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MONITORING AND ANALYSIS OF THE IMPACTS OF CLIMATE CHANGE ON PLANT BIODIVERSITY AND TERRESTRIAL ECOSYSTEMS IN ALPINE AND POLAR ENVIRONMENT

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Cover pictures: the three main study areas discussed in this thesis (from top to bottom): Foscagno valley (Central Italian Alps), west coast of Signy Island (Maritime Antarctica) and Apostrophe Island (Continental Antarctica, one of the study sites of the Latitudinal Gradient Project).

ABSTRACT

High altitude and latitude environments are among those areas of the Planet that are experiencing the most significant changes of the climatic conditions due to the recent global change. Terrestrial ecosystems in these regions are extremely sensitive to climate, and for this reason, well suited for the comprehension, evaluation and monitoring of their responses, and their modelling under different climate change scenarios.

This thesis focuses on the impacts of climate change on terrestrial ecosystems of alpine (Central Italian Alps) and Polar (both Continental Antarctica and Maritime Antarctica) tundra habitats. European Alps and Maritime Antarctica are two of the three areas of the world where have been recorded the greatest air temperature warming in the last 50 years, whereas simultaneously in Continental Antarctica, air temperature was almost stable. Due to different trends of climate and anthropogenic pressures around the world, contemporary global change is characterized by a large spatial variability that makes the planning of adaptation and mitigation strategies particularly complicate. Peculiar habitats have been protected by international, European and national programs (the Foscagno valley belongs to the Nature 2000 network, while the Antarctica ecosystems are protected under the Antarctic treaty and specially protected areas). However, analyzing the dynamics of terrestrial ecosystems in regions that are facing different climate change scenarios, as well as biological and anthropogenic constrains, could improve the knowledge of the dynamics of terrestrial ecosystems, that could be used for modelling future scenarios and to implement the adaptation plans for such protected areas.

The identification of conservation actions and monitoring plans is thus the priority for such threatened environments, to ensure a correct management of the biodiversity and of the ecosystem services that they can provide.

The alpine site is the Foscagno Valley, a high altitude site (>2500 m a.s.l.) located in the central Italian Alps, where since 2007 a field-based project of snow, ground surface temperature and plant phenology monitoring started. This PhD is part of this project, that since summer 2015 was implemented with manipulation experiments on two typical alpine vegetation communities (snowbed and grassland) to simulate potential future climate change related impacts on plant phenology and growth, including increase of nutrient availability (simulated by additions of urea, ammonium sulfate, NPK respectively), water availability (once or twice per week additions of water), lack of reproductive stages (flowers removal).

The primary aim of this PhD was to investigate alpine plant phenology and its relationships with climate change. We monitored phenology of 21 plants typical of alpine environments and representative of different growth forms types. In particular, we hypothesized that: a) the vegetative development (shoot appearance and leaf emergence) is regulated by snow melt timing, while the other phenological stages (i.e. flowering, seed development and ripening, and leaf senescence) are regulated mostly by photoperiod, which should indicate a conservative and adaptive strategy of alpine plants; b) plant phenology shows different plasticity depending on the growth form types and also on the phenological stage; c) extreme events can overwhelm the effect of photoperiod, and can lead to carry over effects in the phenological cycle and plant growth.

Our data indicated that the main predictor of the vegetative development stages was the snow melt, while the photoperiod was the best predictor of phenological stages from flowering peak up to leaf senescence. Therefore, the photoperiodic control on alpine plant phenology should be considered for the evaluation and modelling of the impacts of climate change in alpine region, not only concerning the reproductive stages, but also for the leaf senescence. This constitute a novelty concerning literature data about phenology of alpine plants (which have been always related to snow and/or temperature as triggering factors) because provides new insights on the capability of alpine plants to profit of potential future autumn warming.

Alpine plant phenology showed thus a strong conservative strategy, which differed among growth forms, according to our hypothesis. Over all the investigated phenological stages graminoids were the most plastic and responsive growth form and their higher adaptation capability could help to explain why this growth form is expanding more than forbs in alpine and Polar tundra habitats.

Extreme events showed impact on plant phenology, with differences among growth forms and phenological stage. In particular, we found the leaf senescence of herbaceous species to be highly sensitive to the combination of drought and heat, which led to an advance of almost one month in the season, while deciduous shrubs were not or less sensitive. Moreover, an extreme leaf senescence showed carry over effects on the next season growth rate.

Our results indicate also a statistically significant increase of the height of evergreen shrubs on the period 2010-2016, which was in agreement with the observed range expansion of shrubs in the Alps.

Relating to the long-term ground surface temperature (GST) monitoring, 13 temperature data loggers were installed in the Foscagno valley, under different surface types conditions, covering the most widespread growth forms of the area. In particular, we hypothesized that: a) GST was strongly influenced by the soil coverage types and snow cover, b) although the actual climatic conditions are less favorable, some vegetated soils could lead a ground cooling until to permafrost condition; c) the shrubland expansion could drive to an energetic disequilibrium of soils with thus positive feedbacks on the carbon cycle.

Our data confirmed that the snow cover duration was the main driver of the mean annual ground surface temperature, while the beginning of snow cover deeper than 80 cm influenced the freezing state of the soils during winter, and the timing of snow melt was related to the thawing degree days of the snow free period. Vegetated soils (shrublands and grasslands surface types) were warmer compared to bare ground, except for pioneer species (i.e. *Cerastium uniflorum*), that involved a cooling on soils leading to permafrost condition. Therefore, future changes in vegetation cover can lead to different soil thermal regimes and different spatial distribution of temperatures in alpine terrains. Potentially, the expansion of pioneer species could be related to longer persistence of permafrost conditions; on the contrary, if the shrublands expansion that we are facing in the Alps will continue in the future, soil temperatures will be warmer, which imply positive feedbacks to the carbon cycle.

The main purpose of the manipulation experiments started at the Foscagno Valley in 2015 was to investigate the responses of phenology and plant growth under different simulations of climate change. As many phenophases exhibited a strong photoperiodic control, we aimed to assess and quantify the eventual effects of the different manipulation treatments and identify the most responsive phenophases and communities types. Concerning the quantitative development, we hypothesized that: a) the vegetative development (shoot length, leaf length, maximum plant height) would be influenced by manipulations, with nutrients exerting the higher impacts, compared to flower removal and water addition (since terrestrial ecosystems are N and P limited); b) the above ground biomass (ABG) would be strongly influenced by the addition of nutrients, more than flowers removal or water addition.

Our data showed that manipulation experiments (in particular nutrient additions) involved strong impacts on plant phenology and growth, lengthening (with xNPK) or shortening (with ammonium sulfate) the duration of flowering and leaf senescence, and enhancing the vegetative quantitative phenology of alpine plants (with xNPK). One of the most important findings is that the photoperiodic limitation observed at the long-term phenology monitoring, could be overcome under future climate changes, with potentially consequences on niche competition within communities.

Above all the manipulation we found a strong N and P limitation, in particular concerning the vegetative development, which thus will imply strong consequences also on the carbon budget. Also the flower removal exerted visible effects especially on the quantitative growth, highlighting differences among the vegetation communities, with higher capability for snowbeds species to remobilize nutrients than grasslands species.

Another feedback of the manipulations experiments concerned the occurrence of carry over effects on the quantitative growth of the first shooting stage at the beginning of the season, provided by the enhanced nutrient availability from the previous year.

While in the alpine tundra vascular plants are dominant, in high latitude ecosystems, cryptogams (mosses and lichens) are the major components of terrestrial ecosystems. In particular, in Antarctica only few long-term data are available on the responses of mosses and lichens to climate change.

Comparable to Alps, the Maritime Antarctica is one of the regions of the planet recording the most rapid air warming, and Signy Island (South Orkney Islands) has been identified as a suitable context for the monitoring of biological changes. Here we analyzed the contemporary abundance and distribution of moss banks on the entire island, assessing their ecological requirements, and providing thus a baseline for future monitoring.

Thanks to the availability of previous field-based studies on the spatial distribution of moss banks carried out in the 1960s and 1970s, we assessed long-term and large-scale moss responses to climate change underlying the related ecological processes.

Differently to Alps and Maritime Antarctica, Continental Antarctica in the last 50 years showed a stable air temperature trend. This region is the last pristine environment on Earth, which provides a unique opportunity to assess the natural dynamics and responses to climate. In Victoria Land, in 2002 started a long-term monitoring project of the climate, permafrost and vegetation, of which we present here the results after 10 years of monitoring. Concerning this activity, we aim to: a) identify the patterns of spatial and temporal active layer variability; b) analyze the changes of the associated vegetation; c) identify the climatic forcing of active layer and vegetation changes.

In the Antarctic summer 2014/2015, we installed over a latitudinal gradient (73-77°S) in Victoria Land, some manipulation experiments (additions of snow, water, urea, ammonium sulfate, NPK, guano respectively) coupled with the manipulation of snow accumulation, soil temperature and

precipitation (installing respectively snow fences, open top chambers and snow shield) for the simulation of potential future climate change impacts. We thus briefly evaluated the effects on soil temperatures after the first year of the experiments, providing thus the start point for future further monitoring.

Among all the experiments, we found that the snow cover exerted the largest effect on the GST, thus highlighting its main role in regulating soil temperatures, which effects overcome the influence of air temperature, leading also to changes of soil moisture and water regime.

The results of this study highlight the importance of some of the environmental cues that drive climate change impacts on terrestrial ecosystems (in both alpine and Polar tundra habitats), that should be taken into account when defining models over the coming decades at the local scale, as well as at regional and global scale, and that could be integrated in the management and adaptation plans of these particularly vulnerable ecosystems.

CONTENTS

I. INTRODUCTION

The last IPCC (Intergovernmental Panel of Climate Change) report confirmed that climate is changing across our planet, largely as result of human activities (such as land use and land use change, pollution, etc…) (IPCC, 2014a; 2014b), that will continue to threat terrestrial ecosystems, exacerbating other impacts on biodiversity (IPCC, 2014a).

Globally mean surface temperature has increased since the late 19th century, and is projected to increase also in the next years: the first decade of the 21st century has been the warmest since the start of instrumental recording (IPCC, 2014c). While confidence is low for a global-scale observed trend in drought or dryness (lack of rainfall) since the middle of the 20th century (IPCC, 2014c), extreme weather events (such as heat waves, extreme droughts, heavy rains, frosts, advanced or delayed snow melt) increased since 1950s (IPCC, 2014d).

Climate change (CC) exhibited strong spatial heterogeneity (IPCC, 2014a), and Polar and alpine regions are among those areas that recorded the largest significant changes of the climatic conditions (ACIA, 2005; Turner et al., 2007; IPCC, 2014a; 2014g), and have been identified among the most sensitive and vulnerable ecosystems to the impacts of CC (IPCC, 2014f; 2014g). The main reason of this great vulnerability comes from the prevailing abiotic control of these ecosystems. Indeed, going towards higher elevations/latitudes, the terrestrial ecosystems are more dependent from climate (mostly snow and temperature) and abiotic forcing, which influence their temporal and spatial patterns (e.g., Korner, 2003). In cold biomes, species have adapted their physiological functions to climatic extreme conditions (where also competition processes are reduced) (Crawford, 2008). Therefore, as a paradox, the climate amelioration in these biomes become a limit rather than a facilitation, as already demonstrated by many authors (e.g., Theurillat & Guisan, 2001; Keller et al., 2005; Cannone et al., 2007; Convey, 2011; Elmendorf et al., 2012b; Cornelius et al., 2013; Cannone & Pignatti, 2014; IPCC, 2014f; 2014g).

In the last three centuries the European Alps faced a warming almost double than the mean global warming rate (Böhm et al., 2001; Casty et al., 2005), reaching +1.2°C over the period 1950-2003 (Cannone et al., 2007). Arctic experienced the greatest regional warming on Earth, with an increase in temperatures up to +3°C since 1950s (e.g. ACIA, 2005; Turner et al., 2007), affecting particularly regions such as Alaska (Hinzman et al., 2005) or Siberia (Serrezze et al., 2000). The Antarctic peninsula is the third region of the world where temperature increased at faster rates, with an increase of mean annual temperatures of +0.56°C (Turner et al., 2007) and reaching +1.2°C in summer temperatures compared to the 1950s (Guglielmin et al., 2012; Cannone et al., 2016a). On the other side, in Continental Antarctica, trends indicate even temperature decrease (Doran et al., 2002), or almost stable temperature (Chapman & Walsh, 2007; Guglielmin & Cannone, 2012; Guglielmin et al 2014).

Among the abiotic components of cold terrestrial ecosystems, the cryosphere, which is the dominant element of these environments, showed striking and evident responses to CC (e.g., Chersich et al., 2015). Glaciers retreat has been observed worldwide, with increased rates during the last decades (Oerlemans, 2005; Tuner et al., 2007; Cannone et al., 2008; Convey, 2011; Diolaiuti et al., 2012; Chersich et al., 2015; Carturan et al., 2016; Malecki, 2016; Machguth et al., 2016; Mir et al., 2016), coupled with a reduction of the snow cover depth (Serrezze et al., 2000; Cannone et al., 2007; Bokhorst et al., 2016a; Klein et al., 2016; Kunkel et al., 2016) and its areal extension (Thompson, 2016).

Since the 1990s, permafrost has generally warmed across all over the Globe (Harris, 2003; Wu & Zang, 2008; Smith et al., 2010; Romanovsky et al., 2010; 2011; Christiansen et al., 2010; 2012; Zhao et al., 2010; Guglielmin et al., 2011; 2014; Guglielmin, 2012; Bockheim et al., 2013; Guglielmin & Vieira, 2014; Wang et al., 2014; Chersich et al., 2015; Li et al., 2015; Pogliotti et al., 2015; Balks & O'Neill, 2016, Grosse et al., 2016). However, trends have been weak in several sites, including Alaska (e.g., Osterkamp, 2008), northern Canada (e.g., Smith et al., 2005) and continental Antarctica (McMurdo Dry Valleys) (Guglielmin et al., 2011). Since the 1990s, also a progressive increase of the active layer thickness (ALT) has been recorded in all regions, with the exception of northern Alaska, the western Canadian Arctic, and West Siberia (Christiansen et al., 2012). In northern Victoria Land (Continental Antarctica), the active layer thickened up to 1 cm/y from 1996 to 2009 (Guglielmin & Cannone, 2011; Guglielmin et al., 2014), while in the McMurdo Sound (southern Victoria Land) no clear trend was recognized from 1999 to 2007 (Adlam et al., 2010).

Permafrost warming and active layer thickening were mainly attributed to air warming although in several cases the role of snow cover, soil properties and the overlying vegetation were emphasized (e.g., Harris et al., 2003; Guglielmin et al., 2004; 2014; Osterkamp, 2008; Haeberli et al., 2010; Romanovsky et al., 2010; Chersich et al., 2015). In particular, ALT does not always follow the trend of the underlying permafrost and, in general appears more closely related to summer air temperature (Osterkamp, 2008) or to summer radiation (e.g., Guglielmin & Cannone, 2012), or to the presence of vegetation (e.g., Guglielmin et al., 2008; 2012).

There are ample evidences of the ecological impacts of recent CC going from polar to tropical terrestrial ecosystems (Walther et al., 2002; IPCC, 2014g). Many plant and animal species moved their ranges (mainly towards higher altitude and latitude), altered their abundance and shifted their seasonal activities in response to the observed CC over recent decades (e.g., Walther et al., 2002; Root et al., 2003; Parmesan & Yohe, 2003; Menzel et al., 2006a; Lenoir et al., 2015; Royles & Griffith, 2015; Parmesan & Hanley, 2015).

When CC impacts affect different levels of ecological organization, the competition between species is altered and, over a long-term scale, it could drive to species extinction and consequential loss of biodiversity (Dullinger et al., 2012).

A growing body of literature shows that CC is altering vegetation structure with changes of spatial distribution, phenology, physiology and biogeochemical cycle from the Alps (e.g., Cannone et al., 2007; Cannone & Pignatti, 2014; Cannone & Dalle Fratte, 2016 submitted) to the Arctic (e.g., Callaghan et al., 2013; Farrer et al., 2015; Valolhati et al., 2015; Moffat et al., 2016; Rosa et al., 2016; Schmidt et al., 2016; Walker et al., 2016) as well as Antarctica (e.g., Brabyn et al., 2005; Favero Longo et al., 2012; Guglielmin et al., 2014; Cannone et al., 2016a).

Climate manipulation experiments have been used for evaluating and modelling the impacts of one or more environmental factors on vegetation, from alpine regions (e.g., Carbognani et al., 2016; Wipf & Rixen, 2010) to the Arctic (e.g., Wipf & Rixen, 2010, Cooper, 2011; Elmendorf et al., 2012a; 2015; Johanson et al., 2013) and Antarctica (e.g., Bokhorst et al., 2011).

In the Northern Hemisphere, experiments showed that warming induced a decrease in non-vascular plant biomass (both mosses and lichens), although the declining trend of non-vascular plants with warming has also been assumed to reflect competition with vascular plants instead of the effects of climatic drivers (e.g., Chapin et al., 1995, Cornelissen et al., 2001, Elmendorf et al 2012a).

In the Southern Hemisphere, even if the number of climate manipulation experiments is lower (e.g., Bokhorst et al., 2011), they showed that warming combined with greater snow accumulation exerted negative impacts, largely on lichens more than mosses (e.g., Bokhorst et al., 2016).

Moreover, there are evidences that the sensitivity to climate of terrestrial ecosystems is strongly affected by nutrient limitation, in both Polar and alpine tundra vegetation (e.g., Wasley et al., 2006; Bowman et al., 2006; Petraglia et al., 2014b), and by plants' efficiency on acquiring nitrogen (e.g., Cannone, 2011).

When terrestrial ecosystems are substantially altered (in terms of plant cover, biomass, phenology, or plant group dominance), the local, regional, and global climates are also affected (IPCC, 2014a). While gradual changing of climate parameters (such as gradual warming) could allow species to adapt or at least acclimate to the changing environment, extreme weather works like a stochastic event, with rapid and unpredictable effects on plant fitness and survival (Niu et al., 2014). There are evidences that extremes changed since 1950s, possibly because of anthropogenic influence (IPCC, 2014d). Extreme weather events may adversely affect natural ecosystems, crop productivity and human health, and facilitate biological invasion (Ciais et al., 2005). Unfortunately, even if the number of studies on extreme events and their consequences has recently increased (Jentsch et al., 2007; Wipf et al., 2013), there is a substantial lack of knowledge on how they will affect biodiversity and ecosystems (Jentsch & Beierkuhnlein, 2008). One of the main reason is because plant responses to extreme climatic events of different types and magnitudes are very specific and the number of case studies is still too small to reveal general patterns (Orsenigo et al., 2014). There are evidences that extremes (such as pulse warming – Alatalo et al., 2016) could lead to negative effects on species richness and diversity and thus to a decrease in regional carbon stocks, negating an expected increase in terrestrial carbon uptake in a warming scenario (Reichsten et al., 2013; Arnold et al., 2014; Yuan et al., 2016).

In many cases, increased mean air temperature corresponds to increased variability, leading to more extreme temperatures, and greater heat energy in the atmosphere, which promote the development and intensity of extreme weather and events (Easterling et al., 2000), which are projected to rise (IPCC, 2014d).

The main feedbacks of terrestrial ecosystems to global change regard biogeochemical cycles (gas fluxes and net carbon storage), that can be altered following a modification of plant communities composition and thus of dominant plant growth-forms (Wookey et al., 2009; Cannone et al., 2012; 2015; 2016; García-Palacios et al., 2015). However, the response of the terrestrial carbon cycle to global change remains one of the main uncertainties in current climate change predictions (IPCC, 2014e). Plant traits drive carbon inputs and outputs, firstly trough modifications in leaf litter decomposition rates (Cornelissen et al., 2007; Cornwell et al., 2008), or soil temperatures (e.g.

Klene et al., 2001; Cannone & Guglielmin, 2009) and thus on soil carbon sequestration under global changes (de Deyn et al., 2008; Schmidt et al., 2011).
Concerns are thus for the future projections, that show evidences that global changes will continue to threat terrestrial ecosystems, exacerbating such impacts on biodiversity (IPCC, 2014a; 2014b).

Aims of the study

One of the main topic concerning contemporary global change is its large variability due to different trends of climate and anthropogenic pressures around the world. Analyzing the dynamics of terrestrial ecosystems in regions that are facing different climatic, biological and land-use changes, could improve the comprehension and evaluation of the impacts of CC, emphasizing the different sensitivities and peculiarities for such threatened terrestrial ecosystems. This can contribute to better quantify the real vulnerability of ecosystems to CC and the construction of more realistic and predictive models, that could be used for CC adaptation and mitigation policies, which have been recognized as main elements of the climate policy at the international level (e.g., UNFCC – United Nations Framework Convention of Climate Change), as well as at the EU level (e.g., EU adaptation strategy). The identification of conservation actions and monitoring plans is thus the priority for such threatened environments, to ensure a correct management of the biodiversity and of the ecosystem services that they can provide.

In this study, we focused on the impacts of climate change on the terrestrial ecosystems of alpine (European Alps) and Polar (Continental and Maritime Antarctica) tundra habitats, by analyzing three regions of the world that are facing different pressures concerning climate, environment and land-use change: the European Alps, Continental Antarctica and Maritime Antarctica. The European Alps and Maritime Antarctica are among the areas of the world where have been recorded the greatest rise in air temperature at least in the last 50 years, while simultaneously in Continental Antarctica, air temperature was almost stable.

In cold-environments is necessary to disentangle the impacts and interactions of multiple drivers (climate, permafrost, biotic interactions) and identify the complex processes (competition, facilitation) that can lead to high spatial heterogeneity of species responses (Callaghan et al. 2013). One important forcing that have to be considered is also the land-use management, since it can influence species richness and composition (Blasi et al., 2009; Burrascano et al., 2013). In high elevation areas of the Appenines (central Italy) were recently documented long-term changes of plant species composition and functional traits related to successional dynamics as well as management factors (grazing intensity) coupled with shifts of climate parameters (Giarrizzo et al., 2015; 2016). Moreover, even if Polar and alpine ecosystems are similar under historical climatic conditions, due to the different photoperiodic constraints, they have been hypothesized to produce different responses to CC (Ernakovich et al., 2014), with consequences and feedbacks on species competition, community composition and biogeochemistry.
For example, little is known about the plasticity of plant species in alpine environments, and how they respond to the inter-annual variability of climate parameters (e.g., Abeli et al., 2012; 2014; Petraglia et al., 2014; Vitasse et al., 2016; Cannone & Dalle Fratte, 2016a submitted), while for Antarctic plant species very few long-term studies are available that allow to quantify vegetation responses to CC (e.g., Cannone et al., 2016c submitted).

The analysis of these different systems could thus be useful to identify and quantify the potential variability of terrestrial ecosystems responses, both with similar climatic input (Alps vs Maritime Antarctica) or different (vs continental Antarctica), or under different ecological and biological pressures.

Since summer 2007, at the Foscagno valley (central Italian Alps) started a long-term monitoring project of high elevation vegetation, snow and soil temperature, in order to assess and monitor the impacts of climate change on alpine terrestrial ecosystems above the treeline. This PhD activity thus focused on the prosecution and maintenance of this monitoring, and on the analysis of the long-term data record. This site has been selected among the Nature 2000 network of EU (Directive 92/43/EEC) since it is occupied by habitats of community interest, therefore, the improvement of the knowledge about the ecological dynamics can help to enhance the proper management and to identify the best CC adaptation plans.

The main topic of the project can be divided in subgroups that will be described in details in the next chapters (see chap. III.1): a) high elevation plant phenology and responses to climate in the frame of ITEX (International Tundra Experiment), b) distribution and evolution of the winter snow cover, c) surface soil temperature monitoring and d) manipulation experiments.

Antarctica is the largest protected area at the world being under the Antarctic treaty, which has among the objectives the preservation of the flora, fauna and the ecosystems. In Antarctica, the research activities allowed us to analyze two geographically remote areas belonging to different biogeographic regions, where significant (and opposite) climate changes have been observed: Maritime Antarctica (one of the three regions of the planet recording the most rapid atmospheric warming over the last 50 years according to Turner et al. (2009), and Continental Antarctica, where no trends in air temperature were observed, but changes of the global radiation and active layer thickness have been identified, e.g. Guglielmin & Cannone (2012).

Since 2000, in Victoria Land (Continental Antarctica), started a long-term monitoring project of climate, permafrost, active layer and vegetation along a latitudinal transect (73°S-77°S) (Cannone et al., 2006). In particular, we focused on two main topics (see chap. IV.1): a) impacts of recent climatic changes on vegetation and terrestrial ecosystems in Victoria Land, b) installation of manipulation experiments for the simulation of potential future climate change impacts.

In the 1960s and 1970s, at Signy Island (Maritime Antarctica), field based studies were carried out concerning spatial distribution of moss banks over the entire island (e.g. Edward, 1972; Smith, 1972; Fenton, 1980; Fenton & Smith, 1982). Here, we first analyzed the contemporary abundance and distribution of the moss banks at Signy Island, and we assessed long-term and large-scale mosses responses to climate and environmental change identifying the background ecological processes associated to changes (see chap. V.1).

In these remote areas (Antarctica as well as the Foscagno valley), the land-use and management changes are almost negligible (see detailed descriptions of the study areas) and thus we could observe the natural dynamics and evolution of ecosystems. For this reason, the evaluation and quantification of CC impacts on these ecosystems based on ground observation, could contribute to create more realistic models for the adaptation policies, also in other areas of the world with human settlements, and where vegetation is no longer left at his natural evolution.

II. STATE OF THE ART

II.1. Sensitivity of high elevation/latitude flora and vegetation to recent climate change

Climate impact studies have indicated ecological fingerprints of recent global warming across a wide range of habitats (Hughes, 2000; Walther et al., 2002; Root et al., 2003; Walther, 2010; Parmesan & Hanley, 2015), among which terrestrial ecosystems, both in Polar (Serrezze et al., 2000; Turner et al., 2005; 2009; Hinzman et al., 2005; Convey, 2011; LeRoux & McGeoch, 2008; Callaghan et al., 2013; Cannone et al., 2015; Royles & Griffit, 2015) and tropical alpine regions (Beniston, 2003; 2012; Cannone et al., 2007; Grabher et al., 2010; Pauli et al., 2007; 2012; Gottfried et al., 2012; Vittoz et al., 2013; Chersich et al., 2015).

Going towards higher elevations/latitudes, the terrestrial ecosystems are more dependent from climate (mostly snow and temperature) and abiotic forcing influencing their temporal and spatial patterns (e.g., Korner, 2003), and are thus extremely sensitive to changes in climate parameters (Theurillat & Guisan, 2001; Keller et al., 2005; Cannone et al., 2007; Convey, 2011; Elmendorf et al., 2012b; Cornelius et al., 2013). Moreover, as species from cold environments already live at the range of their physiological tolerance (Crawford, 2008), they are strongly susceptible to CC (ACIA, 2005; Convey, 2011; Elmendorf et al., 2012a; 2012b; Cannone & Pignatti, 2014; Cannone et al., 2015; IPCC, 2014g). For these reasons, the cold biomes constitute the best choice to analyze CC impacts.

Impacts of climate change (CC) have been identified on phenology of terrestrial ecosystems at a global scale, as well as in Polar and tropical alpine regions (e.g. Schwartz, 2003; Chambers et al., 2013; Parmesan & Hanley, 2015; Rosa et al., 2016). In Antarctica most of the phenological studies have been focused to larger organism (seabirds and marine mammals) with few long-term studies on the phenology of plants, invertebrates and other species (Chambers et al., 2003; 2013; 2016), also because of the low fruiting rates of bryophyte flora (e.g. Seppelt, 2004; Ochyra et al., 2008; Casanova-Katny et al., 2016).

Phenology do not relate only to plants and animals, but largely also to all the compartments of terrestrial ecosystems, which in environments like Antarctica were comparatively more investigated. As an example, ice phenology of lakes has been investigated in Antarctica (e.g. Dugan et al., 2006) and frozen-lakes have been identified as sentinels of climate change (e.g. Forte et al., 2016; Castendyk et al., 2016).

A detailed description of the relations between phenology (of alpine and Polar tundra plants) and CC have been given in the next chapter (see chap. II.2). In this section, we focused on the impacts of CC on the vegetation composition and distribution, which constitute another important compartment of the studies about global change impacts.

One of the most relevant responses of plant to climate warming is the range shift towards higher altitudes and latitude (e.g., Walther et al. 2002; 2005; Dullinger et al., 2003; Lenoir et al., 2008; Parmesan & Yohe, 2003; Chen et al., 2011; Lenoir & Svenning, 2015; Parmesan & Hanley, 2015). Over the Alpine regions, changes within plant communities composition has been attributed to climate warming (e.g., Kullman, 2010a; 2010b; Gottfried et al., 2012; Pauli et al., 2012; Cannone & Pignatti, 2014; Matteodo et al., 2016), and an increase of the grasses/forbs ratio has been documented for the main alpine vegetation communities (Cannone & Pignatti, 2014), similarly to what was observed for Arctic tundra plant species (Elmendorf et al., 2012a).

Alpine tundra vegetation (above the tree line) exhibited upward migration of plant species on mountain summits, upward displacement of shrubs, changes in community composition, local extinctions and surface area changes of vegetation, with also some examples of increase of vascular plant species richness (e.g., Keller et al., 2000; Kullman, 2010b; Walther et al., 2005; Pauli et al., 2007; Cannone et al., 2007; Holzinger et al., 2008; Kelly & Goulden, 2008; Lenoir et al., 2008; Erschbamer et al., 2011; Gottfried et al., 2012; Fernandez-Calzado et al., 2012; Gigauri et al., 2013; Cannone & Pignatti, 2014; Gritsch et al., 2016).

Alpine plant species and bioclimatic zones in the past 50 years followed an upward displacement of 120-340 m for tree and woody shrubs species (Kullman, 2002), and upward migration of alpine and nival plant species at a rate of 8-10 m per decade (Grabherr et al., 1994; Walther et al., 2005).

Profound changes in ecosystem functioning and potential losses of high-alpine and Arctic species are expected under climate warming as cold-adapted plants may be outcompeted by taller growing species or lost as their habitats vanish (Rixen et al., 2014).

Klanderud & Birks (2003) comparing flora composition of mountain regions in Norway, found that on the period 1930-1998 the species richness increased, with larger consistence at elevation of 1600-1800 m a.s.l. Similar results were observed by Kullman (2010), who found increasing rate for many species over a 50-y study from Sweden summits, with evidences of higher reproduction rates.

According to Cannone et al. (2007), grasslands are increasing at higher altitudes (2500-2600 m a.sl.), replacing the snowbeds, which in turn shifted upward (2600-2800 m a.s.l.). The upward movement and increase abundance of grasslands (Cannone, 2007; Cannone & Pignatti, 2014), confirms the ability of late successional species, such as *Carex curvula*, to migrate under warming scenario (Elmendorf et al., 2012b).

Consequently, species richness of snowbeds communities could increase, determining important alteration in the community structure and composition (Pickering et al., 2014; Carbognani et al., 2014; Matteodo et al., 2016). On the short-term (6-y), Pickering et al. (2014) demonstrated that grasses invaded snowbed environments in the Australian Alps, thus highlighting threats and potentially rapid changes of Alpine plant communities. However, this invasion not necessarily occur at the cost of snowbed specialist, as demonstrated by Carbognani et al., (2014) always on a 6-y period, but imply higher plant densities and thus higher species segregation, which indicates more competitive plant-plant interactions.

Recently, Matteodo et al. (2016) highlighted how the invasion of snowbed communities was related to a clear shift towards drier conditions and shorter snow cover duration, evidenced by their colonization by species from surrounding grasslands, which are taller and hence more competitive respect snowbed species.

Moreover, new surfaces will be available from the glaciers shrinking in the next future years, and pioneer alpine plants demonstrated fast rates of colonization of these new surfaces (Cannone et al., 2008b; Caccianiga et al., 2011).

Current studies of the impact of CC on plants are based on tracheophytes, i.e. vascular plants. Cryptogams (i.e. non-vascular plants) fundamentally differ from vascular plants in their small size and utilization of a poikilohydric strategy for water and nutrients; their survival and reproduction are highly dependent on their external environment. Thus, the results from studies on tracheophytes cannot be generalized on cryptogams.

He et al. (2016) published a review of all the available information about the influence of environmental factors on bryophytes to understand their relation to climate, especially to temperature at a global scale. Elevated temperature may shorten the time of metabolic activity, and increase desiccation intensity. As a consequence of global warming, significant losses can be expected, particularly in areas harboring a large number of species, such as high latitude boreal forests, alpine biomes and higher altitudes on tropical mountains. The decline of bryophytes diversity will also lead to an alteration of ecosystem structure and function, nutrient cycling and carbon balance.

Mosses are ubiquitous components of plant communities in high latitude ecosystems, becoming dominant in terms of diversity and biomass in the High Arctic (Meltofte, 2013) and, particularly, in the Antarctic, where vegetation is dominated by cryptogams (Longton 1988, Wasley et al., 2006a; Ochyra et al., 2008; Convey, 2013; Pointing et al., 2015). In High Arctic tundra, some reports suggest that the abundance of mosses has increased over recent decades (Hudson & Henry, 2009), while others point to them remaining relatively stable (Prach et al., 2010). Despite the dominance of mosses in the terrestrial vegetation of the Antarctic (Ochyra et al., 2008), few long-term monitoring studies of moss communities are available (Melick & Seppelt, 1997; Brabyn et al., 2006; Wall et al., 2011; Clarke et al., 2012; Royles et al., 2012; Guglielmin et al., 2014), as most studies to date have focused on vascular plant species (e.g. Fowbert & Smith, 1994; Smith, 1994; Parnikoza et al., 2009; Vera, 2011; Cannone et al., 2016).

There is a shortage of data available on vegetation changes in continental Antarctica. In Victoria Land, the only example of long-term vegetation monitoring, carried out at Cape Hallett (Brabyn et al., 2005), showed that, in the period 1960–2004, vegetation expanded (with an increase of algae), although it was not possible to associate this changes with long-term temperature increases, while it is likely that it was driven by local alterations of water supply. In other sectors of continental Antarctica, in Wilkes Land, there was a generalized increase of lichens vegetation and a concomitant decrease of bryophytes due to a drying climate (period 1960–1990; Melick & Seppelt, 1997). In Dronning Maud, Johansson & Thor (2008) reported an increase in both lichen species density and abundance, and a slight increase of lichen taxa of their permanent plots for the period 1992–2002.

Relating to the impacts of recent climate change on vegetation, in maritime Antarctica a large increase of the two native Antarctic vascular plants (*Deschampsia Antarctica* and *Colobanthus quitensis*) has been documented in the past 30–50 years in response to air warming (Parnikoza et., al., 2009, Torres Mellado et al., 2011) and probably also to increased precipitation and active layer thickening (Cannone et al., 2014).

In order to asses and study the impacts of climate change on tundra plants (alpine and polar) the scientific research network of International Tundra Experiment (ITEX, e.g. Elmendorf et al., 2012a) carried out experiments at more than 40 sites in Arctic and Alpine regions. The ITEX research combines long-term and short-term experimentations with monitoring, and aims to understand ecosystems responses and vulnerability to changes (see chap. II.4).

Across all sites, ITEX found that vegetation height and abundance are destined to increase under warming (e.g. Walker et al., 2006; Elmendorf et al., 2012b), and results from their long-term changes in control plots were largely consistent with these predictions (Elmendorf et al., 2012a). Elmendorf et al. (2012a) stressed that responses of vegetation showed large inter-site variability: shrubs (particularly deciduous shrubs) were increasing over time, primarily in sites that were warming rapidly, while vegetation in cold tundra sites was relatively insensitive to climate warming.

Concerning the cryptogamic flora, in Northern Hemisphere, experiments showed that warming decreased both mosses and lichens, although has also been assumed to reflect competition with vascular plants instead of the effect of climatic drivers (e.g. Chapin et al., 1995, Cornelissen et al., 2001, Elmendorf et al 2012a). In Southern Hemisphere, warming (and the combined effect of greater snow accumulation due to the design of the experiments) exerted negative impact, largely on lichens more than mosses (e.g. Bokhorst et al., 2016).

Changes in species distribution and community composition relative to global changes in cold biomes has been analyzed by many other projects (e.g., Rixen et al., 2014). For instance, across European summits, evidence for so-called thermophilization was found, i.e., more warm-adapted species increased whereas more cold-adapted species declined (Gottfried et al. 2012). In the short period between 2001 and 2008, this upward migration has caused an increase of local species richness in many boreal-temperate mountain regions, but a decrease in Mediterranean mountain regions (Pauli et al. 2012). Looking at longer time scales, i.e. more than a century, the vegetation change has even accelerated in recent decades, most likely in line with accelerated climate warming (Wipf et al. 2013).

The recent observed increases in the growth and abundance of shrubs are undoubtedly one of the most prominent ecological changes currently occurring in many tundra ecosystems (Sturm et al., 2001; Tape et al., 2006; 2012; Verbyla, 2008; Jia et al., 2009; Post et al., 2009; Forbes et al., 2010; Naito & Cairns, 2011; Myers-Smith et al., 2011; 2011a; Daniëls et al., 2011; Ropars & Boudreau, 2012; Elmendorf et al., 2012b; Macias-Fauria et al., 2012). In the Italian Alps, as a response of a +1.0°C air temperature increase (or +1.2°C depending on the station considered) over the period 1950-2003, Cannone et al. (2007) indicated an increase of shrubs coverage from 33% (between 2230 and 2400 m a.s.l.) to +28% (between 2400 and 2500 m a.sl.).

The shrub expansion is of relevant interest (e.g. Myers-Smith et al., 2011) because they can alter the energy partitioning in summer (Chapin et al., 2000; 2005), the trapping and distribution of snow in winter (Sturm et al., 2001b; 2005a; 2005b), leaf litter decomposition rates (Cornelissen et al., 2007; Cornwell et al., 2008) as well as increasing the amount of carbon stored in a region that is believed to be a net source of carbon dioxide (Oechel et al., 2000; Wookey et al., 2009; Block et al., 2010).

Shrubs canopies thus alter the microclimate and therefore soil (and permafrost) temperatures (Myers-Smith et al., 2011). Consequently, there is a growing need to understand the drivers of Arctic and alpine shrubs growth and population dynamics to improve projections of tundra vegetation change (Myers-Smith et al., 2015). Shrub growth measurements have been used to: (1) quantify climate-sensitivity of growth; (2) reconstruct climate; (3) establish linkages to satellite-derived vegetation greening; (4) document advances of the shrub line ecotone; and (5) investigate landscape-level disturbances (e.g. Myers-Smith et al., 2015).

Many studies also focused their attention on the treeline ecotone, indicating enhanced conifer recruitment during the twentieth century (e.g. Kullman, 2002; 2010a; 2010b; MacDonald et al., 2008; Chersich et al., 2015).

One method to evaluate the relationships with plant growth and climate is the dendrochronological analysis, of which there are many example in literature concerning trees expansion (e.g. Huges et al., 2011), while comparatively less studies relating to shrubs. In the Arctic, shrubs showed a positive correlation with the summer mean air temperature (Woodcock & Bradley, 1994; Forbes et al., 2010; Hallinger et al., 2010; Blok et al., 2011). However, also the duration of snow cover also influences the shrubs growth rate (*Salix arctica*) (Schmidt et al., 2006; 2010). Shrubs dendrochronology highlighted an increased growth rate in the last decades (Forbes et al., 2010; Rixen et al., 2010; Hallinger et al., 2010; Blok et al., 2011), with evidences also of exceptional growth after extreme warming events, such that of summer 2003 in Europe (Rixen et al., 2010).

Concerning European Alps, by the end of the XXI century most models forecast species extinction risk and habitat fragmentation (e.g., Theurillat & Guisan, 2001; Thuiller et al., 2005; Dirnböck et al., 2011; Engler et al., 2011; Dullinger et al., 2012) with a species loss estimated of about 60% by 2100 (Dullinger et al., 2012). However, responses within a community may be idiosyncratic (Lenoir et al., 2010). Often, the upward migration is difficult to recognize as the vegetation may "lean" upslope within the existing ranges (Breshears et al., 2008). Lenoir & Svenning (2015) recently reviewed the climate related range shifts observed over the last decades. They underlined that, even if the most frequently reported range shifts are poleward and upward, is now increasing the literature about movement in other directions (i.e. across longitude or, even more unexpected, towards tropical latitudes or lower elevation).

Because of the typical conical shapes of mountains, upslope movements mostly results in range loss (in extreme cases so called “mountain top extinctions” – Colwell et al., 2008; LaSorte & Jetz, 2010), even if often, the upward migration is difficult to recognize as the vegetation may “lean” upslope within the existing ranges (Breshears et al., 2008; Cannone & Pignatti, 2014) and responses within a community may be idiosyncratic (Lenoir et al., 2010).

Gradual warming will affect plants and vegetation over short (decades), medium (centuries), and long (millennia and over) timescales (Dullinger et al., 2012). Plant must constantly adapt to the environmental conditions in which they are, and although plants don’t have the ability to move, they can respond to environmental pressure in 3 ways (Theurillat & Guisan, 2001): a) persistence, developing adaptive mechanism (phenotypic plasticity); b) migration, not about individuals but subsequent generation – germination in other place with suitable conditions; c) extinction, individual who fail to adapt or migrate will disappear from that site.

Moreover, persistent species could be classified in three categories (Cannone & Pignatti, 2014): a) species shifting from their original community to another with different ecological requirements; b) species increasing their coverage within their original community; c) species declining without shifting in other communities.

Since the forcing events, species can show a delay in the extinction rate (extinction debt) (Cannone & Pignatti, 2014). Dullinger et al. (2012) predicted for the European Alps average range size reductions of 44–50 % by the end of the XXI century, creating an extinction debt, with the highest losses for the endemic species.
Moreover, the additivity of different forcing (climate, geomorphology, biotic and human disturbance) can results in unexpected feedbacks among vegetation communities (Cannone et al., 2007; Cannone & Pignatti, 2014).

In contrast to the phenological literature, where the overall signal of response is strong (see chap. II.2), the range shift literature contains multi-species studies where the signal is weak, non-significant, or counter to expectation from known regional warming (e.g. Parmesan & Hanley, 2015). Idiosyncratic or unexpected changes can be the consequence of different limitation to plasticity of alpine and polar tundra plants, which come for example from soil disturbances, topography, nutrients, phenology, altitude, species competition, seed longevity and reproductive success.

As an example, in the Italian Alps was observed an unexpected regression of pioneers communities related to an increase of bare ground coverage, most likely due to the degradation of permafrost which trigger disturbances, such as debris flow and landslides (Cannone et al., 2007).

The soil topography can thus influence the responses to changing environment. Anschlag et al. (2008) considered this effect while studying seedling recruitments of *Betula* ssp., and found limited growth on the wind-swept ridges. This high microclimate variability of alpine terrains could counterbalance the effect of warmer temperatures predicted for the future by IPCC scenario (Scherrer & Korner; 2010; 2011).

One recent example of phenotypic plasticity come from the study of Bienau et al. (2014), who studied trait plasticity of the crowberry, *Empetrum hermaphroditum*, under a range of different snow and climate conditions. Across two latitudes ranging from Northern Sweden to central Norway, snow cover displayed highly consistent effects on growth and reproductive traits. Plants from snow-poor sites had a higher number of flowers and fruits, but smaller ramets and lower above-ground biomass than plants from snow-rich habitats. The authors suggest that *Empetrum hermaphroditum* may have the potential to cope with changing snow conditions due to its large plasticity of traits. However, some authors stressed that evolution is too frequently ignored in predicting responses to climate change in relation to plasticity (Hoffmann & Sgro, 2011; Anderson et al., 2012). For a detailed literature, about phenology and plasticity refer to the next chapter (II.2).

Mountain plant species with wide elevation ranges are expected to be exposed to different selection pressures at low and high elevation, depending on the extent of genetic population differentiation (e.g. Frei et al., 2014). Rosback et al. (2014) found that over the past 50 years, richness increased and functional and taxonomic vegetation composition changed most at lowest sites in the subalpine, while the high-alpine sites showed a decrease in richness and few changes in composition. Potentially, permafrost thawing and thus, increasing soil instability at the highest sites may foster this seemingly counter-intuitive result (according also to Cannone et al., 2007). This illustrates that vegetation changes may vary at the local scale, and that understanding complex interactions between environmental drivers is crucial to understand ecosystem processes in complex alpine terrains.

Another possible factor limiting the expected range expansion could be the physical difficulty for plants to colonize surfaces outside the existing range limit. To test this possibility, Mondoni et al. (2015), using experimental seed planting, showed that range expansion could occur even into historically unvegetated areas exposed by retreating glaciers. Their results indicate that these alpine species may increase recruitment with moderate levels of warming, due primarily to an extended snow-free season. Therefore, the absence of these same species in the wild at lower elevation sites that are naturally warmer than current habitat suggests that the establishment success may be dependent more on competitive interactions with other species in plant communities than on climate alone.

Moreover, the soil nutrients availability can be one of the main factor regulating species responses to environmental change. Indeed, nutrient limitations have been widely reported, from Antarctica (Bokhorst et al., 2007a; Wasley et al., 2006; Cannone, 2011), to Arctic (Bilbororugh et al., 2000; Myers-Smith et al., 2013) and Alpine regions (Gerdol et al., 2004; Bowman et al., 2006; Petraglia et al., 2014b).

Climate change, by driving shifts in species ranges, has directly caused the introduction of exotics into new geographic areas. Walther et al. (2009) reviewed studies of climate-mediated shifts of plants, invertebrates, fish and birds into novel lands. They found that these newly exotic species have varied impacts on their recipient communities.

Moreover, the expansion of vegetation must be related with biotic interactions that comes from both natural variability and anthropogenic effect, such as land use change. In a warming scenario, for example, the expansion rate of shrubs is higher without the presence of herbivory (Olofsson et al., 2009; Ropars & Boudreau, 2012; Callaghan et al., 2013) and the counterbalancing effect of invertebrate herbivory can strongly influence vegetation dynamics (e.g. Barrio et al., 2016).

In Antarctica, the proximity of birds' colonies can strongly influence the nutrients availability for terrestrial ecosystems (Bokhorst et al., 2007). Moreover, in the sub-Antarctic Islands, as result of the abandonment of whale hunting activities, there was an increase of the fur seals population with important consequences on the vegetation communities distribution (Favero Longo & Cannone, 2012; Cannone, 2016)

Gerigh-Fasel et al. (2007) underlined the effects of human influence on climate forcing on regulating the treeline. They found large evidences of the increase of forest coverage, but in large part (90%) due to in-filling processes (i.e. ri-appropriation of tree species of previously woody areas), and only a small part of the increase (10%) was due to upward migration. Similar results were observed from Motta et al. (2006) for the western Italian Alps, where the treeline expansion was mainly attributable to land use changes, while climate was found as the main factor influencing the rate of colonization.

The ability of species to respond to environmental changes will depend largely also on their ability to colonize new territory, and thus on seeds longevity and productivity (e.g. Mondoni et al., 2011; 2012; 2015). Indeed, climate warming could increase seed longevity of alpine plants (Bernareggi et al., 2015), and seed maturation and dispersion (Bernareggi et al., 2016).

The alteration of species distribution and thus of communities composition can alter the ecological functions of terrestrial ecosystems (e.g. Wookey et al., 2009; Chapin et al., 2006). One of the most important could be the carbon cycle, which alteration can display positive or negative feedbacks to atmosphere and thus to climate change (Hick et al., 2007; Wookey et al., 2009; Myers-Smith et al., 2011). According to Wookey et al. (2009) the plant functional types strongly influence the carbon balance, because of their structure, and, physiological and ecological characteristics.

Higher rates of respiration in terrestrial ecosystems are mainly observed as response to climate warming (Welker et al., 2004; Mendonca & LaScala, 2011; Cannone et al., 2012; 2015).

There are many evidence from Polar (Arctic and Antarctic) and alpine regions that species richness and diversity, in combination also with soil properties, influence the carbon fluxes (e.g. Welker et al., 2004; Eugster et al., 2005; Hooper et al., 2005; Kabwe et al., 2005; Adams et al., 2006; Jones et al., 2006; Johansson et al., 2006; Choi et al., 2008; Wohlfahrt et al., 2008a; 2008b; Bahn et al., 2009; Johnson et al., 2010; Mendonca & LaScala, 2011; Cannone et al., 2012; 2015; Shanun et al., 2012; Calvagno et al., 2013; Sturtevant et al., 2013; Puma et al., 2013; Risk et al., 2013; Wohlfahrt, 2013). It is thus of relevant interest the evaluation of the dynamics of community evolution and species competition in order to assess and quantify the feedbacks of vegetation to climate change.

II.2. Alpine plant phenology and recent climate change

Phenology is the study of the timing of the occurrence of biological events, the causes of their occurrence in relation to biotic and abiotic factors and the interrelationships between the phases of the same species or different species (Lieth, 1974). For long time the man observed plant phenology: there are traces of phenological observation in ancient China and Japan, Greece and Roman times (e.g. Demaree & Rutishauer, 2011).

The perception regarding the discipline of phenology has definitely changed over time. Especially with the advent of the systematic scientific model, under which impulse started the recording of the life cycle for a large number of species that are today fundamental as proxy data to study the past climatic variations and that make this discipline as a critical element for global change research (e.g. Richardson et al., 2013; Schwartz, 2013).

The last IPCC report (IPCC, 2014a) assessed that there are now many evidences, mainly on the Northern Hemisphere, that phenology shifts have occurred in response to climate changes.

The availability of long-term datasets, has led to the recognition that phenology is one of the most sensitive and tangible biological responses to climate change across several biomes over the Northern Hemisphere (e.g. Sparks & Yates 1997, Menzel & Fabian, 1999; Ahas et al., 2002; Penuelas et al., 2002; Walther et al., 2002; Parmesan & Yohe, 2003; Root et al., 2003; 2005; Badeck et al., 2004; Parmesan, 2006; 2007; Defila & Clot, 2005; Menzel et al., 2006a; Cleland et al., 2006; 2007; Hoye et al., 2007; Wipf, 2010; Primack et al., 2009; Cook et al., 2008; 2012; Ma & Zhou, 2012; Iler et al., 2013a; 2013c).

Plants have advanced their spring phenology even faster than average temperature has increased (Ovaskainen et al., 2013). Such results come from ground-based studies, but there is ample evidences of phenological changes also from remote sensing satellite studies (e.g. Jeong et al., 2011; Garonna et al., 2014; 2016; Liu et al., 2016; Mao et al., 2016; Zhu et al., 2016).

The expansion of the growing season length (GSL) has been observed over the last decades (e.g. Menzel & Fabian, 1999; Cannone & Dalle Fratte, 2016), with a large contribute from both spring advances and autumn delays (Jeong et al., 2011; Garonna et al., 2016).
Satellite based analyses emphasized the role of the advances of the spring green-up as well as of the delays of the end of season in contributing to the growing season lengthening (Garonna et al 2014; 2016; Jeong et al., 2011).
Spring events clearly indicate an advance of 2-3 days per decade in the last fifty years (Peñuelas et al., 2002, Defila & Clot, 2005, Menzel et al., 2006a, Gordo & Sanz, 2009), while autumn events provided more heterogeneous and less consistent patterns (e.g. Menzel & Fabian, 1999; Penuelas et al., 2002; Menzel et al., 2006a; Defila & Clot, 2005; Gordo & Sanz, 2009; Yang et al., 2014).

At a global scale, climate change affects some regions more than others, and high latitude and high altitude environments have been recognized to be among the most sensitive systems to climate change impacts (IPCC, 2014a; Elmendorf et al., 2012a; 2012b). Alpine regions have been identified as one of the best context to quantify climate change impacts, as at high altitudes changes in temperature could be used as an early detection tool of the signal of global warming (Giorgi et al., 1997).

Changes in phenology may be especially prominent in alpine and Arctic ecosystems because they are experiencing higher than average rates of temperature increase under global climate change, and projected changes indicate greater warming for this region in the future (Root et al., 2003; Cannone et al., 2007; Callaghan et al., 2011; IPCC, 2014a).

Many studies from Arctic and alpine tundra plants phenology focused on greening and flowering phenomena (Keller & Körner, 2003; Molau et al., 2005; Hulber et al., 2010; 2011; Wipf & Rixen, 2010; Cooper et al., 2011; Abeli et al., 2011; Dullinger & Hulber, 2011; Cornelius et al., 2013; Petraglia et al., 2014a; 2014b; Bjorkman et al., 2015; Straka & Starmozski, 2015; Walder & Erschbamer, 2015; Bernareggi et al., 2015; 2016). Only few addressed also autumn phenology (Marchand et al., 2004; Shi et al., 2014; Filippa et al., 2015; Rosa et al., 2015; De Boeck et al., 2016), which have been comparatively neglected (Gallinat et al., 2015).

In the last two decades started a large number of field manipulation experiments which increased our knowledge about responses of plants phenology to modelled future climate change (e.g. Arft et al., 1999; Aerts et al., 2004; 2006; Walker et al., 2006; Wipf & Rixen, 2010; Cooper et al., 2011; Cornelius et al., 2013; Rumpf et al., 2014; Rosa et al., 2015; De Boeck et al., 2016; Carbognani et al., 2013; 2016).

Air temperature warming in combination with an anticipation of the snow melt can alter the phenology of alpine and Arctic plants, to a degree that is site and species-specific (Aerts et al., 2006; Walker et al., 2006; Rumpf et al., 2014; Rosa et al., 2015). Most studies indicate that warming advanced reproductive phenology as indicated by the timing of budburst, flowering and fruiting (Walker et al., 1999; Dunne et al., 2003; Aerts et al., 2006; Cleland et al., 2006).

In contrast, long-term observations from control plots of the ITEX (International tundra experiments) project, reveals minimal phenological advancement when coupled with 1°C of warming, likely due to strong inter-annual variability in temperatures and variability among sites in long-term climatic trends (Oberbauer et al., 2013). Phenological responses can vary among sites (Hollister et al., 2005; Hoffmann et al., 2010) and may even be delayed by warming (Hollister et al., 2005; Yu et al., 2010).

However, the degree of potential phenological advance within the lifespan of the individual is controlled, after all, by limits to phenotypic plasticity (Anderson et al., 2012; Gratani, 2014), which may lead to not linear responses to climate (Iler et al., 2013a; Ernakovich et al., 2014).

Our general understanding of phenological responses to climate change is based almost solely on the first day on which an event is observed (Parmesan, 2007; Cook et al., 2012; Ovaskainen et al., 2013; Menzel et al., 2006a; 2006b), limiting our understanding of how communities may respond as a whole.

In addition to the first day of manifestation for a single phenophase, there are other components of the entire phenological response (CaraDonna et al., 2014; Menzel et al., 2006a): timing of the ending of a biological event and peak abundance. For example, the number of species changing their flowering times can be underestimated and the magnitude of phenological change overestimated when documenting the changes of all the distribution curve of the flowering phase (CaraDonna et al., 2014).

There appears to be a significant taxonomic, spatial, and temporal variability in the magnitude of these changes, with some species showing no change, or opposite trends (e.g. Fitter & Fitter, 2002; Menzel et al., 2006a; Parmesan, 2007; Gordo & Sanz, 2009; Primack et al., 2009).

Estimates of phenological change are sensitive to the specific time period used (Bolmgren et al., 2013), and species may show different responses in different parts of their range (Schwartz & Hanes, 2009) or within the same community (Cleland et al., 2006; Miller-Rushing & Primack, 2008; Crimmins et al., 2010).

Moreover, different communities may vary in the direction and strength of responses to climate (Aldridge et al., 2011). The biological organization level, together with the spatial scale, is the main driver to be considered when analyzing and forecasting phenology (Diez et al., 2012). However, the development of forecasts at these different scales is constrained by our poor understanding of phenological variability, within and among communities (Ibanez et al., 2010; Pau et al., 2011).

Changes in phenology can be an adaptation to climate change, but also the limits to phenological adaptation (IPCC, 2014a). Species unable to adjust their phenological behavior will be negatively affected, particularly in highly seasonal habitats as alpine and Polar tundra ecosystems (Elmendorf et al., 2012a; 2012b). There is high confidence that in these regions, climate change-induced phenological shifts will continue to alter the interactions between species (IPCC, 2014a).

The phenology of any species needs to be linked to the phenology of other species with which it interacts, such as competitors, food species, and pollinators (Ehrlen, 2015; Forrest et al., 2015). For example, biotic interactions exacerbate the effect of climate change on plant reproductive phenology and success (Hulber et al., 2011; Kudo, 2014; 2016; Forrest et al., 2015).
Increasing temperatures may bring species either more into or out of synchrony, depending on their respective starting positions in the season (Høye et al., 2007; Singer & Parmesan, 2010), although evidence is more toward a loss of synchrony (Thackeray et al., 2010; Kudo, 2014).

Plant-herbivore interactions are also central to the functioning of tundra ecosystems (with high variability over space and time), and their effects on biodiversity, energy flows, nutrient cycling, and the role in structuring these ecosystems is increasingly being recognized (e.g Barrio et al., 2016).

Systematic cross-taxa studies indicate different rates of phenological change for different species and trophic levels (Parmesan, 2007; Cook et al., 2008; Thackeray et al., 2010, Iler et al., 2013b; Doiron et al., 2015), which could bring to trophic mismatches (i.e. lack of synchrony between phenology of consumers and that of their resources).
If adaptation is insufficiently rapid or coordinated between interdependent species, disruption of ecological features such as trophic cascades, competitive hierarchies, and species coexistence is inferred to result (Nakazawa & Doi, 2012; Rafferty et al., 2013).

Lack of coordination can occur if one of the species is cued to environmental signals that are not affected by climate change, such as day length (Hulber et al., 2010; Keller & Korner, 2003; Parmesan, 2006; Cannone & Dalle Fratte, 2016 submitted).

Phenology has a key role for the structure and functionality of ecosystems at different trophic levels (Miller-Rushing & Weltzin, 2009), from species (Zhu et al., 2016), up to the community (Diez et al., 2012) with thus large potential implications on nutrient and carbon storage.

Despite similar convergences in their responses to climate, alpine and polar tundra plants are subjected to different photoperiodic limitation (Ernakovich et al., 2014). However, the role of photoperiod has been neglected and underestimated, particularly in alpine regions (Keller & Korner, 2003; Vitasse et al., 2016; Cannone & Dalle Fratte, 2016). However, a deeper knowledge of its role on contributing to phenotypic plasticity could be helpful to assess non-linear responses to climate (Iler et al., 2013a).

Another aspect of global changes, other than gradual changes, are the extreme events. Current climate models predict the increasing frequency and severity of extreme climatic events, like heat waves, drought and heavy, irregular rainfalls (e.g. Orsenigo et al., 2014, IPCC, 2014b; IPCC, 2014d). The responses of tundra plant species to extreme weather events mainly focused on germination or reproductive stages (Wipf & Rixen, 2010; Orsenigo et al., 2014, 2015; Walder & Erschbamer, 2015), even if there are evidences that extremes can influence also the autumn senescence (De Boeck et al., 2016; Cannone & Dalle Fratte, 2016) and thus the growing season length (Cannone & Dalle Fratte, 2016).

Moreover, the climate change induced phenological shifts showed important implications also for agriculture (Menzel et al., 2006a; Stoate et al., 2009; IPCC, 2014f).

In conclusion, the timing of phenological events influences a wide range of ecological processes, including species demography (Miller-Rushing et al., 2010), species interactions (Hegland et al., 2009a; 2009b), ecosystem functions such as carbon cycling (Morrisette et al., 2009; Richardson et al., 2010) and ecosystem services (Morisette et al., 2009; IPCC, 2014a) and thus constitute a key component for the human livelihoods (IPCC, 2014a).

II.3. Ground surface temperature and sensitivity to climate change

The World Meteorological Organization recognizes permafrost (perennially frozen ground) and active layer among the essential abiotic variables for quantifying the impacts of climate change (e.g. Harris et al., 2001). Moreover, permafrost degradation and active layer thickening, play a crucial role in terms of surface instability (Gruber et al., 2004; Huggel, 2009; Einhorn et al., 2015; Haeberli et al., 2016). Natural hazards related to permafrost retreat are expected to become more frequent (Gobiet et al., 2014), and can reach exceptional amount of disturbed material with high relevance for the risk management (e.g. Dramis et al., 1995; Bodin et al., 2016; Phillips et al., 2016), but also for the vegetation stabilization (Cannone et al., 2007; 2008).

With the ongoing climate change, a number of monitoring sites has been established through the Alps during the last decades (e.g. Guglielmin et al., 2001; Guglielmin, 2004; Cremonese et al., 2011; Paro & Guglielmin, 2011; Haeberli, 2013; Pogliotti et al., 2015), as well as in Arctic (e.g. Nelson et al., 2008) and Antarctic tundra (e.g. Guglielmin et al., 2012; 2014; Guglielmin & Vieira, 2014).

The active layer dynamics are controlled by a number of variables such as air temperature, solar radiation, topography, ground surface characteristics, ground ice/water content and the timing, distribution and physical characteristics of snow cover (Zhang, 2005; Luetschg et al., 2008; Scherler et al., 2010; Wollschläger et al., 2010; Zenklusen Mutter & Phillips, 2012). Consequently, the active layer thickness has a high spatial and temporal variability (Anisimov et al., 2002; Wright et al., 2009) which in the Alps may occur at very small scale (Pogliotti et al., 2015).

Active layer changes can indirectly modify the overlying vegetation through variations of the frost heave, cryoturbation, ice segregation or gelifluction disturbance, or through the different water availability linked to the active layer thickness (Cannone & Gerdol, 2003; Cannone et al., 2004; 2007; Guglielmin et al., 2014).

Conversely, vegetation affects the energy balance of the soils and, therefore, vegetation changes can have feedbacks on the active layer thickness and underlying permafrost temperature (Klene et al., 2001; 2008; Cannone & Guglielmin, 2009; Walker et al., 2003, Guglielmin et al., 2012; Guglielmin et al., 2014). Indeed, different vegetation associations produce a different organic layer thickness, which affect the conductivity of temperature through soils (Mazhitova et al., 2004, Smith et al., 2009).

Studies from Antarctica revealed that cryptogamic vegetation provides an insulating effect on the ground surface temperature (GST), with a net cooling (Cannone & Guglielmin, 2009; Guglielmin et al., 2012). The degree of cooling varies with differences in vegetation types, structure, coverage and thickness (Cannone & Guglielmin, 2009). Similarly also in Arctic, tundra vegetation involves a net ground surface cooling (e.g. Klene et al., 2001).
Mosses play an important role in permafrost stability by buffering the surface soil temperature (Guglielmin et al., 2008; Soudzilovskaia et al., 2013), which is negatively related to the thickness of organic soil layers (Cannone et al., 2006; Harden et al., 2006; Romanovsky et al., 2007; Guglielmin et al., 2008).

The ground surface temperature (GST) is of relevant interest because it has crucial implications on the initialization, calibration and validation of numerical models for predicting permafrost spatial distribution (e.g., Guglielmin et al., 2003; Noetzli & Gruber, 2009; Hipp et al., 2014). Indeed, the mean annual ground surface temperature (MAGST) is one of the best indicator of permafrost presence (e.g. Guglielmin et al., 2003; Guglielmin, 2004; Gruber et al., 2011).

One of the main challenges in the study of GST variability is the quantification of the thermal effect of snow cover given the influence that it can have on thermal regime trough different processes (Zhang, 2005; Luetschg et al., 2008; Guglielmin & Vieira, 2014).
On gentle slopes, snow cover mostly causes a net increase of MAGST due to the insulating effect during winter, but timing of snow cover onset and melt out, duration, thickness and interaction with ground surface characteristics strongly control the local magnitude of this effect (Hoelzle et al., 2003; Brenning et al., 2005; Gruber & Hoelzle, 2008; Pogliotti, 2010; Gubler et al., 2011; Rödder & Kneisel, 2012).

Although a number of studies focused on snow-GST interaction exists (e.g.,Zhang, 2005), little is known on its spatial and temporal variability especially over complex alpine terrains (but see Gubler et al., 2011; Pogliotti et al., 2015).
The snow cover is subject to a high spatial and temporal variability, from the beginning of its formation until the spring melt out. Firstly, the amount of precipitation has a fundamental role, but other factors are important, as wind and landscape morphology (Zhang, 2005), and thus variation in the snowpack duration and permanence on the ground have important implications on soil energy budget (Zhang, 2005).
In Alpine environment is fairly well known that the snow thickness increases with altitude, but the distribution can vary according to the above explained forcing. Thus, many works have been done in an attempt to apply statistical analysis and models to recreate the snowpack distribution (Lopez-Moreno & Nogues-Bravo, 2006, Lopez-Moreno et al, 2009). These models are useful also for avalanche hazard modelling (e.g. SnowPack model, Bartelt & Lehning, 2002). Plattner et al (2004) applying a geostatistical analysis between the snow distribution, topographical and climatic variables, identified the altitude as determining factor between 2750 and 3000 m a.s.l., while above 3050 m a.s.l. the wind redistribution played the most important factor, with regard to both erosion (wind exposed ridges) and accumulation (leeward sites).

Also the vegetation, in terms of canopy structure, influences the snow distribution. Pomeroy (2006) studied the tundra shrubs, and concluded that they facilitate the snow accumulation (+147%) respect the patchy tundra vegetation. At the same time, the snow melt is 47% greater than tundra sparse vegetation, because the heat flow transmitted through longwave radiation from the shrubs facilitate the melting. The net radiation increase with the increase of shrubs because of lower reflectance of the short radiation. In general, the snow accumulation in the shrub is greater than other tundra sites because of the larger retention of the snowfall and wind distribution in the lower part of the shrubs. The authors in particular identified three classes of interaction between shrubs and snow: tall shrubs exposed above the snow, tall shrubs sub-emerged from the snow, lower shrubs covered by snow.
Beck et al (2005) develop models predicting the distribution of shrubs in the Arctic environment, based precisely on the snow distribution and duration. Vegetation, wind and snow, may help in the prediction of climate change. Walker (1993) studied the distribution of 50 species along a gradient

of snow cover, to investigate the relationship between the topography, the distribution of the snow by wind and distribution of vegetation, underlying that the comprehension of these relationships may help to predict effects of climate change.

The timing, depth and duration of the snow cover are of special importance to upland ecosystems, as they define the start and duration of the potential growing season (Inouye & Wielgolaski, 2003), as well as the temperatures under the snow (Pomeroy & Brun, 2001). Snowmelt and water infiltration are two important processes of the hydrological cycle in alpine basins (Zhang et al., 2016).

In alpine and polar ecosystems there is a close association between the spatial patterns of snow distribution and the occurrence of vegetation types or plant species (e.g. Evans et al., 1989; Walker et al., 1993; Odland & Munkejord, 2008; Guglielmin et al., 2014), illustrating the importance of snow depth, snowmelt and season length in structuring communities (Galen & Stanton, 1995).

Due to its effects on plant and soil temperatures and soil freezing processes, the snow depth controls biochemical, microbial and plant processes in winter (e.g. Campbell et al., 2005; Sturm et al., 2005), the effects of which can persist well into the growing season (Jones et al., 1998; Weih & Karlsson, 2002). Therefore, changes in the snow cover can have a wide range of species-specific effects on alpine tundra plants (e.g. Wipf et al., 2009), especially when considering that the snow cover has declined at a global-scale (IPCC, 2014), as well as for the European Alps (e.g. Edwards et al., 2007; Durand et al., 2009; Klein et al., 2016).

The soil thermal regime is conditioned by the soil surface conditions and thus by the types of vegetation, which can influence greatly on individual processes of the surface energy regime. In particular, it is the microclimate that determines the variation in the average surface temperature (e.g. Scherre & Korner, 2011), and, where soil temperatures are close to 0 °C, the local factors determine the presence or absence of permafrost (e.g. Klene et al., 2001).

The surface soil thermal balance can be simplified to only one index, the *n-factor* (Klene et al., 2001). This index is calculated as the ratio between the thawing degree-days (TDD) of the soil (s) and those of the air (a): TDDs/TDDa. For a given period, TDD is the temperature sum of daily mean above 0°C. This implies that: values of n-factors close to unit indicate little difference between the degree-days of soil and that in the air, while values below the unit reflect higher air temperatures than those of the soil.
Klene et al. (2001) found a wide inter-site variability in relation to the vegetation cover type, but also a large inter-annual variability. Moreover, grouped summer n-factor according to vegetation categories: the bare soil had higher n-factor, than the wet tundra, and last the shrubs have the lowest values. The shading effect of the canopy of shrubs would be responsible for the portion of the direct radiation that reaches the surface.

Similarly to the TDD, for a given period the FDD (Freezing Degree Days) are the cumulative sum of mean daily temperature below 0°C (Cannone et al., 2006, Guglielmin et al., 2008). Antarctic tundra vegetation studies revealed by using these cumulated indices that the vegetation influence considerably on the soil thermal balance (Cannone & Guglielmin, 2009).

The moderating effect of vegetation on the GST is well documented in the literature (e.g. Balisky & Burton, 1993). The vegetation mainly affects the soil thermal regime and diminishes the solar radiation. The albedo of the various types of vegetation is also very variable, but in general, within the canopy there is an attenuation of the light, and thus of the radiant energy, that is function of the plant architecture.

Little is known about the effects of specific growth forms on the soil thermal regime. Balisky and Burton (1993) analyzed three species in British Columbia: *Alnus rubra*, *Rubus sp*. and *Epilobiom angustifolium*. They measured air and soil temperature during the growing season, and use as a base temperature in the calculation of degree-days of 8 °C. After a statistical analysis (ANOVA) they observed that the average temperature of the soil was attributable to the daily energy and humidity input, and indicated greater temperatures for bare ground and lower with *A.rubra.*

Snow cover can be the key factor in determining the presence or absence of permafrost in sporadic discontinuous permafrost areas (e.g. Zhang, 2005). Individual measurements of the BTS (Haeberli, 1973; Brenning et al., 2005; Isaksen et al., 2002; Lewkovicz & Ednie, 2004) and/or monitoring of ground surface temperature (GST) at the snow-ground interface are simple techniques recommended for the investigation of mountain permafrost distribution and development (Hoelzle et al., 1999; Ishikawa, 2003; Gadek & Kedzia, 2008).
The BTS is a geophysical based methods applied since 1970s to investigate permafrost distribution (Haerbeli, 1973). It consists in measuring the temperature under the snowpack, when it reaches a depth higher than 80 cm, at the end of the winter season. At this moment, the measured value is function only of the soil energy balance of the previous year.

It 'also widely recognized that the soil temperature in winter depends on the previous summer heat balance. One of the methods of mapping permafrost developed in the Alps (Haeberli, 1973) is based on this concept. It provides, in fact, the measurement of the temperature of the soil at the base of the snow cover in the winter period, when the snow has a thickness of at least 80 cm at a radius of 10 m. The measured values are then divided into classes: <-3 ° C permafrost present, between -2 °C and -3 °C permafrost likely present and > -2 ° C permafrost absent.
Guglielmin & Tellini (1994) applied this method in the Foscagno area, identifying 3 classes of permafrost presence according to their BTS values: T<-3°C = probable presence of permafrost, -3°C<T<-1.7°C = possible permafrost, T>-1.7°C = absence of permafrost.

The actual model for mapping mountain permafrost distribution, normally do not consider vegetation as a factor to be included in permafrost modeling (Keller et al., 1998; Wright et al., 2003; Guglielmin et al., 2003), or included vegetated areas as proxy of permafrost free areas (Boeckli et al., 2012).
Different types of vegetation have been attributed to the presence/absence of permafrost and for example allowed to discriminate active/inactive rock glaciers (Burga et al., 2004; Cannone, 1997a; 1997b; Cannone, 1999).

The temperature under plant cover depends thus from their leaf density; normally it is assumed that more compacted growth forms, such as cushion plants, could achieve higher temperature during the day and prevent rapid cooling during the night (e.g. Sklenar et al., 2016). It is thus therefore crucial to disentangle the effect of the vegetation types on the soil surface temperatures, in order to assess the evolution of GST in the future climate change scenarios.

However, in a climate change scenario, independently from the warming or the cooling of air temperature, we may expect shifts of vegetation ecology and composition with consequences on the GST and the active layer thickness and further feedbacks on the carbon cycle in both alpine and Polar tundra (Welker et al., 2004; Oberbauer et al., 2007; Myers-Smith et al., 2011; Cannone et al., 2012; 2015).

II.4. Evaluating climate change impacts. Long term monitoring or simulations through manipulative experiments?

Researchers have adopted two main strategies to predict plant and terrestrial ecosystems responses to climate change: a) spatial and/or temporal monitoring and b) climate change simulation.

Spatial and/or temporal monitoring

Ground observations

The first approach relies on observations over time or space to quantify sensitivities to climate variability and change (e.g. Menzel et al., 2006a; Schwartz et al., 2006; Parmesan et al., 2007; Høye et al., 2007). Such information were useful in the recent decades to assess impacts of climate change on biodiversity.

Long-term field observation are usually based on field measurements of individual plants or plots (Cleland et al., 2006; Hoye et al., 2007; Inouye, 2008), or larger portion of vegetation communities (Aldrige et al., 2011; Diez et al., 2012; CaraDonna et al., 2014).

Field observations are based also on short-term studies focused along natural gradients, such as latitude (e.g. De Frenne et al., 2013; Bienau et al., 2014) or altitude (e.g. Ziello et al., 2009; Cornelius et al., 2012; 2013; Jochner et al., 2012; Frei et al., 2014).

Ultra-sonic sensor data have been used for the evaluation of plant communities' growth rate in response to climate (Jonas et al., 2008; Vitasse et al., 2016), and digital image analysis also proved to be a valuable tool for the computation of phenological index, such as greenes index (e.g. Richardson et al., 2009; Migliavacca et al., 2011; Julitta et al., 2014; Filippa et al., 2015).

Walther et al., (2002) reviewed studies on climate change impacts on shifts in species range, invasion, community shifts and phenology over the period 1950-2000. For all these traits, many examples were reported of changes in the direction expected to occur under ongoing climate change.

At the beginning of the 2000s, in two studies (Parmesan & Yohe, 2003; Root et al., 2003) meta-analysis techniques were applied to test if a coherent fingerprint of global warming on wild plants and animals could be detected. References to nearly 100 individual studies reporting trend analysis on phenological phases are given in these two papers and in Walther et al. (2002).

Root et al. (2003) analyzed results from 143 studies on changes in species densities and ranges, morphology, genetic frequencies, and phenology. Analysis showed that significant changes occurred in the direction expected for the given climatic-change trends. For the studies on spring phenology within the past 50 years, linear trends were calculated and the regression slopes analyzed. The analysis is based on 61 studies reporting results on 694 plant and animal species. The studies included had to meet the following three criteria: they examined a time series of at least 10 years; they found a change for at least one trait analyzed; and they found either a temporal trend in temperature or a strong association between the trait and site temperature. The estimated mean number of days of advancement in the phenological phases per decade was 5.1 (± 0.1 SE). Because the warming trend is higher in higher latitudes, separate analyses were performed for the latitudinal belts 32–49.9° and 50–72 °N that resulted in trends per decade of 4.2 (± 0.2 SE) and 5.5 (± 0.1 SE), respectively. Trees, on average, responded less (3.0 ± 0.1 SE) than non-tree plants that had a response ratio close to 5 as the overall result.

Parmesan & Yohe (2003) analyzed results on more than 1700 species on changes in species abundance; range boundary shifts; and phenology. Observations of birds, butterflies and alpine herbs resulted in an overall significant trend for northward and upward elevational shifts in range boundaries at the poleward and upper distribution limits. Trends in phenology were analyzed for 172 species, for which time series of at least 17 years and observations over large geographical regions were available. Meta-analysis resulted in a mean advancement of spring phases by 2.3 d per decade.

Based on the basic and robust hypothesis about the causal link between temperatures and spring phenology, an acceleration in the advancement of spring phenology in the late 20th century is to be expected (Badeck et al., 2004), as confirmed by the work of Walther et al. (2002).

Penuelas et al. (2002) made the same observation in analyzing the time series for a mesic Mediterranean site in northern Spain.

Several analyses of the inter-annual variability in phenophases (Forchhammer et al., 1998; Chmielewski & Rötzer, 2001; D'Odorico et al., 2002; Scheifinger et al., 2002) demonstrated a correlation with the NAO Index. In positive phases of the NAO, when winters are warmer in northern and middle Europe, phenological phases tend to be triggered earlier.

In conclusion, ground observations of phenology not only bear a clear and consistent warming signal, but also indicate parallelism in the phases of warming and advancement of phenology.

Satellite observations

Remote sensing has been widely used to explore land surface phenology at the landscape level (e.g. Studer et al., 2007; Garonna et al., 2014; 2016; Jeong et al., 2011; Ma & Zhou, 2012; Henebry & DeBeurs, 2013; Mao et al., 2016).

Analysis of the normalized difference vegetation index (NDVI) temporal cycle provides an indication of the seasonal greenes. Badeck et al. (2004) provided a review of the main works from satellite data since the last decade and compared these results with evidence from ground-based data.

Using methods of correlation analysis, Buermann et al. (2003) showed that the spatial patterns of covariability of spring temperature and greenness in the northern hemisphere are associated with the influence of large-scale atmospheric circulation patterns. Particularly, the effect of ENSO is that of a general warming at northern latitudes, while the Arctic Oscillation (AO) in its positive phase, adds additional warming in Eurasia but not in eastern North America. The additive effect of these patterns may explain differences between vegetation activity in Eurasia and North America visible in greening trends and spring timing.

Schwartz et al. (2003) provided in their book the frame of the main phenological observation network existing all around the world, comparing also remote sensing phenology results and the main application of phenological studies.

Climate change simulations

The second approach relies on experiments that directly manipulate in the field at the plot-scale one or more environmental factor: temperature, precipitation, growing season length, nutrients load (e.g. Arft et al., 1999; Chapin et al., 2006; Aerts et al 2006, Wipf & Rixen, 2010; Wahren et al., 2005; 2013; Bokhorst et al., 2007b; 2009; 2011; 2013; Wipf & RIxen, 2010; Cooper et al., 2011; Bassin et al., 2012: Anadon-Rosell et al., 2014; Cooper, 2014; Elmendorf et al., 2012; Oberbauer et al., 2013; Cornelius et al., 2013; 2014; Petraglia et al., 2014a; 2014B; Bjorkman et al., 2015; Rosa et al., 2015; Li et al., 2015; Bokhorst et al., 2016; Livensperger et al., 2016; DeBoeck et al.., 2016; Zhu et al., 2016).
On the contrary, only few studies focused their attention also on the most neglected photoperiod limitation (Heide, 2005; Keller & Korner, 2003) or on the cost of reproduction (e.g. Obeso, 2002, Xiao et al., 2016).

Climate change simulations: soil and air temperature

Future higher temperature conditions have been simulated with open-top chambers (OTCs), which are easy to handle and have been widely used in many ecosystems from Arctic and Antarctic tundra (Marion et al. 1997; Hollister & Webber 2000; Dennis et al., 2013; Bokhorst et al., 2011; 2013; 2016; Livensperger et al., 2016; Rosa et al., 2016), to alpine meadows (Totland 1999; Kudernatsch et al. 2008; Zhao et al., 2014) and also deciduous forests (De Frenne et al. 2010).

In the frame of the ITEX project (Molau & Molgaard, 1996), it was started a network of climate change simulation experiments over alpine and polar tundra ecosystems: open top chambers have been used to experimentally warm soils and plants and to quantify the responsiveness of tundra plants (e.g. Arft et al., 1999; Elmendorf et al., 2012a; 2012b; Oberbauer et al., 2013).

Climate change simulations: snow cover

Another topic largely studied by mean of simulation experiments is the snow cover. In their review, Wipf & Rixen (2010) provided a frame of the effort already done in relation to snow cover field-experiments. The snow manipulation experiments can roughly be divided in 3 categories, differing in the climate scenario they actually simulate (Wipf & Rixen, 2010): a) delayed snow melt, b) earlier snow melt, c) earlier snow melt combined with warming.

a) Increase snow and/or delayed snow. Most snow manipulation experiments that simulated increased quantities of snow have done so by either manipulating snow depth manually (i.e. shoveling snow), decreasing snow melt rates (i.e. using reflective cloth covers), or accumulating wind-drifted snow, e.g., behind snow fences or within open-top chambers (OTCs) (Wipf & Rixen, 2010; Cooper et al., 2011; 2014; Frei et al., 2014; Rumpf et al., 2014).
b) Earlier snow melt. This scenario is created by either manipulating snow manually (i.e. shoveling away snow), increasing snow melt rates (i.e. using dark clothes), or by mean of transplanting experiments (Wipf & Rixen, 2010; Carbognani et al., 2012; Petraglia et al., 2014a; Sedlaceck et al., 2015).
c) Earlier snow melt combined with a summer warming treatment. This scenario was simulated by applying a warming treatment that starts before the snow has melted, and therefore accelerates and advances snowmelt. However, in this case is not easy to quantify separately the responses to earlier snowmelt and to the subsequent warming (e.g. Wipf & Rixen, 2010; Livensperger et al., 2016).

Climate change simulations: water

Plant responses to water (changes liquid precipitation and soil moisture) have also been analyzed. We can divide studies about this topic in two main categories: water table manipulations (e.g. Strack et al., 2006; Cornelius et al., 2014) or drought manipulation experiments (e.g. De Boeck et al., 2016).

Kong et al. (2013) examined the response of aboveground and fine root biomass to water and N addition in two consecutive years. They showed that inter-annual precipitation fluctuations resulting from the emergence of an extreme rainfall event could have the potential to modify plant response to water and N enrichment.

Additions of water to terrestrial ecosystems was done for a wide range of ecosystems from Alps (Cornelius et al., 2013) to Antarctica (Simmons et al., 2009; Day et al., 2009; Dennis et al., 2013; Ball & Virginia, 2014; Sylvain et al., 2014; Wasley et al., 2006).
In maritime Antarctica for example, temperature and the availability of water and organic substrates will probably increase, and soil microbial activity will lead to more rapid C and N cycling with a positive feedback on these biogeochemical processes, particularly where or when these factors increase concurrently (Benhua et al., 2014). However, from past climate change manipulations, is fairly well known that Antarctic flora is more strongly affected by elevated nutrients more than water (Wasley et al., 2006).

Climate change simulations: nutrients additions

Tundra plants are adapted to survive stressful abiotic limitations, such as low mean annual temperature, short growing season, and low soil nutrient availability (Billings, 1987; Korner, 2003). We could expect environmental factors to affect production and evolution of tundra ecosystems only if they are able to alter nutrient availability (Jonasson, 1992; Shaver et al., 1992). In particular, nitrogen (N) and phosphorous (P), which are the two most essential and growth-limiting elements in terrestrial ecosystems (Chapin et al., 1995; Elser et al., 2007, Petraglia et al., 2014b; Li et al., 2016).

The growth of global population and of anthropogenic activities (industrialization and agricultural intensification) have significantly altered and influenced the N and P cycles in terrestrial ecosystems (Galloway et al., 2004; Liu et al., 2013; Smil, 2000). It is estimated that N wet deposition accounts for 40–80% of total atmospheric N deposition in most regions (Holland et al., 2005; Lü and Tian, 2007; Vet et al., 2014). Unlike carbon (C) and N, P doesn't have a stable gaseous phase in the atmosphere, and thus atmospheric P deposition has been thought to be relatively small (Smil, 2000). However, atmospheric P deposition (as direct dust deposition or dust entrained in precipitation) is potential source of new P input to terrestrial ecosystem and could be ecologically important due to frequent limitation of primary productivity by P in many ecosystems (Elser et al., 2007).

Therefore the implication from dust deposition are double in tundra biomes: it could bring in an earlier snow melt with consequences on the start of the growing season (Steltzer et al., 2009), and it could potentially amplify the fertilizing effect of atmospheric N deposition, due to the higher P input (Elser et al., 2007; Harpole et al., 2011).

The warming-induced increase in nutrient mineralization and the further increase in atmospheric N and P depositions raise the topic of whether and how alpine plants will react to enhanced nutrient availability (e.g. Petraglia et al., 2014b).

Some manipulation experiments for this reason focused on other aspects of global changes, such as: rising CO2 concentration, or increasing soil nitrogen and phosphorous availability (e.g. Yin et al., 2016; Li et al., 2016; Gasarch & Seastedt, 2015; Dunne et al., 2003; Fuhrer 2003; Hautier et al. 2009; Johnson 2010; Liancourt et al. 2009; Cornelius et al. 2013; Spence et al. 2014), or their combination with other environmental factors such as warming, light, water (Chapin et al., 1995; Gough et al., 2002; Campioli et al., 2012; Kong et al., 2013).

The additional N source by melting snow contributes substantially to alpine plants N uptake, particularly during periods when N demands are highest (Hiltbrunner et al., 2005; Bombonato & Gerdol, 2012). Nitrogen addition demonstrates that most alpine plants are particularly responsive to increased N supply (Schappi & Korner, 1996; Heer & Korner, 2002),
The consequences of an excessive N load, can be altered growth, altered organism chemistry composition, shifted phenology, changed nutrient cycling and, ultimately, alteration in plant community composition (Xia, 2008; Xi et al., 2016), even if is still lacking an adequate knowledge of the impacts of nutrients on plant phenology (Jochner et al. 2013).

Global warming can accelerate the decomposition of soil organic matter in ecosystems with typically low temperatures, which may lead to an increase in soil nutrient availability (Chapin et al., 1995; Cornelissen et al., 2014).

Nutrient availability in the soils is not related to nutrient concentrations in the leaves: there are environmental cues that influence nutrient uptake and translocation rates. Variations in soil temperature modify the activity of soil microorganisms and nutrient mineralization (Koch et al., 2007; Rinnan et al., 2009; Li et al., 2014; 2015; Zhao et al., 2014; Puissant et al., 2015; Wang et al., 2015).

Experiments on Alpine tundra showed that manipulating the snow cover can change the N:P ratio in the microbial biomass, which declined after increasing snow cover (Bombonato & Gerdol, 2012). The potentially enhance of absorption of P, rather than N, by microbes may eventually reduce P availability for plant uptake.

Moreover, plants from low fertile environments displayed specific and evolutive adaptive mechanisms for nutrient resorption from senescing leaves and facilitate transport of photosynthetic products to other part of the plant (Aerts et al., 2007; Freschet et al., 2010; Lang et al., 2014).

However, caution should be used in estimating soil fertility and specific nutrient limitations of growth based on foliar nutrient concentrations in herbaceous communities (Bowman et al., 2003). The N addiction did not linearly increased the biomass production of alpine vegetation (Bowman et al., 2006). Case studies have been conducted to examine responses of ecosystem biomass production to P addition, which vary significantly among different studies or ecosystems (Davidson et al., 2004; Huang et al., 2012).

Similarly Antarctica ecosystems have been investigated in related to nutrient limitation (e.g. Smith, 1994; Dennis et al., 2013; Ball & Virginia, 2014; Wasley et al., 2006).
In Antarctica, large but spatially localized and mostly coastal bird and seal colonies are known to influence vegetation in their vicinity through extra nitrogen deposition (e.g. Bokhorst et al., 2007a; Favero Longo & Cannone, 2010; Favero Longo et al., 2012). Penguin colonies, in particular, are associated with large guano deposits. Local presence of bird colonies have been identified as the most significant external mineral nitrogen input to Antarctic terrestrial ecosystems (Bokhorst et al., 2007a).
Furthermore, productivity of the canopy can be measured by sampling the plant biomass that could be subsequently weighted (biomass estimation) or analyzed for the determination of leaf area index (LAI) (Cornelissen et al., 2003; Gerdol et al., 2004; Studer et al., 2007; Petraglia et al., 2014; Filippa et al., 2015; Livensperger et al., 2016).

Climate change simulations: photoperiod

One of the most important environmental factor regulating tundra plant phenology is photoperiod (Keller & Korner, 2003; Heide, 2001; 2005; Hulber et al., 2010) and constitutes the major forcing that shapes responses between mid-latitude and high latitude tundra ecosystems (Ernakovich et al., 2014). Some species are able to flower only after a critical photoperiod threshold is achieved or can be photoperiod-independent (Heide, 1989; 1990; 1992; 2001; 2005; Keller & Korner, 2003).

The importance of photoperiod is relevant also towards the end of the growing season, when the number of light hours is shortening, and it can play a crucial role in determining a conservative strategy for alpine tundra plants (Cannone & Dalle Fratte, 2016).
Darkness is frequently used in physiological studies to initiate and maintain senescence processes in intact leaves (Thomas & Stoddart, 1980). Nevertheless, among the simulation experiments, few

studies to our knowledge are dedicated to photoperiod or light manipulation in the field (but see Chapin & Shaver, 1985; Shaver et al., 1986; Chapin et al., 1995; Campioli et al., 2012; Gough et al., 2002).

Climate change simulations: flower removals

To our knowledge, very few studies addressed the topic of flower or fruits removal (but see Obeso, 2002), in order to assess nutrient remobilization and distribution among plant compartments, particularly in tundra plants.

Obeso (2002) reports on the processes associated with costs of reproduction, including some theoretical considerations, definitions and methodological aspects, followed by a list of the situations where costs are difficult to find. Despite some exceptions, case studies, examined by trade-offs between reproduction and other life-history traits, generally support the predictions of the cost of reproduction hypothesis. The cost of reproduction as an evolutionary determinant of sexual dimorphism in life history traits in dioecious species was specifically tested, considering that the higher cost of reproduction in females has driven the life history traits related to sexual dimorphism. Finally, the mechanisms that enable the compensation of the reproductive costs are detailed, including the plastic responses of photosynthesis and growth, the effects of the timing of investment, plant architecture and plant physiological integration

In a flower removal experiment Karlsson et al. (2006) look for relationships and potential trade-offs between vegetative growth, i.e., branching, and fruit production in two contrasting sub-Arctic populations (growing at low and high altitude) of *Rhododendron lapponicum*. The high-altitude population showed several characteristics indicating that this population gave priority to vegetative growth over sexual reproduction

Flower removal increased the number of ramets, and biomass allocation to stolon and roots, on an experiment on the herbaceous species *Duchesnea indica* (Xiao et al., 2016). Moreover, onset and median date of flowering phenology shifted after organ removals.

Selas et al. (2011) combined N-fertilization and flower removal experiments during a three year period on bilberry (Vaccinium myrtillus), finding that the N-concentration increased with both fertilization but also flower removals.

Other evidences of higher vegetative growth as consequence of flower removal come from agronomic experiments (e.g. Snow, 1989; Polisetty & Singh, 1994; Zobolo & Van Stadeb, 1999). Zobolo & Van Staden (1999) for example investigated the effects of deflowering and defruiting on the growth and senescence of the annual herbaceous species *Bidens pilosa* (a plant use for commercial use to treat malaria disease). Deflowered plants were generally taller, had a greater shoot weight and higher chlorophyll concentration than those that were only defruited. Fruit and flower heads were responsible for the reduction in leaf and stem growth after flowering. Deflowering is essential if the leaves are to be harvested commercially because it retarded senescence and maintained growth.

Reliability of climate change manipulation experiments

Such experiments have been used to extrapolate to future climate conditions, assuming that plant responses to experimental manipulations match long-term responses to climate change (Elmendorf et al., 2012).

Testing this assumption is an important first step to assess the utility of warming experiments for long-term forecasting and prediction, and for this reason, the reliability of manipulation and simulation experiments results is still an open debate (e.g. Wolkovich et al., 2012; Elmendorf et al., 2012).

Some authors found coherence across methods (warming or not) and in plant responses to warming (Dunne et al., 2003; Wahren et al., 2013), while others demonstrated that warming experiments largely underpredicted the advancing of phenological events (e.g. timing of flowering and leafing, Wolkovich et al., 2012).

These significant mismatches seem to be unrelated to the study length or to the degree of manipulated warming experiments (Wolkovich et al., 2012). Long-term and short-term warming experiments might have similar effects on the soil nutrient levels, microbial biomass, and enzyme activities in the alpine meadow of the Tibetan plateau (Wang et al., 2014), and thus on plant communities.

The discrepancy between experiments and observations, however, could arise from complex interactions among multiple drivers in the observational data, or it could arise from remediable artefacts in the experiments that result in lower irradiance and drier soils, thus dampening the phenological responses to manipulated warming (Wolkovich et al., 2012).

Moreover, experimental studies typical applied static warming treatments, without incorporating future climatic variability (such as extreme events) which have a greater impact on ecological systems than changes in means alone (Thompson et al., 2013). The timing of extreme events is critical regarding their impact on plant communities and their synergism can aggravate negative effects, for example, when heat waves and drought happen simultaneously large effects on plant activity have been detected (De Boeck et al., 2016).

III. ALPS

III.1. Introduction

High elevation alpine areas have been identified among the most sensitive and vulnerable ecosystems to the impacts of CC (IPCC, 2014f; 2014g), and are also characterized by high biodiversity due to the elevation gradient, complex topography, edaphic conditions and complex evolutionary history (Korner, 2003). In high elevation areas of Europe, the biodiversity is threatened by climate change (CC) and land use change (IPCC, 2014a; 2014b; 2014f). The Nature 2000 network has been established to protect biodiversity of species and habitats in Europe and may provide a sort of “insurance” in particular for the conservation of species threatened by climate and anthropogenic changes. For all Nature 2000 sites specific monitoring and managing plans has been elaborated. Therefore, the improvement of the knowledge on the biodiversity of these sites and on the responses of species and ecosystems to climate and environmental change may provide key information both for the implementation of the existing planning and for the elaboration of suitable strategies focusing on species adaptation to CC. Our study site (the Foscagno valley) belongs to the Nature 2000 network and could be considered as a template of high elevation alpine ecosystems characterized by very low anthropogenic impacts. Therefore, the ecosystem responses and dynamics detected at this site may be used as a proxy and/or contribute to fill the knowledge gaps on the behavior of these ecosystems and for the development of adaptation strategies and management plans.

The vulnerability of alpine vegetation has been demonstrated by several studies providing evidences that the impacts of CC on the alpine vegetation already occurred at different levels of organization, thus implying also altered competition between species and consequently local extinctions (Dullinger et al., 2012). The main impacts have been observed concerning species physiology and metabolism (Brancaleoni et al., 2007; Carbognani et al., 2012; Mondoni et al., 2011; 2012; Bernareggi et al., 2015; 2016; Orsenigo et al., 2015) and plant phenology and growth (Defila & Clot, 2005; Ziello et al., 2009; Hülber et al., 2010; Orsenigo et al., 2014; Petraglia et al., 2014a; Straka & Starzomski, 2015; Filippa et al., 2015; Vitasse et al., 2016; Cannone & Dalle Fratte, 2016 submitted). Evidences from studies of spatial distribution and communities composition highlighted higher rates of shrubs encroachment and an upward migration of tundra plants as response to climate change (Walther, 2003; Walther et al., 2005; Tape et al., 2006; Cannone et al., 2007; 2008; Pauli et al., 2007; Gehrig-Fasel et al., 2007; Holzinger et al., 2008; Kelly & Goulden, 2008; Lenoir et al., 2008; Parolo & Rossi, 2008; Grabherr et al., 2010; Gottfried et al., 2012; Kullman, 2010a; Cannone & Pignatti, 2014; Carbognani et al., 2014; 2016), with consequential important changes in productivity and biogeochemical cycle (Körner et al., 1997; Koch et al., 2008; Gerdol et al., 2008; Zeeman et al., 2010; Fóti et al., 2016; Kirk, 2016).
Profound changes in ecosystem functioning and potential losses of high-alpine and Arctic species are expected under climate warming as cold-adapted plants may be outcompeted by taller growing species or lost as their habitats vanish (Rixen et al., 2014).

Above all, plant phenology has become one of the most reliable indicators of the ongoing climate change, since phenological cycle of organism is strongly controlled by climate (Schwartz, 2003; Menzel et al., 2006a; Cleland et al., 2007; Chuine, 2010).

Recent studies of plant phenology, mainly of greening and flowering phenomena, indicated that timing of vegetation is changing faster in the recent years (Walther et al., 2002; Root et al., 2003; Parmesan & Yohe, 2003; Menzel et al., 2006a; 2006b; Cleland et al., 2007; Cook et al., 2012; Wolkovich et al., 2012; Iler et al., 2013a; 2013b).
There are also ample evidences about alteration in inter-specific (plants, birds, herptiles, insects and fungi) phenological synchrony (e.g. Ovaskainen et al., 2013; Forrest, 2015; Kudo, 2016), with consequences on ecosystem functioning and services. The timing of plants life cycles are shifting (e.g., flowering – CaraDonna et al., 2014) with discrepancies from their pollinators or herbivores, and thus reduction of insects abundance (Pyke et al., 2016).

Field based long-term phenological observations clearly indicated an average advance of spring events of 2-3 days per decade in the last fifty years in response to earlier snow melt (Defila & Clot, 2005; Menzel et al., 2006a; Penuelas et al., 2002; Gordo & Sanz, 2009). On the other side, autumn events provided more heterogeneous and less consistent patterns (e.g., Menzel & Fabian, 1999; Penuelas et al., 2002; Defila & Clot, 2005; Menzel et al., 2006a; Gordo & Sanz, 2009). However, overall the Northern Hemisphere the autumn phenology was delayed in the last three decades (Liu et al., 2016), leading to an expansion trend in the growing season length (even if with spatial heterogeneity – e.g. Wang et al., 2016). There are also evidences that the growing season lengthening is fastening over the last decades (Jeong et al., 2011; Garonna et al., 2014; Kolarova et al., 2014; Wang et al., 2016), with effects clearly visible also on the net carbon uptake and carbon sequestration rate (e.g. Calvagno et al., 2013).

In Alpine environments, the complexity of topography, ground surface types, snow cover distribution, subsurface hydrology and geology strongly influence the permafrost thermal regime (e.g., Guglielmin, 2004; Scherrer & Korner, 2010; 2011; Gruber et al., 2011; Apaloo et al., 2012; Pogliotti et al., 2015), altering the response of terrestrial ecosystems to changing environmental conditions. Also the thermal variability related to plant communities (Lenoir et al., 2013) and plant growth forms (e.g., Klene et al., 2001; Scherrer & Korner, 2011) at local scale is determinant in a climate changing context, because it may strongly increase the local spatial buffering to climate warming (Lenoir et al., 2013). The topographically induced mosaics of micro-climatic conditions are associated with local plant species distribution and the risk of overestimating alpine habitat losses in isotherm-based model scenarios (Scherrer & Korner, 2011): species depending on the very coldest microhabitats will find thermally suitable ‘escape’ habitats within short distance.

The European Alps are facing strong climatic and vegetation changes since the late 1950s (Cannone et al., 2007; Cannone & Pignatti, 2014), which have been showed to be comparable to the Arctic tundra (Elmendorf et al., 2012b; Cannone & Pignatti, 2014). Therefore, even if the variability of the Alpine system is great, the microclimate variability could counterbalance the effects of warmer temperatures predicted for the future by IPCC scenario (Scherrer & Korner, 2010; 2011), and long-term observations at one site could be representative of changes of vegetation occurring at larger scales (Elmendorf et al., 2012b).

Since 2007, a field-based long-term monitoring project of snow, ground surface temperature and plant phenology started at the Foscagno valley, a high elevation alpine site of the Italian central Alps. The study area covers an elevation gradient of almost 250 meters, from grasslands to snowbeds, with observation sites distributed among all the topographic conditions (aspect and slope), and is thus constituted by the typical microclimate variability of alpine terrains.

Our data were analyzed in relation to the climatic dataset (1996-2016) provided by LaFoppa AWS (Automatic Weather Station), located <1km far from the study area, in order to assess the inter-annual variability of phenology in relation to climate, and to quantify the degree of plasticity of alpine plant species, both in years characterized by “normal” climatic conditions, as well as with extreme years. Indeed, due to the largest photoperiodic limitation at tropical latitudes, alpine plants are expected to be less able to profit from growing season lengthening (compared to polar regions) particularly if coupled with decrease water availability (Ernakovich et al., 2014). However, few studies focused on the importance of photoperiod on providing the ranges of natural variability of alpine plants (e.g., Gugger et al., 2015).

The Foscagno valley provides a suitable context to study the evolution and dynamics of terrestrial ecosystems and to assess the plasticity/responses of alpine species and ecosystems to the natural inter-annual climate variability. Indeed, in this area, the land use change in the recent year it is almost negligible and, therefore, the observed responses and eventual changes are exclusively related to natural inputs, in particular to climate. This area was only marginally devoted to livestock pasture in the last years (only one-two weeks per year, normally at the end of August), and more precisely, only sheep grazing has been documented at least in the last two decades (about 400 heads each year, personal communication by the shepherd) (see also chapter III.2.D.e).

Plant phenology can provide a clear and imminent response of plants to the inter-annual variability of climate, however most studies are devoted to few species, while ground observations of large dataset are still missing. The main aims of the long-term snow and phenology monitoring was to investigate the relationships between climate and alpine plant phenology in the frame of ITEX (International Tundra Experiment). We monitored phenology of 21 plants species typical of alpine environments and representative of different growth forms types. In particular, we hypothesized that:

-the vegetative development is regulated by snow melt timing, while the other phenological stages (i.e. flowering, seeds development, seeds ripening and leaf senescence) are regulated mostly by the photoperiod, thus implying a conservative strategy, which provided a specific intervals for the phenophases to allow to cope with the inter-annual climate variability;

- plant phenology shows different plasticity depending on the growth form types and also on the phenological stage; plastic species will respond to the inter-annual variability of climate parameters, while aplastic species follow a defensive strategy and respond to climate only with extremes;
- extreme events can overwhelm the effect of the photoperiod, and can lead to carry-over negative effects in the phenological cycle and plant growth the following year.

Concerning the long-term ground surface temperature (GST) monitoring, 13 temperature data loggers were installed in the Foscagno valley, under different surface types condition, covering the most widespread growth forms of the area. The main purpose was to investigate the GST under different soil coverage types, in order to assess the relations of GST with climate, and the impacts on the spatial distribution of temperatures. Specifically, we hypothesized that:

- GST could be strongly influenced by the soil coverage types and snow cover distribution and persistence;
- even if actual climatic conditions are less favorable for permafrost aggradation, some vegetated soils could lead in a soil cooling, and thus to permafrost condition;
- the shrublands expansion could drive to an energetic disequilibrium of GST with thus feedbacks on carbon cycle.

In summer 2015, the long-term monitoring was implemented with manipulation experiments that simulated impact related to potential future climate change including the increase of nutrient availability (simulated by additions of urea, ammonium nitrate, NPK respectively), of water availability (once or twice additions per week), lack of reproductive stages (flowers removal).

The main purpose of the manipulation experiments was to investigate the responses of phenology and plant growth under different simulations of anthropogenic related climate change. This could help to implement the results from the long-term observations concerning the plasticity of species to climate and environmental pressures, and their inter-annual and intra-annual variability. In particular, we hypothesized that:

- plants phenological cycles will not be affected by manipulations, for those stages where we hypothesized a photoperiodic limitation;
- on the contrary, the quantitative vegetative development (shoot length, leaf length, maximum plant height) is influenced by the treatments, with the nutrient additions exerting the higher impacts, compared to flower removal and water addition;
- the above ground biomass (ABG) is strongly influenced by the addition of nutrients, more than flowers removal or water addition.

For the nomenclature of plant species we referred to the annotated checklist of the Italian vascular flora (Conti et al., 2005) and to the Italian vegetation database of the VegItaly project, coordinated by the Italian Society of Vegetation Science (Lucarini et al., 2015; http://www.vegitaly.it/). For the nomenclature of syntaxa we referred to the Italian vegetation prodrome (http://www.Prodroquetia.it, Biondi & Blasi, 2013; Biondi et al., 2014), a project of the Italian Botanist Society built on the classification of the Italian vegetation proposed by Blasi (2010).

III.2. Study area

III.2.A. The Foscagno Valley

The study area is a high elevation alpine site (>2300m a.s.l.) located above the treeline in the Foscagno Valley (Italian Central Alps) (46.4°N, 10.2°E). The valley is close to the Foscagno pass (2291 m a.s.l.) and neighboring with the Stelvio National Park (Fig. III.2.1). Although this area extends beyond the boundary of the National Park, it is characterized by habitats of great natural and environmental relevance. Indeed, it has been recognized has a site of community importance (SIC "Passo and Monte Foscagno") by the European Union, in the frame of the ecological network "Nature 2000", established under the Habitats Directive (92/42/EEC). It is a typical alpine environment, characterized by the presence of several habitats of high quality: from bog vegetation, pastures, grasslands and shrublands up to the characteristic habitats of the snowbeds and pioneer communities of the high alpine belt. Moreover, these habitats constitute a source of livelihood for the alpine fauna that colonize the area. It is easy to observe protected species, like eagle (*Aquila chrysaetos)*, bearded vulture (*Gypaetos barbatus*) and many other species typical of alpine environments, like chamois and marmots.

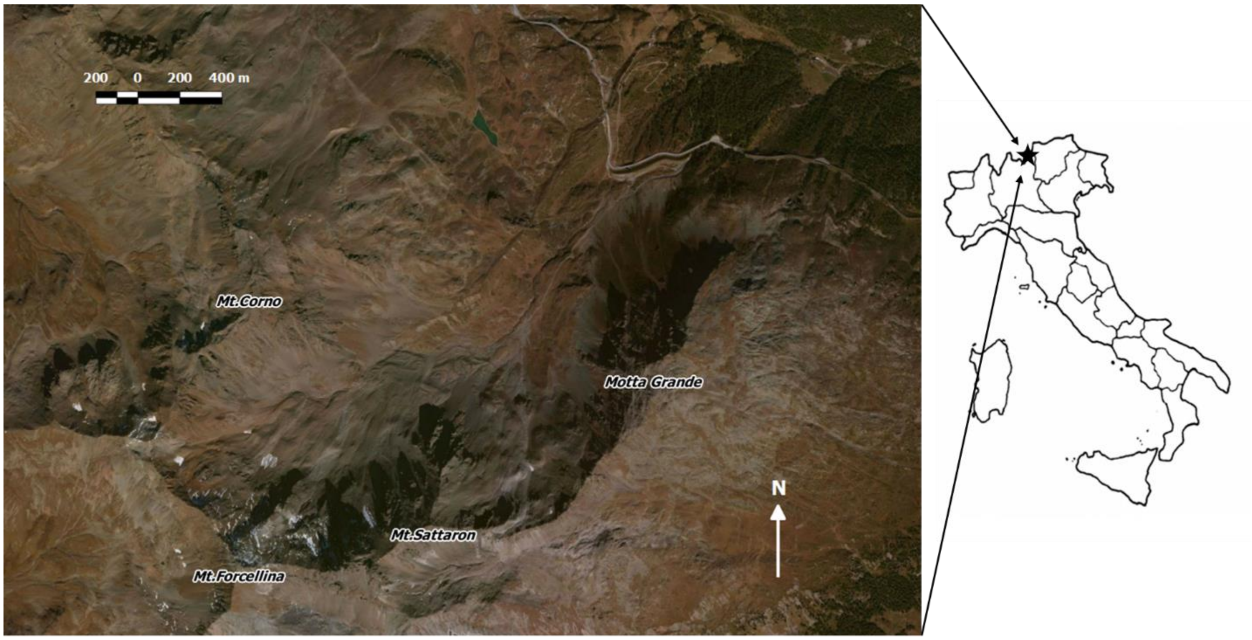


Figure III.2.1. Location of the Foscagno Valley (Bing Aerial photography, 2015).

The Foscagno valley is also characterized by a great morphological diversity: several glacial and periglacial features, relict, inactive or still active, are well widespread and make it an area of high geomorphological significance. In the valley, a patchy occurrence of permafrost has been described, mostly within the Foscagno rock glacier, which is the most important topographic feature of the study area, and one of the most studied rock glacier of Europe (e.g. Guglielmin et al., 1994; Cannone, 1999; Hauck et al., 2001; Guglielmin et al., 2001; Guglielmin et al., 2003; 2004; Stenni et al., 2007; Ribolini et al., 2010).

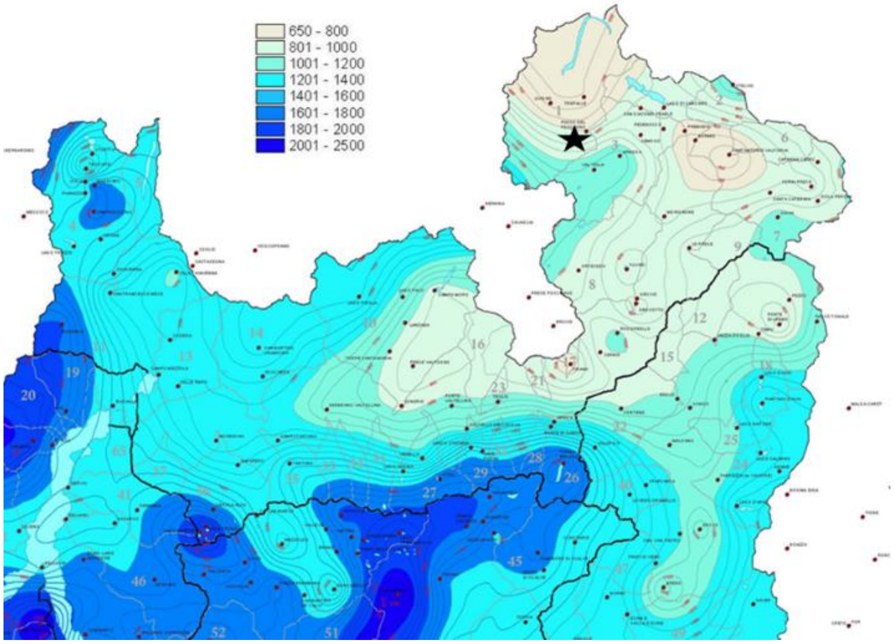


Figure III.2.2. Clip of the Lombardia region mean annual precipitation map obtained with Kriging method (Ceriani & Carelli, 2000). The Foscagno valley is indicate by the black star.

III.2.B. Geography and Climate

The Foscagno area is located in the northeastern sector of central Italian Alps (Alps Retiche), in high Valtellina, southeast from Livigno. It lies in the province of Sondrio (SO), in the country of Valdidentro and Livigno, and is included in the table D1b5 of regional technical maps (CTR) of Lombardia region. The study area is situated in a valley that from the Foscagno pass goes towards the Val Viola Bormina in the direction NE-SW (Fig. III.2.1).

The Foscagno valley is a lateral valley of Viola Bormina valley, by which is separated by the ridges of Mt. Forcellina (3087 m a.s.l.), Mt.Sattaron (2735 m a.s.l.) and Motta Grande (2714 m a.s.l.). On the Northern side, the Vallaccia pass link the Foscagno valley with the Vallaccia valley, by which is separated by the ridges of Mt.Corno (2986 m a.s.l.) (Fig. III.2.1). The whole Foscagno valley covers an area of about 3 km^2, with an elevation range of about 1000 metres, spreading from the main road SS301 (2140 m a.s.l.) up to the summit of Mt. Forcellina. The hydrological catchment is defined by the Foscagno river basin, the only one tributary from east of the Viola river, which waters feed the river Adda.

The climate here is characterized by a continental regime (Ceriani & Carelli, 2000): January is the coldest and driest month while July is the warmest and wettest. Because of the complex orography in Valtellina, the average annual precipitation values are highly variable (Fig. III.2.2). The driest areas are those surrounding the Foscagno valley: the area of Livigno-Trepalle (657 mm/years) (Ceriani & Carelli, 2000). The Foscagno valley in particular, is characterized by a more severe climate due to the northeastern exposure, which strongly limits the insolation, especially in winter.

The mean air temperature (MAT) is of -0.1°C (computed on the period 1996-2015) and there is a persistent snow cover of about 8 months (since September-October to May-June).

III.2.C. Geology and Geomorphology

This region is part of the Campo-Languard fault that belongs to the Upper Austroalpine domain. The bedrock is completely acidic and the lithology mainly consists of paragneiss (with prevalent andalusite) and amphibolite, which compose the rocks of the highest portion (Mt.Corno, Mt.Corno-Mt.Forcellina glacial cirque), while in the basal zone predominate low-grade paragneiss and micaschist (Guglielmin, 1989). Moreover, the Mt.Forcellina ridge has a small Late Hercynian granite-granodiorite intrusion (Guglielmin & Notarpietro, 1992). The rocks of both lithological units are very deformed and rock masses are therefore generally degraded.

Figure III.2.3. Morphological drop on the lateral moraine located on the left of the Foscagno valley.

The Foscagno valley is a glacial basin with slightly asymmetrical section, as evidenced by the presence of erosion (roche moutonnée and striated rocks) and glacial accumulation: glacial circle edges and moraines characterize the landscape of this valley. The conservation status of these features is not optimal, since the intense gravitational and crioclastic activities has partially erased the traces. Despite this, well preserved are the lateral and frontal moraine ridges that are related to the high Late Glacial Period pulse, but also the "fluted moraine" that border the western side of the valley. The presence of these features would testify the past existence of slope glaciers in this valley (Guglielmin, 1989; 1997).

Furthermore, the lateral moraine on the left shows numerous forks and branching, sharing the same abrupt morphological drop of about 70 m between 2300 and 2370 elevation a.s.l. (Fig. III.2.3). This drop is at the same level of an alignment of counterslopes hedges on the eastern side of Mt.Corno and could be due to phenomena of neotectonics. According to Guglielmin (1997), it is not possible to exclude that the moraine ridges that begin at an elevation of 2300 meters are related to a more ancient glacial event than the one represented by the higher elevations glacial deposit. On the opposite, the recent glacialism (Little Ice Age, LIA) did not leave such evidences, even if there is an historical and iconographic documentation of the presence of a small glacier up to year 1932 A.D. (Nangeroni, 1933), that covered an area of about 7 ha between 2650 and 2800 m a.s.l (Fig. III.2.4).

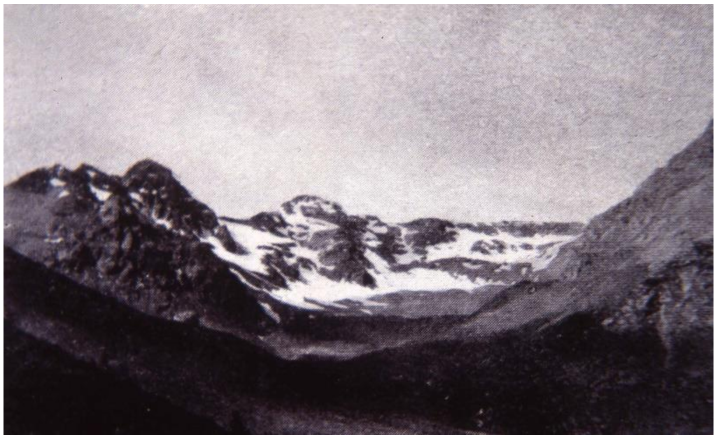


Figure III.2.4. Picture of the small glacier still present in 1932 (Nangeroni, 1933). Source: SGL-Servizio Glaciologico Lombardo: http://www2.sgl.cluster.it:81/archivio_storico/dosde/dosde_anni.asp?anni=1932**.**

A large number of periglacial features (Pietracaprina, 1963; Guglielmin, 1997) also characterize the Foscagno valley (Fig. III.2.5). The greatest geomorphological shape of the area and one the most studied of all the Alps occupies the Mt.Forcellina cirque: the Foscagno rock glacier (Fig. III.2.5). It's a complex rock glacier: the higher part has been classified as active, in contrast to the lowest and inactive part (Guglielmin, 1997). The active area extends from 2450 up to 2730 m a.s.l. covering an area of about 0.3 Km^2. The rock glacier morphology is highly variable; on the higher side, the edges are not well defined and on its surface, there are lobes and roughness, longitudinal furrows and small concavity. Its surface is characterized by the presence of large blocks (from decimeters up to meters) with a gravelly-sandy matrix localized only in few points. Blocks are mainly not colonized by lichens or mosses, but where the sandy matrix is more abundant, it is starting the vegetation colonization by pioneer plants. The massive face of the active rock glacier, large more than 300 meters (Fig. III.2.5) has a slope that goes over the material angle of repose, and that join the inactive rock glacier, which extends until 2390 m a.s.l. The inactive rock glacier is characterized by a more advanced state of pedogenesis, the rocks are well covered by lichens and mosses, pioneers communities are more developed and structured with evidence of colonization of individuals from lower altitudinal vegetation belts (Guglielmin et al., 2001). The active layer on the rock glacier varies from 1 to 2 meters in the frontal zone and on the right lobes, while it becomes thicker on the left lobes. Permafrost here shows variable thickness; on average is about 12 meters, with a tendency to diminish towards the apical part of the body. In correspondence of the right lobe, a high ice content has been found (Guglielmin et al., 2001; 2004). On the higher lobes on the left instead the permafrost is largely degradated, and was present at depth of about 10 meters (Guglielmin, 1997).

Other periglacial features in this site are small sorted polygons and striated soils, present on slopes and ridges at depth higher than 2600 m a.s.l. A small boulder stream is present also in the Sattaron cirque. Non-sorted shapes also occur, like turf hummocks, located close to a bog area (2400 m a.s.l.) at the beginning of the flat area that brings to the rock glacier.

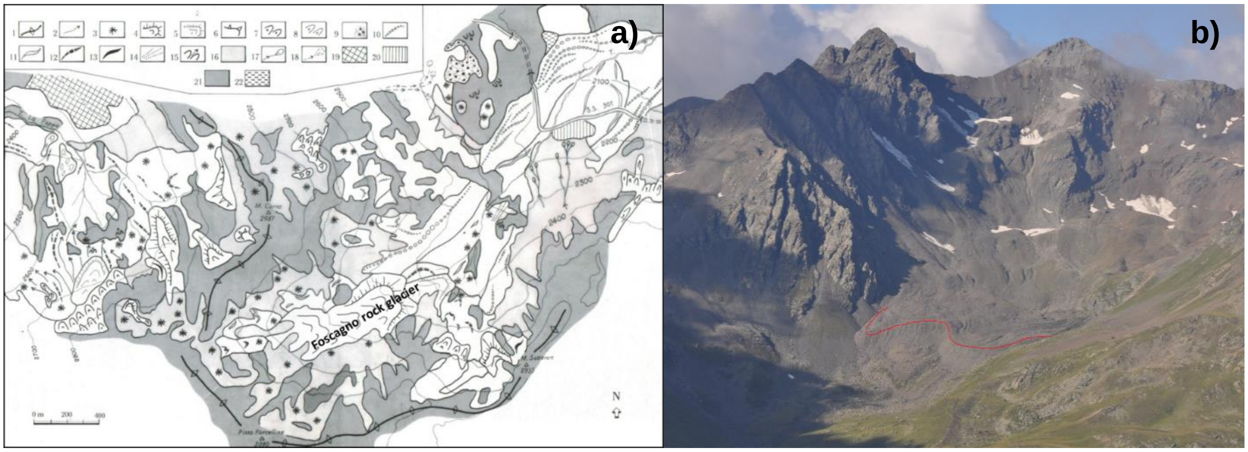


Figure III.2.5. a) Geomorphological map of the Foscagno valley (Guglielmin, 1997). Legend: 1) ridge; 2) boulder stream; 3) sorted soils; 4) active rock glacier; 5) inactive rock glacier; 6) protalus rampart; 7) active gelifluction lobe; 8) inactive gelifluction lobe; 9) fluvioglacial deposits: pre-Tardi Glaciale Foscagno I; 10) deposits and moraines: Tardi Glaciale Foscagno I; 11) depostis and moraines: Tardi Glaciale Foscagno II; 12) deposits and moraines: Tardi Glaciale Foscagno III; 13) Olocenic moraines; 14) fluted moraine; 15) roche moutonnée; 16) Olocenic deposits 17) active debris flow; 18) inactive debris flow; 19) collapsed slope; 20) anthropic deposit; 21) rock substrate; 22) Olocenic lacustrine deposits; b) Picture of the Foscagno rock glacier, with highlighted in red the massive face of the active rock glacier.

Characteristics of the valley are also landslides deposits, situated on the slopes of the valley as well as on the lateral moraine. Other gravitational phenomena are observable on the mountainsides: avalanche furrows and debris flows, mostly active but in some places inactive. Many dating have been done on buried soils and peats trying to understand the morphological evolution of the valley (Calderoni et al., 2008). These reconstructions indicated that the moraine ridge (Fig. III.2.3) should be of the Late Glacial (Egesen), dating back to 6190±80 years BP. Dating of soils of the moraine buried by the rock glacier (active or inactive) indicated its origins back to 2200±60 and 2700±70 BP. All these elements indicated that more probably the rock glacier formation is possibly related to the glacial expansion of 5800-4300 years BP.

III.2.D. Flora and vegetation

III.2.D.a. *Alpine landscapes: general characteristics*

The Foscagno valley is a suitable site to observe the distribution of the alpine vegetation belts and communities, from the coniferous forests, in the lower side of the valley, up to the subalpine

shrublands and grasslands, and the pioneer and snowbed communities at higher elevation (Fig. III.2.6).
The rigid and selective climatic context of the mountains areas merges many limiting ecological factors that determine the presence of vegetation. For this reason, only species that developed specific adaptations (genetic, morphological, physiological and phenological) could persist and live in such uncomfortable environments.

Figure III.2.6. Foscagno valley (view from Mt.Rocca). It is evident the altitudinal vegetation gradient that characterize the valley, from coniferous forest up to shrublands, grasslands, and then snowbeds.

In particular for what concerns climate, plants must adapt to several limiting condition (e.g. Bliss, 1962; Korner, 2003): low winter temperature and high thermal difference with the summer; mainly snowy precipitation,; high radiation and insulation during summer; significant wind effect (also for the snow re-distribution); large differences due to the topographic variability (implying significant effects, e.g. on the ground surface temperature; Scherrer & Korner, 2010).

Moreover, climatic factors become more limiting towards higher elevations: air temperature is colder due to the thermal vertical gradient (-0.6°C/100m). For this reason, the alpine vegetation shows a large variation with elevation (Fig. III.2.6), according to the equivalence: higher elevation= lower temperature. This equation is the analogous of what happens going toward the poles: higher latitude = lower temperature; thus, it is the main reason why alpine vegetation could be considered at the same ecological level of the polar tundra vegetation, besides showing similar responses to the climate forcing (Cannone & Pignatti, 2014).
The environmental conditions are similar comparing alpine and Polar environments and the same species sometimes occur in both biogeographical regions (Arctic-Alpine species).

Thus, alpine species developed some peculiar characteristics allowing them to live in these habitats: resistance to low temperature and frost damage, short growing period (due to the long duration of snow cover), drying resistance, efficiency in nutrient absorption. To improve their adaptation these species developed many strategies: dwarf or cushion growth form, perennial organs, efficient vegetative and clonal reproduction, cold-resistant leaves (thicker, white cuticles or hairs), higher photosynthetic efficiency, higher shoot:leaves ratio (Fig. III.2.7) (e.g. Bliss, 1962; Billing & Mooney, 1968; Walker et al., 2001; Korner, 2003).

Figure III.2.7. *Pulsatilla vernalis* (spring anemome or lady of the snow) is a species of Ranunculaceae, native of mountain habitats in Europe, and it is a nice example of high elevation adaptation strategy. The hairs cover all flowers and leaves, creating an insulating layer, that prevent at the same time the freezing due to cold temperature and the desiccation due to high evapotranspiration.

III.2.D.b. *Elevation belts and vegetation elements in the Foscagno Valley*

For the reason explained above, the Foscagno valley is a suitable example to observe the characteristic vegetation of the Alps and all the vegetation elevation belts typical of high elevation landscapes: subalpine (2200-2400 m a.s.l.), alpine (2400-2800 m a.s.l.) and snow belts (>2800 m a.s.l.) (Table III.2.1).

For a detailed syntaxonomic frame and nomenclature of the vegetation assemblages that characterize the Foscagno valley, please refer also to the next chapter (III.2.D.c).

Concerning the subalpine belt, the lower side of Mount Motta Grande shows the geosigmetum typical of subalpine acidophilus soils, which is a transition between the montane and subalpine coniferous forest (*Piceion excelsea*, dominated here mainly by *Larix decidua*) and shrublands/grasslands.

Soon after the limit of the coniferous forest, shrublands become the dominant communities with the *Rhododendro ferruginei-Vaccinion myrtilli* alliance. The dominant species are *Rhododendron ferrugineum*, *Empetrum hermaphroditum*, *Vaccinium myrtillus* and *Vaccinium uliginosum*. The snow depth during the winter season is enough to protect shrub leaves from the cold and freezing air.

In areas with less snow accumulation during winter, it is present the ecological vicarious community of the *Juniperion nanae*. Here *Juniperus communis* dominates, growing preferentially on southern facing slopes, where the snow melt is anticipated.

In areas with little accumulation of snow cover, especially in wintertime, the exposure to low temperatures and cold winds enhance the risk of frost damage. The only plant community able to tolerate such extreme conditions is the dwarf alpine shrubland of *Loiseleurio procumbentis-Vaccinion microphyilli*. *Kalmia procumbens* is the distinctive and dominant species of this association, which is characterized by high hedges of macrolichens, mainly *Cetraria* ssp and *Cladonia* ssp. Among the vascular plant species, here occur diagnostic species such as *Arctostaphylos alpinus*, *Empetrum hermaphroditum*, *Luzula lutea*, *Juncus trifidus*, *Vaccinium vitis-idea*, while other frequent species are *Vaccinium uliginosum*, *Vaccinium myrtillus*, *Rhododendron ferrugineum*. In areas even more subject to wind, and with limited duration of snow cover, the lichen coverage and thickness increase considerably.

In areas where instead the snow cover tends to increase, there are transition mosaics between *Loiseleurio procumbentis-Vaccinion microphyilli* and *Rhododendro ferruginei-Vaccinion myrtilli*.

In the Alpine belt the vegetation dynamics would lead, in the absence of environmental disturbance and with constant climatic conditions, to the formation of high-alpine grasslands, which constitute the natural potential vegetation. Due to local topographical and edaphic conditions (e.g. long permanence of the snow cover, or limited drainage of water with consequent stagnation, or the presence of instability of the surface), the most common condition is the presence of a mosaic of different plant communities (geosigmetum).

In fact, where the snow cover persists for more than eight months a year (for example in the hollows or on slopes facing north) snowbeds communities develop; but where the water drainage is reduced and the degradation of organic matter is prevented, marsh areas form with typical bog vegetation.

At sites with bare soil or surface instability, the vegetation presents pioneering characteristics, which enable it to colonize new substrates and/or to tolerate the disturbance of surface movements.

The alpine meadow occupies, with continuous coverage, both the sides and the bottom of the valley, and is mainly constituted by the alliance of *Caricion curvulae*, which dominant and representative species is *Carex curvula*. Among the characteristic species there are several graminoids (Graminae, Cyperaceae and Juncaceae) including *Agrostis rupestris*, *Anthoxanthum alpinum*, *Helictochloa versicolor*, *Avenella flexuosa*, *Juncus trifidus*, *Oreochloa disticha* and many other vascular plants including *Campanula scheuchzeri*, *Geum montanum*, *Homogyne alpina*, *Leontodon helveticus*, *Minuartia sedoides*, *Pedicularis kerneri*, *Phyteuma hemisphaericum*, *Bistorta vivipara*, *Primula glutinosa*, *Ranunculus alpestris*, *Senecio carniolicus*, *Silene acaulis*, *Veronica alpina*, *Veronica bellidioides*.

Elevation (m a.s.l.)	**Belt**	**Vegetation communities**
>3000	Snow belt	pioneers *Androsacion alpinae* and *Androsacion vandellii* Cryptogameae communities (algae, fungi, mosses and lichens)
2800–3000	Sub-Snow belt	Discontinuos grasslands *Caricion curvulae*
2600–2800	High-Alpine	grasslands *Caricion curvulae* snowbeds *Salicion herbaceae* pioneers *Androsacion alpinae* pioneers/rocky substrate *Androsacion vandellii*
2400–2600	mid-Alpine	grasslands *Nardion strictae* dwarf shrublands *Loiseleurio procumbentis-Vaccinion microphylli*
2200–2400	low-Alpine	shrublands *Rhododendro ferruginei-Vaccinion myrtilli* grasslands *Aveno-Nardetum*
2000-2200	Subalpine	Coniferous forests *Piceion excelsea*

Table III.2.1. Typical elevation belts on high mountains siliceous substrate.

Where the snow remains longer or the soil moisture is higher, it is observed the hygrophilic variant of the association *Caricetum hygrocurvuletosum*, which represents a transition between the *Caricetum curvulae* and *Salicetum herbaceae* and is characterized by the presence of *Salix herbacea*, *Luzula spicata* and *Bistorta vivipara*.

In areas subject to grazing in the past, it is observed the *Nardion strictae*, typical alliance of alpine pastures dominated by *Nardus stricta*, and its transition to the *Caricion curvulae*, the *Curvulo-Nardetum*, which is observed mainly in the lower part of the Foscagno valley.

Snowbed communities are observed where the snow cover remains on the ground for at least 8 months. Depending on the duration of snow cover, they are colonized by different plant communities, with different species composition. The main association at the Foscagno valley is the *Salicetum herbaceae*. Characteristic species are *Salix herbacea* and *Soldanella pusilla*, with *Veronica alpina*, *Ligusticum mutellina*, *Gnaphalium supinum*. This association is present between 2200 and 2800 m a.s.l., both with continuous and discontinuous coverage, on the Northern side of the Mt. Sattaron, at the base of the active rock glacier and in the inactive rock glacier.
Where the snow remains for longer periods (up to about 10 months a year), mosses dominate the plant communities, with the selection of *Polytrichetum sexangularis* association.

The vegetation of rocks and instable substrate, which largely colonize the rock glacier area, includes three main plant associations of the *Androsacion alpinae* alliance, characterized by a different degree of evolution in the succession dynamic series and different characteristics (function of elevation and snow): *Androsacetum alpinae*, *Oxyrietum digynae* and *Luzuletum spadiceae*.
The *Androsacetum alpinae* represents the initial stage of vegetation development and the typical variation of the highest elevations. Its existence in the valley is reported only in some areas of the active rock glacier (about 2470 m a.s.l.), apart from small patches on Mt.Sattaron slopes.

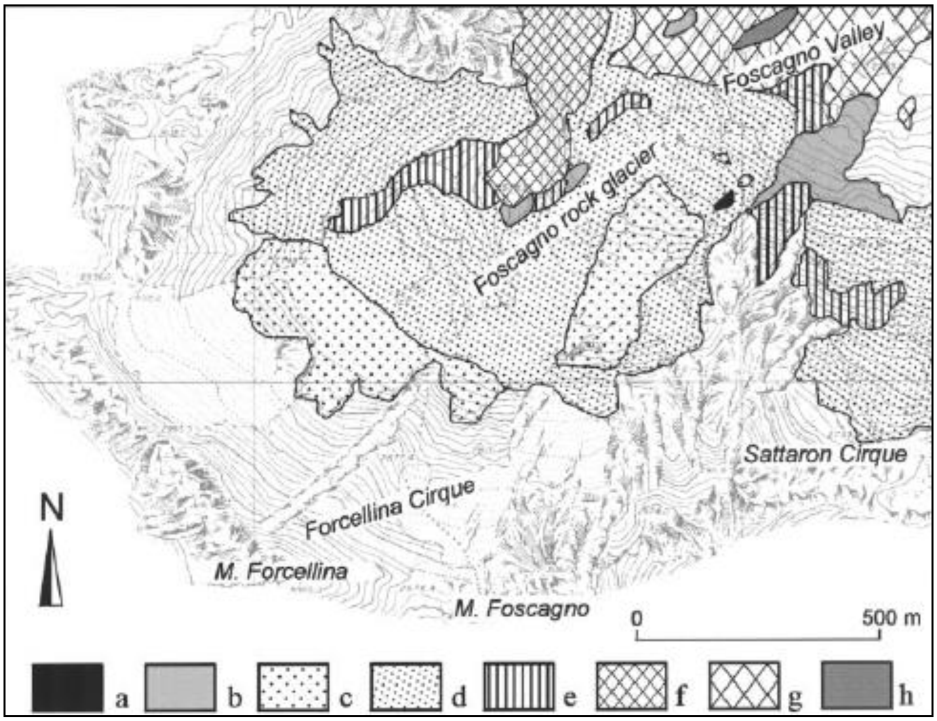


Figure III.2.8. Phytosociological map of the Foscagno Valley (Guglielmin et al., 2001). Legend: a) *Polytrichetum sexangularis*; b) *Salicetum herbaceae*; c) *Androsacetum alpinae* discontinuous; d) *Oxyrietum digynae* discontinuous; e) *Luzuletum spadiceae* discontinuous; f) *Caricetum curvulae* discontinuous; g) *Caricetum curvulae* continuous h) *Vaccinium-Rhododendretum ferruginei* continuous.

The *Oxyrietum digynae* characterizes stages of greater maturity and evolution in the succession and is present with different variants. It is the dominant association of this environment and it is always present in the Foscagno valley with discontinuous coverage (<25%). The species characteristics of this association are *Oxyria digyna*, *Geum reptans*, *Cerastium uniflorum* and *Cerastium pedunculatum* accompanied by species of superior orders such as *Ranunculus glacialis*, *Poa laxa*, *Saxifraga bryoides* and *Cardamine resedifolia* and from companion species *Leucanthemopsis alpina*, *Sedum alpestre*, *Veronica alpina* and *Senecio incanus* ssp *carniolicus*. In the Foscagno valley, this association cover a large part of the active rock glacier (Fig. III.2.8).

The *Luzuletum spadiceae* grows in areas where the slope increases. This association has a more advanced dynamic term than *Oxyrietum digynae*; moreover, being characterized by a greater permanence of snow cover is considered a transitional phase between the pioneers and the snowbeds. The characteristic species is *Luzula alpinopilosa*. It extends from 2150 up to 2600 m a.s.l. in a large part of the area, and on the eastern slopes of Motta Grande.

Moreover, in some location, there are also patches with series of transition between the main pioneers associations and variants with typical species of alpine meadows such as *Agrostis schraderiana*.

In conditions of water stagnation, it occurs a shortage of oxygen in the soils, which makes difficult the processes of degradation of the organic substance, causing the accumulation of peat in the surface layers of the soil. It is in this environmental context that are formed bog environments, characterized by the presence of species whose ecological characteristics are high hygrophilous (total and continuous flooding), very acidic pH (both that of the water and of the soil) and the partial anoxia of the terrain.

The main plant alliance is the *Caricion nigrae*, which represent communities composed of oligotrophic to mesotrophic small sedges and bryophytes that grow in acid fens. The most abundant species are *Carex nigra*, *Eriophorum scheuzeri*, *Juncus triglumis*, *Juncus filiformis* with the *Sphagnum warnstorfii*. The *Caricetum nigrae* can also be generated as regression of pastures vegetation respect an increase in the amount of water stagnation or flow.

III.2.D.c. *Syntaxonomic structure of the vegetation in the Foscagno valley*

In this section is reported the syntaxonomic frame of the main elements of the Foscagno valley vegetation, according to the Italian vegetation prodrome: http://www.prodromo-vegetazione-italia.org/introduzione.

- *Coniferous forest of montane and subalpine areas on acidic and oligotrophic soils*

Cl: *VACCINIO MYRTILLI-PICEETEA ABIETIS* Br.-Bl. in Br.-Bl., Sissingh & Vlieger 1939
Ord: *PICEETALIA EXCELSAE* Pawłowski in Pawłowski, Sokołowski & Wallisch 1928
    All: *Piceion excelsae* Pawlowski in Pawlowski, Sokolowski & Wallisch 1928
        Ass: *Piceetum excelsae* Pawlowski in Pawlowski et al. 1928

- *Alpine shrublands and dwarf shrublands*

Cl: *LOISELEURIO PROCUMBENTIS-VACCINIETEA MICROPHYLLI* Eggler ex Schubert 1960
Ord: *RHODODENDRO FERRUGINEI-VACCINIETALIA MICROPHYLLI* Br.-Bl. in Br.-Bl. & Jenny 1926
    All: *Loiseleurio procumbentis-Vaccinion microphylli* Br.-Bl. in Br.-Bl. & Jenny 1926
        Ass: *Empetro hermaphroditi-Vaccinietum gaultherioidis* Br.-Bl. in Br.-Bl. & Jenny 1926 corr. Grabherr 1993
    All: *Rhododendro ferruginei-Vaccinion myrtilli* A. Schnyd. 1930
        Ass.: *Rhododendretum ferruginei* Rübel 1911
    All: *Juniperion nanae* Br.-Bl. in Br.-Bl., Sissingh & Vlieger 1939
        Ass: *Junipero alpinae-Arctostaphyletum uvae-ursi* Br.-Bl. ex Haffter in Br.-Bl., Sissingh & Vlieger 1939.

- *Snowbeds vegetation*

Cl: *SALICETEA HERBACEAE* Br.-Bl. 1948
Ord: *SALICETALIA HERBACEAE* Br.-Bl. in Br.-Bl. & Jenny 1926

All: *Salicion herbaceae* Br.-Bl. in Br.-Bl. & Jenny 1926
  Ass: *Polytrichetum sexangularis* (Rübel, 1912) Br.-Bl.,1926
  Ass: *Salicetum herbaceae* Rübel 1911

- *Alpine meadow acidophilic vegetation*

Cl: *CARICETEA CURVULAE* Br.-Bl. 1948 nom. cons. propos. Rivas-Martínez, Diaz, Fernández-González, Izco, Loidi, Lousa & Penas 2002
Ord: *CARICETALIA CURVULAE* Br.-Bl. in Br.-Bl. & Jenny 1926
All: *Caricion curvulae* Br.-Bl. in Br.-Bl. & Jenny 1926
  Ass: *Caricetum curvulae* (Kerner,1863) Borckm.-Jer.,1907
  Ass: *Caricetum hygrocurvuletosum* Br.-Bl.,1948-50
All: *Nardion strictae* Br.-Bl. in Br.-Bl. & Jenny 1926
  Ass: *Nardetum alpigenum* Br.-Bl.;1949
All: *Agrostion schraderianae* Grabherr 1993
  Ass: *Pediculari recutitae-Agrostitetum schraderianae* Grabherr 1993

- *Alpine vegetation on scree and debris*

Cl.: *THLASPIETEA ROTUNDIFOLII* BR.-BL. 1948
Ord.: *ANDROSACETALIA ALPINAE* Br.-Bl. in Br.-Bl. & Jenny 1926
All.: *Androsacion alpinae* Br.-Bl. in Br.-Bl. & Jenny 1926
  Ass.: *Androsacetum alpinae* Br.-Bl.;1918
  Ass.: *Oxyrietum digynae* (Lüdi,1921) Br.-Bl.;1926
  Ass.: *Luzuletum spadiceae* (Brockm.-Jer.,1907) Br.-Bl.;1926

- *Alpine vegetation on rocks*

Cl: *ASPLENIETEA TRICHOMANIS* (Br.-Bl. in Meier & Br.-Bl. 1934) Oberdorfer 1977
Ord: *ANDROSACETALIA VANDELLII* Br.-Bl. in Meier & Br.-Bl. 1934 corr. Rivas-Martínez, T.E. Díaz, Fernández-González, Izco, Loidi, Lousã & Penas 2002
Sub-Ord.: *ANDROSACENALIA VANDELLII* Loisel 1970
All: *Androsacion vandellii* Br.-Bl. in Br.-Bl. & Jenny 1926 corr. Rivas-Martínez, T.E. Díaz, Fernández- González, Izco, Loidi, Lousã & Penas 2002
  Ass: *Androsacetum vandelii* Br.-Bl.;1918

- *Marsh vegetation*

Cl: *SCHEUCHZERIO PALUSTRIS-CARICETEA NIGRAE nom. mut. propos.* ex Steiner 1992
Ord: *CARICETALIA NIGRAE* Koch 1926 *nom. mut. propos.*
All: *Caricion nigrae* Koch 1926 em. Klika 1934 *nom. mut. propos.*
  Ass: *Caricetum nigrae* Br.-Bl. 1915 *nom. mut. propos.*

III.2.D.d. *The vegetation colonization of the Foscagno rock glacier*

The characteristics (type of community, floristic composition, percentage of coverage and continuity) and the spatial distribution of vegetation are not only influenced by enviromental factors such as elevation, exposure, snow conditions, but also by the age of the surface and deglaciation or by the presence of surface instability phenomena, such as those that characterize the rock glacier (Cannone, 1999). Indeed, the vegetation in the Foscagno valley shows a high diversity of plant communities, with different coverage percentages (Guglielmin et al., 2001) (Fig. III.8).

The inactive part of the Foscagno rock glacier (between 2350 and 2480 m a.s.l.) is characterized by typical vegetation of stable substrates, with evolved soils such as *Caricion curvulae* that form mosaics with the alpine heath vegetation (*Rhododendron ferruginei–Vaccinion myrtilli*, *Juniperion nanae*) and dwarf alpine shrublands (*Loiseleurio procumbentis-Vaccinion microphylli*). The active the rock glacier (from 2480 to 2730 m a.s.l.) is characterized by a greater surface movement, which allows colonization only by associations of pioneer species, typical of scree slopes and snowbeds, which consists primarily in the *Oxyrietum digynae*, which covers much of the active rock glacier area (Fig. III.8). On the contrary, areas with less surface movement are colonized by the *Luzuletum spadiceae*.

In the Foscagno rock glacier, the vegetation has also been used as a support to the study of permafrost and surface soil movement (Cannone, 1997a; 1997b; 1998; 1999). Types of vegetation have been attributed to the dynamic movement of the rock glacier surface. Some plant species are well adapted to the presence of surface movement, tolerating movements up to 35-40 cm/year, with species-specific differences depending on the extent of the measured movement (Cannone & Gerdol, 2003). Especially *Geum reptans* and *Saxifraga bryoides* on coarse substrates, and *Cerastium uniflorum* on fine substrates can tolerate very intense movements (up to 35 cm/year), while other species such as *Linaria alpina*, *Veronica alpina*, *Sedum alpestre* can tolerate minor movements and mostly on medium-fine substrates.

Moreover, investigations on vegetation have allowed the reconstruction of the maximum extension of Foscagno glacier during the LIA (Guglielmin et al., 2001). Indeed, following the altitudinal vegetation belts in a normal gradient the *Oxyrietum digynae* should be replaced by *Androsacetum alpinae* at higher elevations, and that is what happens for the Foscagno rock glaciers at elevations between 2600 and 2750 meters. However, at the same elevation outside the rock glacier, vegetation shows an inverse gradient, with the *Androsacetum alpinae* at lower elevations than the *Oxyrietum digynae*, and this is attributable to the disturbance linked to the advance of the glacier during the LIA.

III.2.D.e. *Pasture management in the Foscagno Valley*

In the Foscagno valley grasslands, the sheep pasture was documented for the last two decades (Fig. III.2.9). Each year, sheep are moved in the valley towards the end of the season for a period of almost 2 weeks (late August – early September, depending on the year). The sheep grazing occurs on the grasslands on the flat area at the foot of the rock glacier, on the lateral moraine, and the basal slopes of the Motta Grande.

Figure III.2.9. Grazing disturbance in the Foscagno valley: chamois in the higher slopes (left) and sheep on the downward grasslands (right).

The number of sheep brought to graze in the Foscagno valley each year since the last two decades was almost constant (about 400 heads) (personal communication by the shepherd). For this reason, we can exclude any impact of sheep grazing/nutrient input on the study period concerning the vegetation communities' dynamics.

One other grazing impact (even if of less important) comes from the chamois. There are not data about the exact chamois population size each year and their movements in the Foscagno area over the study period. In the study area (from grasslands up to the active rock glacier) no more than 2-3 chamois each year have been observed during the whole study period. Usually they remain at the top of the valley, coming downward only in early and late summer, with thus a small impact (compared to climate forcing) on the vegetation dynamics in the study area. Only in summer 2012, a larger and anomalous number of individuals (about 100 heads) have been observed moving around the higher ridges of the valley, even if they never went down to the study area (Fig. III.2.9).

III.2.D.f. *Relevance of the selected plant species in the frame of Habitat Directive*

In the supplementary materials (chapter III.7, table S2) is given a list of the monitored species at the Foscagno long-term phenology monitoring and manipulation experiments.

The selected species are representative of the most widespread vegetation communities of the Foscagno valley, as well as of the siliceous vegetation of the Alps. Moreover, these species are characteristic of habitats of community importance, as identified by the Habitats Directive (92/43/EEC). In this section, are described the habitats of community relevance that are represented by the species selected for our study (according to the Habitats Directive and the manual for Habitat interpretation by Biondi et al., 2010), as indicated by the Italian Vegetation prodrome (Biondi & Blasi, 2013; Biondi et al., 2014) and by the Italian manual of interpretation of the Habitats Directive (Biondi et al., 2010).

- Alpine and boreal heats (Habitat 4060)

Small, dwarf or prostrate shrub formations of the alpine and sub-alpine zones of the mountains of Eurasia dominated by ericaceous species (*Rhododendron ferrugineum*, *Kalmia procumbens*, *Vaccinium uliginosum*, *Empetrum hermaphroditum*) and dwarf junipers (*Juniperus communis*). All these species are attributable to the *Rhododendro ferruginei-Vaccinietalia microphylli*.

- Siliceous alpine and boreal grasslands (Habitat 6150)

Siliceous alpine and boreal grasslands. Acidophilic grasslands, sometimes discontinuous, in high elevation and / or stations with prolonged snow cover, in the Alps, and very rarely in the northern Apennines (also in Scandinavia and Carpathians), developed on soils derived from silicate or decalcified substrates. They include plant communities of the *Caricetalia curvulae* (mainly represented by *Carex curvula* and *Nardus stricta*), as well as of the alpine snowbeds of the *Salicetalia herbaceae* (mostly represented by *Salix herbacea*). The physionomic combination comprises other important species, such as: *Agrostis alpina*, *Anthoxanthum alpinum*, *Helictochloa versicolor*, *Carex sempervirens*, *Gnaphalium supinum*, *Leontodon helveticus*, *Ligusticum mutellina*, *Luzula alpinopilosa*, *Potentilla aurea*, *Senecio incanus*, *Veronica alpina*. Other companion species of this habitat are: *Bistorta vivipara*, *Leucanthemopsis alpina*, *Poa alpina*, *Soldanella pusilla*, *Cardamine resedifolia*

- Species-rich Nardus grasslands, on siliceous substrates in mountain areas (and submountain areas, in Continental Europe) (Habitat 6230)

Closed, dry or mesophile, perennial *Nardus* grasslands occupying siliceous soils in Atlantic or sub-Atlantic or boreal lowland, hill and montane regions. Species-rich sites should be interpreted as sites remarkable for a high number of species. This habitat is of high interest due to its high biodiversity; it is severely threatened by the lack of a correct management that could favor invasion by shrubland species, with consequential loss of biodiversity.

- Siliceous scree of the montane to snow levels (Habitat 8110)

In the Foscagno valley, consist of siliceous scree communities of the upper montane level to the permanent snow level, growing on more or less moving "cryoclastic systems" with variable grain size and belonging to the order *Androsacetalia alpinae*. The physionomic combination comprises the following species selected in our study as representative of these habitats: *Geum reptans*, *Oxyria digyna*, *Cerastium uniflorum*, *Ranunculus glacialis*, *Doronicum clusii*, *Poa laxa*, *Luzula alpinopilosa*, *Senecio incanus*

III.3. Materials and Methods: data collection

III.3.A. Plant phenology: field monitoring

The phenological data collected during this PhD field activity are part of a long-term monitoring project of high elevation plants, started in 2007, which focus on the most representative phenological events of the life cycle of 21 plants species typical of tundra and Alpine environment (see also chap III.2.D).

Individuals of these species are distributed among 53 square permanent plots (50x50cm), spread along a 250 meters elevation gradient (2360-2610 m a.s.l.) over an area of about 0.6 km^2 (Fig. III.3.1, Table S1-S3).

Species were selected at the beginning of the project, according to the following criteria (Cornelissen et al., 2003): a) to obtain the best representation of the whole ecosystems and communities over the study area and b) to provide enough information to scale up the traits values from the plant to the community level.
In order to gain a more robust analysis, each species had at least three replicates for each year, distributed among 53 permanent plots, for a total of 133 replicates (Fig. III.3.1, Table S2-S3).

The species selected for the phenological monitoring belong to different vegetation communities and growth forms (Table S3), well widespread over the study area and typical of alpine environment (a list of the selected species and a brief ecological contextualization is given in supplementary material, Table S2).
The selected species belong to six main growth forms, according to Elmendorf et al. (2012): graminoids (6 ssp, n=38), forbs (9 ssp, n=67), deciduous shrubs (1 ssp, n=4), deciduous dwarf shrubs (1 ssp, n=7), evergreen shrubs (2 ssp, n=8), evergreen dwarf shrubs (2 ssp, n=9) (Fig. S4-S9). As “dwarf shrubs”, we intend here all those shrubs with vegetation height less than about 20 cm (Myers-Smith et al., 2015).
Species were also attributed to five different vegetation communities: pioneers (29 plots, n=70), snowbeds (5 plots, n=12), grasslands (7 plots, n=19), shrublands (9 plots, n=22), dwarf shrublands (3 plots, n=10) (Table S3).

The phenological data were collected in the field twice a week, according to the ITEX protocol (Molau & Edlund, 1996), starting from the snow melt (SM) until the beginning of the permanent snow cover in Fall.

The monitoring includes both qualitative and quantitative observations. The record of qualitative data started since 2007, while the quantitative data were collected since 2010. Some implementations respect to the original ITEX protocol were added during the monitoring period in 2014 and 2015 in order to improve some key information on the selected phenophases.

The qualitative data recorded since 2007 referred to the timing (DOY, Day Of the Year) of appearance of the following phenophases: First Shoot (FS), New Leaves (NL), Main Shoot (MS), Flower buds (FB), First Flowering (FF), First Anthers (FA), First Stigma (FSt), Main Flowering

(MF), Seed Development (SD), Seed Ripening (SR), Leaf Senescence (LS). The qualitative data implementation concerned the recording of seed dispersal (SDisp) (since 2014), flower senescence (FSe) and leaf falling (LF) timing (since 2015) (Table III.3.1).

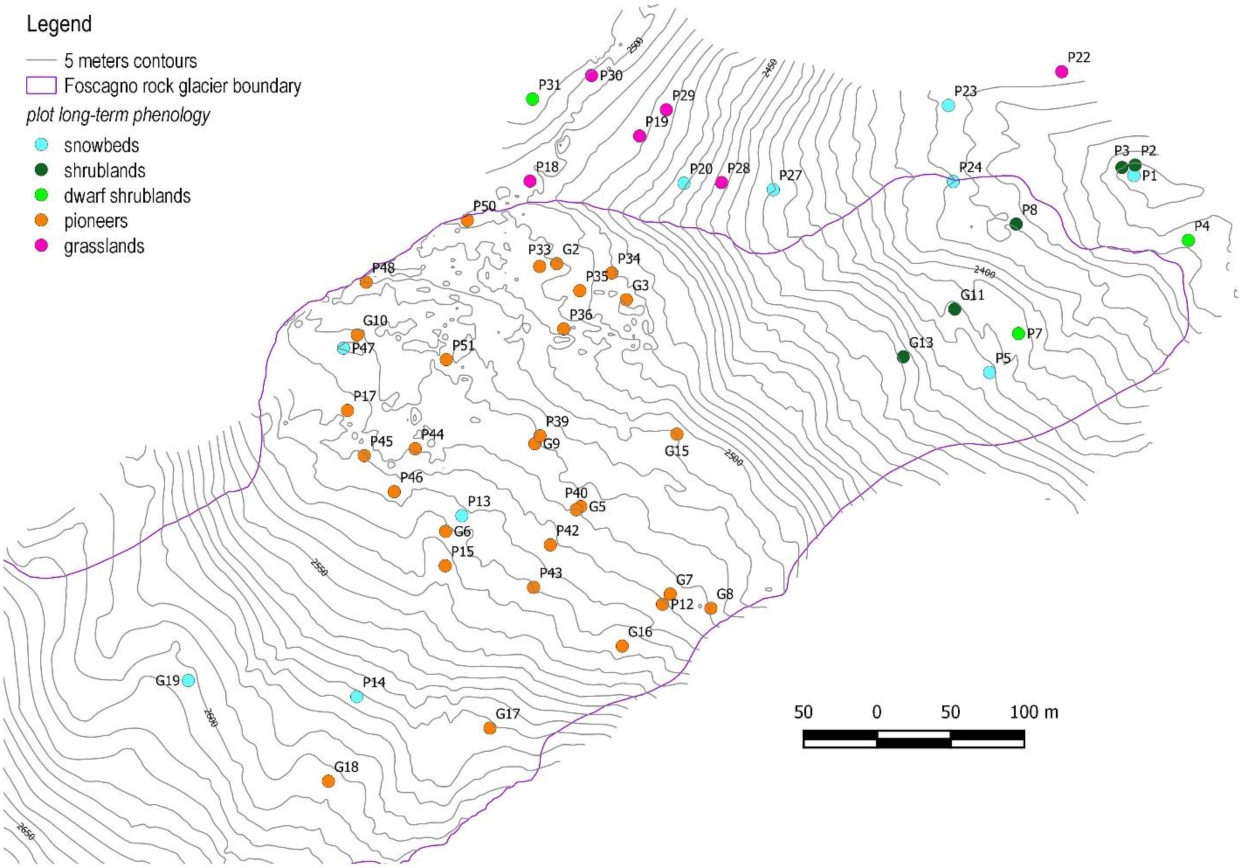


Figure III.3.1. Spatial distribution of the long-term phenology monitoring permanent plots, grouped by vegetation community types.

Since 2010, we started also the recording of quantitative data relying on the observation of a) the duration and b) the quantitative features of each phenophase.

The duration of each phenological stage is the number of days between the first and the last day of appearance of the phenophase (e.g. Iler et al., 2013; Caradonna et al., 2014). Over the season, we obtained the start, maximum and the end DOY for each phenological events. The entire distribution over the time was recorded for each phenophase, allowing us to study the behavior of the phenology over the course of the season.

The quantitative data represent the size of the object of each phenophase (e.g. shoot length, leaves number, flowers number, seeds number, etc…). Since 2010 we also collected data about the plant height according to Cornelissen et al. (2003) as this parameter was found to be a significant indicator of global warming (Walker et al., 2006; Elmendorf et al., 2012).

In total, during the course of this PhD were executed 89 days of field activity, that, considering the 133 replicates of each year corresponded to 11837 observations (considering the growing seasons 2014, 2015 and 2016).

Table III.3.1. Schematic description of the main phenological events monitored at the Foscagno valley**.**

phenophase	Brief description	Main references
SM – snow melt	Complete absence of snow on the ground	Webber & Walker, 1991
FS – first shoot	First vegetative shoot (herbs) or start of buds elongation (shrubs)	Anadon-Rossel et al., 2014; Cooper et al., 2011; Cornelius et al., 2012; Haggerty & Mazer, 2008
NL – new leaf	First leaf fully expanded	Anadon-Rossel et al., 2014; Cooper et al., 2011; Cornelius et al., 2012; Haggerty & Mazer, 2008; Molau & Mølgaard, 1996
MS – main shoot	Start of shoot elongation (only for shrubs)	Anadon-Rossel et al., 2014; Molau & Mølgaard, 1996
FB – flower bud	First flower budding: inflorescence or flower buds visible, but not in anthesis	Anadon-Rossel et al., 2014; Cooper et al., 2011; Denny et al., 2014; Dorji et al., 2013; Hulber et al., 2006; 2010; Ladining et al., 2013; Molau & Mølgaard, 1996
FF – first flower FSt - first stigma FA - first anther	First flower open: stage at which flowers begin anthesis or is receptive to pollen. Stigma and/or anthers are visible.	Abu-Asab et al., 2001; Anadon-Rossel et al., 2014; Anderson et al., 2012; Caradonna et al., 2014; Cook et al., 2012; Cooper et al., 2011; Cornelius et al., 2012; 2013; Craine et al., 2011; 2012; Crimmins et al., 2009; Denny et al., 2014; Dorji et al., 2013; Haggerty & Mazer, 2008; Hulber et al., 2006; 2010; Iler et al., 2013; IPG guide; Ladining et al., 2013; Molau et al., 2005; Molau and Molgaard, 1996; Schwartz et al., 2003
MF – main flowering	Maximum number of flowers, obtained by counting the number of flower at each plot for each census	Anderson et al., 2012; Caradonna et al., 2014; Haggerty & Mazer, 2008; Iler et al., 2013; Schwartz et al., 2003
FSe – flower senescence	Senescence of the stigma or anthers	Cooper et al., 2011; Molau and Mølgaard, 1996
SD – seed development	One or more unripe fruits/seeds are visible, seeds undergo histogenesis.	Denny et al., 2014; Dorji et al., 2013; Hulber et al., 2006; 2010; Ladining et al., 2013
SR – seed ripening	One or more ripe fruits/seeds are visible, ripe color and/or beginning of fruit dropping	Denny et al., 2014; Haggerty and Mazer, 2008; Hulber et al., 2006; 2010; Ladining et al., 2013; Schwartz et al., 2003
Sdisp – seed dispersal	Dispersal of ripe seeds/dropping of ripe fruits	Cooper et al., 2011; Denny et al., 2014; Molau & Mølgaard, 1996; Schwartz et al., 2003
LS – leaf senescence	Date on which at least 50% of the leaves on an individual plant had changed color	Kolarova et al., 2014; Schuster et al., 2014; Panchen et al., 2015
LF – leaf fallen	Beginning of leaf fall	Denny et al 2014; Haggerty & Mazer, 2008; Schwartz et al., 2003

III.3.B. Climate data collection

Climatic data were collected from La Foppa AWS of ARPA (environmental regional agency), located close to the study area (< 1 km) at comparable elevation (2650 m a.s.l.). At this station, a continuous climatic dataset has been recorded since 1996.

The climate parameters provided by La Foppa AWS include: snow depth (m), liquid precipitation (mm), air temperature (°C), global solar radiation (W/m^2), wind direction (°N) and wind speed (m/s).

Direct link to La Foppa AWS: http://www2.arpalombardia.it/siti/arpalombardia/meteo.

As photoperiod has been identified as a key factor of alpine plant development (e.g. Keller & Korner, 2003), we collected the daylight length (i.e. photoperiod) for each day of the monitoring period, at the following link: www.sunrise-and-sunset.com.

III.3.C. Winter snow cover monitoring

Since winter 2006/2007, the evolution of the winter snow pack has been manually monitored at the Foscagno valley in 69 plots along a 250 meters elevation gradient (2360-2610 m a.s.l.) over an area of about 0.6 km^2 (Fig. IV.2).

A detailed description of the topographic characteristic for each permanent plot is given in the supplementary material (Table S1).

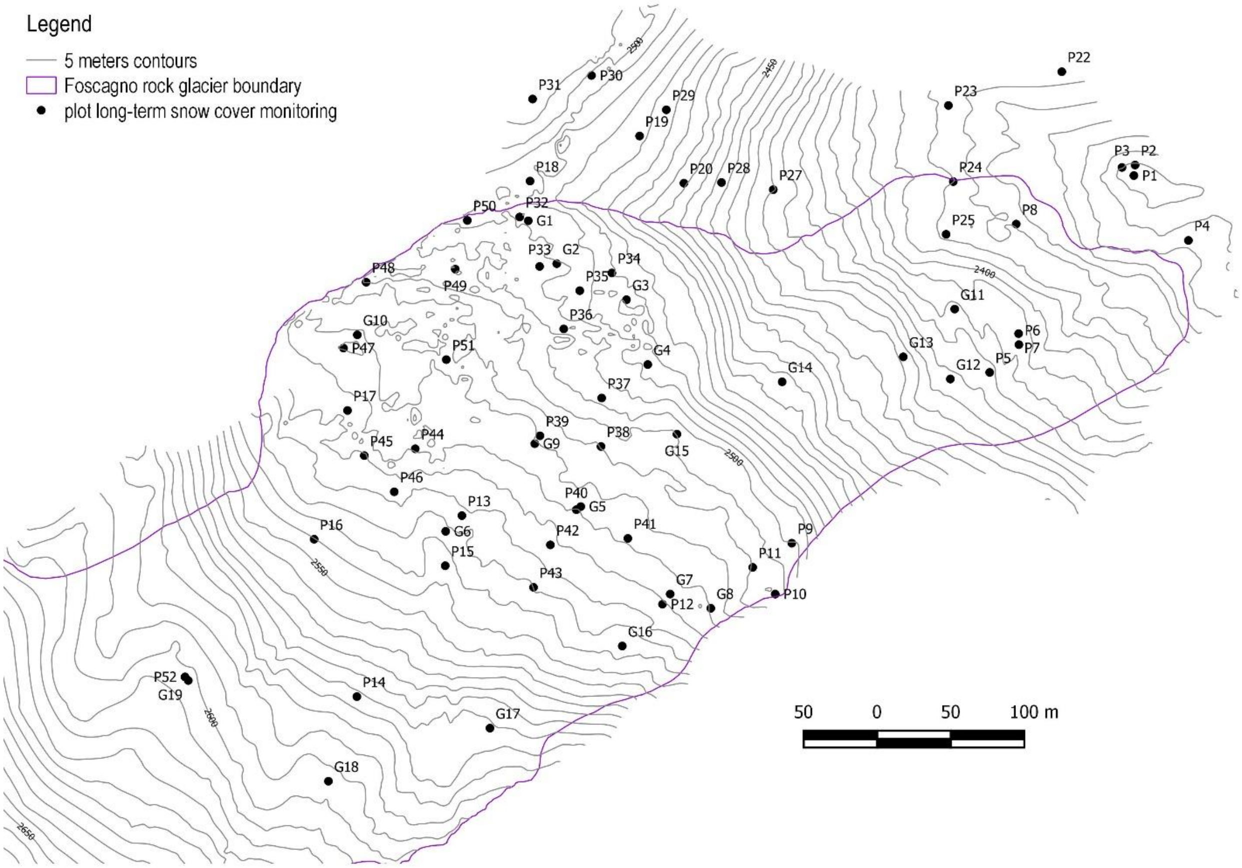


Figure III.3.2. Spatial distribution of the long-term snow cover monitoring plots.

The snow depth was measured in each single plot since the start of the permanent snow cover in Fall up to the melt out date in Spring.

The measurements were performed using a graduated probe (5 cm resolution). In correspondence of each plot, a plastic pole (2 meters high) was installed to indicate with large accuracy the position of the plot under the snowpack (Figure III.3.3). When the snow was higher than 2 meters or when the pole was damaged by the snow movement (and thus not visible), the GPS (±3m) was used to get to the coordinate of the plot. In that case, at least three different measures were made randomly within a circle 3 meters radius.

Figure III.3.3. Example of a plastic pole installed close to the plot to indicate the position of the plot under the snow pack.

While in winter the measurements were performed once every ten days or once a month (depending on the safety condition of the snow pack), in the springtime were performed twice per week. Because the insulating effect of the snow cover over 80 cm is well know (e.g. Haeberli, 1973; Guglielmin & Tellini, 1994; Zhang, 2005), and for safety condition of the snow pack, during the middle winter period the observation were not executed till when the melting period started.

In total 63 field days of measurements were carried out during the winters 2013/2014, 2014/2015 and 2015/2016, which corresponded to 4347 data.

IV.1.D. Ground surface temperature monitoring

The spatial variability of the ground surface in the alpine environment is very high, because morphology and grain size distribution produce a relief largely variable. Moreover, also the different vegetation associations and growth forms can influence strongly the ground surface temperature and therefore the ground thermal regime and the permafrost distribution (e.g. Guglielmin, 2004; Guglielmin et al., 2008; 2012; Gubler et al., 2011). The topographically induced mosaic of micro-climate conditions in an Alpine landscape are associated with local plant species distribution, and such thermal variability can exceed IPCC warming projections for the next 100 years (Scherrer & Korner, 2010; 2011).

Figure III.3.4. Example of 4 study sites with different vegetation cover: P23-*Rhododendron ferrugineum* (a); P31-*Kalmia procumbens* (b), P39-*Cerastium uniflorum* (c), P41-bare ground (d). Painted pebbles indicate where data loggers are buried.

The ground surface temperature (GST) is a good proxy for the evaluation of the soil thermal regime (e.g. Cannone & Guglielmin, 2009; Gubler et al., 2011; Guglielmin et al., 2012). Since the summer 2008 (and during the two following years 2009 and 2010, see table III.3.2) temperature loggers were installed at 2 and 10 cm depths (according to the protocol in Guglielmin, 2006) in correspondence of 13 vegetation plots within the study area.

Data loggers were distributed taking into account both the topographic variability and the ecological context: bare soil (P32, P41, P52) or occurrence of plant species representative of the typical growth forms of the Alpine environment [i.e. deciduous shrubs (G11, P27), evergreen shrubs (P20, P23), evergreen dwarf shrubs (P31), deciduous dwarf shrubs (G19, P47), graminoids (P29), forbs (G17, P39)] (Table S4, Fig. III.3.4).

Table III.3.2. List of the GST monitoring sites at the Foscagno valley, with the hydrologic years with available data.

plot	2009	2010	2011	2012	2013	2014	2015	2016
P20		x	x	x	x	x	x	x
P23	x	x	x	x	x	x	x	x
G11		x	x	x	x	x	x	x
P27		x	x	x		x	x	x
P31		x	x	x	x	x	x	x
G19			x	x	x	x	x	x
P47	x	x	x	x	x	x	x	x
P29		x	x	x	x	x	x	x
G17		x	x	x	x	x	x	x
P39	x	x		x	x	x	x	x
P32		x	x	x	x	x	x	x
P41		x		x	x	x	x	x
P52			x	x	x	x	x	x

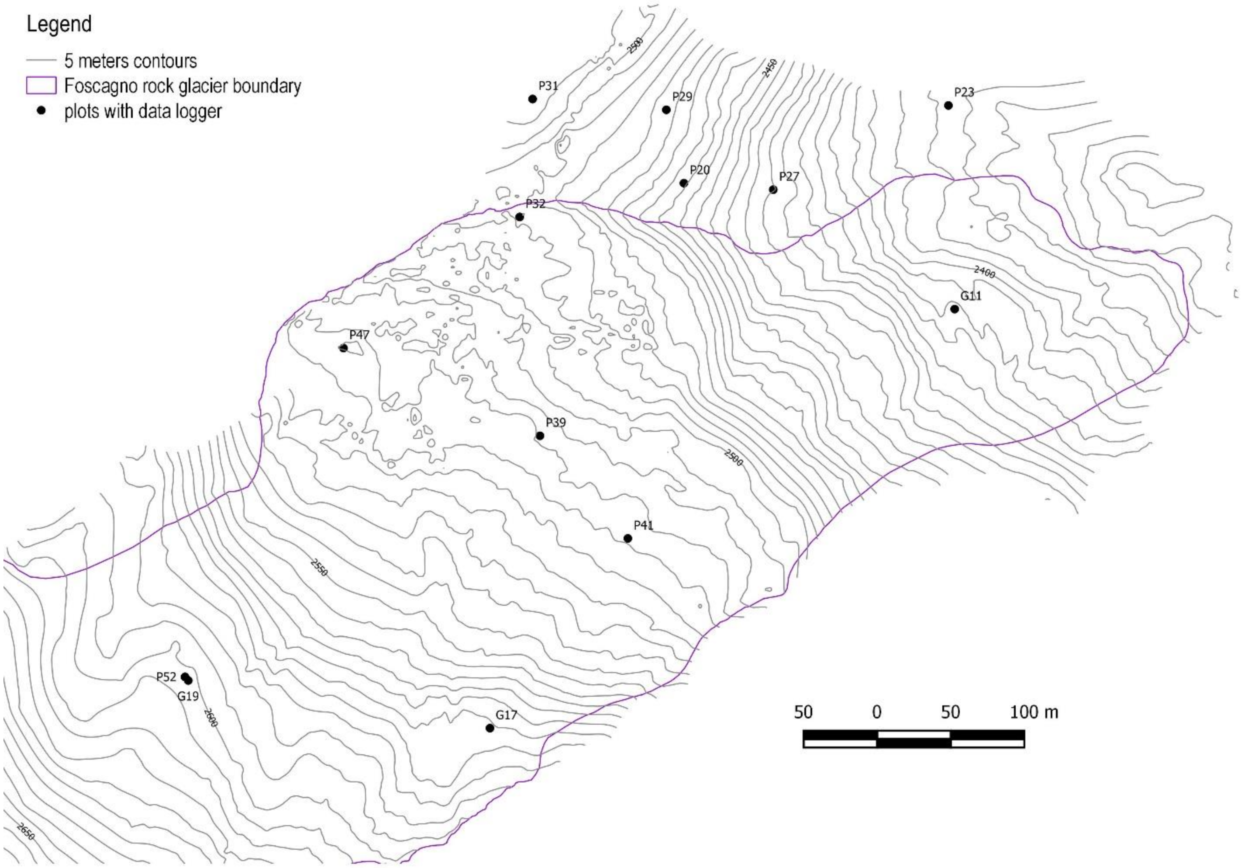


Figure III.3.5. Spatial distribution of the permanent plots with an installed data loggers.

These locations cover an elevation gradient of 221 meters (2388 - 2609 m a.s.l.), a slope range between 7 to 24 degree, and with variable aspects (Table S4 and Fig. III.3.5).

Two different types of two channels data loggers were used for this purpose: Hobo Pro Series (H08-031-08) by Onset and Tynitag TGP4520 by Gemini. The sensor accuracy is ± 0.20 °C for Tynitag and ± 0.25°C for Hobo, with a resolution for both types of 0.02°C. The loggers were programmed to record measures every hour.

Note that during the study period, for maintenance reasons, at some locations the data loggers have been replaced also changing the model and the type of thermistor. These are the points P47, P29, G17, P39, and P41. In all these points a data loggers Tynitag were installed instead of the old Hobo Pro. Unfortunately, some years have missing data, due to the malfunctioning during the winter periods of some data loggers. These occurred in P27 (2013), P39 and P41 (2011) (Table III.3.2).

The thermistors were placed parallel to the surface, avoiding as much as possible the noise due to the roughness of the ground, according to the standard procedure developed for polar regions, from Arctic (Osterkamp, 2003) to Antarctica (Guglielmin, 2006) and also applied in the mid latitude mountain regions (Hoelzle et al, 2003; Pogliotti et al, 2015).

The topographic features (elevation, slope, aspect) were derived from a 2.5 m resolution DEM (Digital Elevation Model) available for this area. We then used these topographical variables to compute the potential solar radiation received in each of our study area (Table S4). All the analysis were done using the spatial analyst tool provided in ArcMap 10.1.

Concerning the plants coverage we measured the average heights of the individual concerned and the degree of coverage expressed as a percentage (Table S4), that are the best proxy as indicator of the plant biomass (Cornelissen et al., 2003), and consequently of the vegetation heat fluxes (Harris, 1998).

IV.1.E. Manipulation experiments

Since 2015 we started at the Foscagno valley some manipulation experiments (Figure III.3.6), focusing on the effects of different aspect of the anthropogenic global change: nitrogen and phosphorous deposition, increase of liquid precipitation and nutrient partitioning among plants compartments.

The experiments were replicated among two of the most widespread vegetation communities: snowbeds (*Salicetum herbaceae* – SH) and grasslands (*Curvulo Nardetum* – CN). The two sites are distant each other about 100 m, and were located at approximately the same elevation. Also the subreplicates among each communities were almost at the same elevation and on flat areas, in order to get comparable data, unbiased from topographically effects.

For each of these communities we applied seven treatments (with three sub-replicates within each community) with a mono-factorial design: cc (control), FL (removal of flowers), xN (Solfate Ammonium addition), xNPK (Plant Food addition), xU (Urea addition), xW (one weekly addition of water), x2W (twice weekly addition of water) (Table III.3.3).

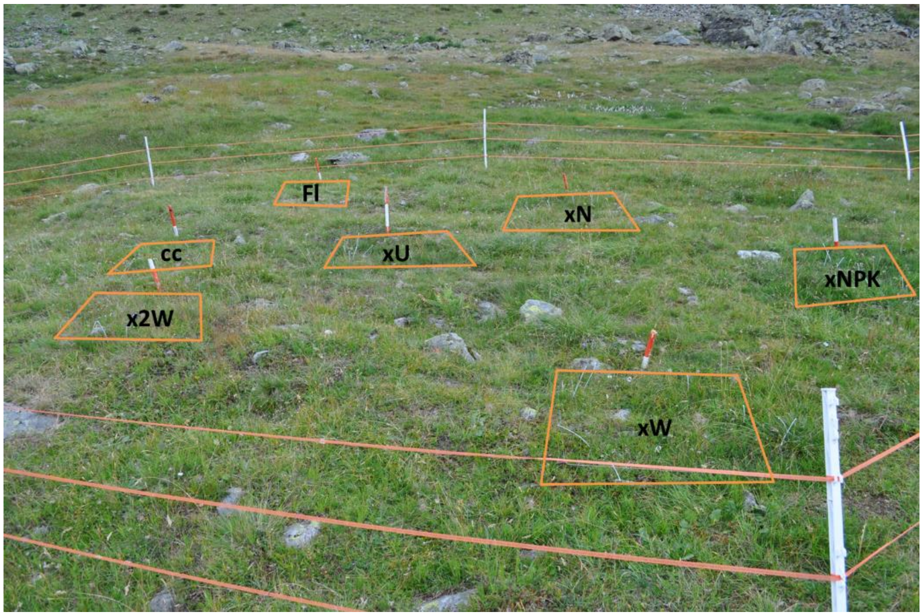


Figure III.3.6. Manipulation experiments: example of one of the sub-replicates on *Curvulo-Nardetum*.

The nutrients we added contains the following proportion of chemical elements (N:P:K:S): U = 46(Urea):0:0:0; N = 21(NH_4):0:0:65(SO3); NPK = 14(12Urea, 2NH_4):10:27:0. For the plant food (NPK) we also added a specific quantity of Urea (Table III.3.3) in order to get comparable quantity of nitrogen among the different treatments.

The plot size of the treatment was of 100x150cm (Bowman et al., 2006; Farrer et al., 2015), within which a surface of 100x100cm was delimited for the vegetation monitoring (Brancaleoni et al., 2007; Smith et al., 2012; Keuper et al., 2012; Hou et al., 2013; Brancaleoni & Gerdol 2014; Petraglia et al. 2014; Farrer et al., 2015). The remaining surface (100x50cm) was used for the harvesting of biomass (20x20cm) in order to quantify the effects on the plant's production (Bowman et al., 2006; Farrer et al., 2015).

The nutrient additions were done in three moments: at the beginning of the season, few days after the snow melt (early July), and the second and third addition respectively 10 and 20 days later (Table III.3.3).

All the nutrients additions were diluted in 1 liter of water and the same amount of water was added to cc and FL plots (Bassin et al., 2012; Bowman et al., 2006; Kong et al., 2013). We executed the dilutions directly in the field, by using the water taken from a spring located at the foot of the rock glacier.

The amount of water for the addition (xW and x2W) was calculated by laboratory experiments of soils water holding capacity (from samples collected in the study area close to our experiments) and incremented of 25% considering the potential runoff due to the gentle slope. We added 10L and 6L of waters per each plot respectively for snowbeds (SH) and grasslands (CN).

Table III.3.3. Amount of nutrients addiction for each single treatment.

treatment	Early July	Late July	Early August	Total (nutrient/m^2yr)	references
U (Urea)	10.25g	8g	8g	26.25g	Bowmann et al., 2006 Bassin et al., 2012 Kong et al., 2013
N (NH_4)	10.25g	8g	8g	26.25g	Bowmann et al., 2006 Kong et al., 2013 Bassin et al 2012
NPK +Urea	25g (+9.5 U)	10g (+5 U)	10g (+5 U)	45g (+19.5 U)	Bowmann et al., 2006 Petraglia et al., 2014 Kong et al., 2013 Bassin et al 2012

The treatments xW and x2W consisted in the same amount of water, but while in xW, the water was added once per week, in x2W the addition was done twice per week. The water was added slowly (in different times covering almost 2 hours) to avoid runoff and facilitate the absorption from the soil.

For all the additions, we used a spray bottle to better distribute the nutrients/water on the plot surface. All the addiction were done in early morning (before 10 A.M.) or late afternoon (after 4 P.M.) to avoid potential evapotranspiration.

The flower removal (FL) was done every time flowers appeared in the plots: for each species of the plot, they were harvested and counted.

Moreover, during all the growing season we fenced the two areas of the experiment, to avoid grazing by sheep or chamois (Figure III.3.6).

During the growing season, we harvested the ABG (Above Ground Biomass) (Liancourt et al., 2009; Bassin et al., 2012; Kong et al., 2013). In particular, we focused on three different moments of the growing season (approximately beginning-middle-end). The first harvesting was done each year before the start of the additions. The collected biomasses were weighted directly in the field by using a portable dynamometer and transferred to the laboratory, where they were dried at 60°C for 48 h (Bowman et al., 2006; Bassin et al., 2012; Farrer et al., 2015).

For each plot, we also monitored the phenological response of some selected target plant species, using the basic ITEX protocol, already applied for the long-term phenological monitoring (see above, Table III.3.1).

The ITEX protocol was implemented in order to intensify the observations for the senescence stages and autumn processes, which have been identified as the most neglected in climate change literature (Gallinat et al., 2014).

Indeed, we observed the leaf senescence evolution for selected individuals according to percentage of the leaves lamina color changes: 0-10%, 10-25%, 25-50%, 50-75%, 90%, and 100%, and for deciduous species, we observed also the timing of leaves abscission.
Moreover, during the growing season we measured the leaves dimensions (c. two or three times per months): length and width, picking up randomly 5 individuals inside the plot.

The species observed for the phenology monitoring were selected in order to satisfy the following requirements: a) they should be the most representative of the selected vegetation communities, b) they were representative of different growth forms, c) they were present in all the three sub-replicates of the same community and d) they were deciduous species. In total, we selected 10 ssp on grassland communities (n=210) and 7 ssp for snowbed (n=147) for a total of n=357 replicates (Table S5). The selected species were thus also representative of 4 growth forms: deciduous dwarf shrubs (1 ssp, n=21), deciduous shrubs (1 ssp, n=21), forbs (8 ssp, n=189) and graminoids (6 ssp, n=126) (Table S5).

III.4. Materials and methods: data elaboration

III.4.A. Plant phenology

For the analysis concerning the long-term phenology monitoring, we selected the main qualitative phenological events (i.e. SM, FS, NL, FB, FF, MF, SD, SR, LS) and two samples of the plant quantitative traits, i.e. FS length (FS_beg_n) and maximum plant height (Hmax).

Phenological data were first analyzed at inter-specific level to examine the overall intra-annual and inter-annual variability of each phenophase and identify eventual trends with time.

The same analyses were also executed at the intra-growth forms level, in order to compare responses among the different selected growth forms.

For this aim were used the main qualitative phenological data since 2007. However, for each specific selected phenological stage, we used data from a specific subgroup of replicates, in order to avoid the interpretation of uncertain data, following this scheme:
a) SM, FS: n=133 replicates x 10 years (2007-2016), all the dataset;
b) NL: n=116 replicates x 10 years (2007-2016). Since evergreen species exhibit specific patterns of leaves unfolding, we decided to select only the data referred to deciduous species (i.e. deciduous dwarf shrubs, deciduous shrubs, forbs, and graminoids);
c) FB, FF, MF: n=127 replicates x 10 years (2007-2016). Since in some years *Empetrum hermaphroditum* and *Juniperu communis* did not produce flowers (<50% of years), we removed this two species from the analysis of flowering pattern;
d) SD, SR: n=123 replicates x 9 years (2007-2015). Since in some years *E.hermaphroditum*, *J.communis* and *Vaccinium uliginosum* did not produce seeds (<50% of years), we removed these three species from the analysis of seeds development and ripening. Moreover, as the seeds development and ripening were still occurring when we performed our analysis, data were not available for all the species, and thus the data of the last year (2016) was excluded from the elaborations;
e) LS: n=116 replicates x 8 years (2007-2015, excluding 2008). Since evergreen species exhibit specific pattern of leaf senescence, we decided to select only the data referred to deciduous species (i.e. deciduous dwarf shrubs, deciduous shrubs, forbs, and graminoids). Likewise SD and SR, as the leaf senescence was still occurring when we performed our analysis, data were not available for all the species, and thus the last year (2016) was excluded from the elaborations. Moreover, in summer 2008 in the Foscagno valley occurred a masting event of a defoliator lepidopter (*Zygaena alpina*), which damaged the leaves of many of the analyzed deciduous species (Figure III.4.1). The LS data recorded in 2008 were thus excluded from our analyses.

We selected also two quantitative phenological data available since 2010, that were among the most sensitive of the vegetative development and thus the best indicator of plant growth and biomass. In particular, we selected the following measures:
a) first shoots length soon after the SM (FS_beg_n): n=133 replicates x 7 years (2010-2016).
b) maximum plant height reached during the season (Hmax): n=133 replicates x 7 years (2010-2016).

Figure III.4.1. *Zygena alpina* on a flower of *Carex curvula*. In 2008, a masting event of this defoliator lepidopter was recorded at the Foscagno valley.

For each qualitative and quantitative phenophase, we run the following analyses for the selected period (see above) at both inter-specific and intra-growth forms levels:
a) One-way analyses of variance (ANOVA; $p<0.05$) during the entire monitoring period at inter-annual level to assess inter-annual and inter-growth forms variability (Gill et al., 2015; Rosa et al., 2015);
b) Non-parametric statistics including: minimum, maximum, median, 25% and 75% quartiles, plus mean (± SE and ± 1.96 SE) (both inter-annual and intra-annual) (Maggini et al., 2011);
c) t-test to identify statistically significant differences between different years (to identify extreme years) and growth forms (VanVliet et al., 2014);
d) Trends with time (advances or delays) were computed through linear regressions between DOY and year (Rosa et al., 2015), or between number of days (for growing season length: GSL, and pre-unfolding period: NL-SM) and year, excluding the extreme years (see above).

Non parametric statistics, in particular median and 75% quartile, provide information on the behavior of the largest part (50% and 75%) of the population data and are hence well representative of biological patterns (Maggini et al., 2011), also considering that the median is less sensitive than the mean to extreme (and potentially wrong) observations (VanVliet et al., 2014). For these reasons, we decided to use the median value (instead of the mean) as representative of the pattern of the population data of each year. Trends with time of each phenophases (both inter-specific and intra-growth form level) were thus computed through linear regression between median values and year.

We also computed the inter-quartile differences (i.e. difference between the 75% and 25% quartiles) in order to provide the mid-phenophase duration (Jentsch et al., 2009) or the duration of the phenophase peak.

The length of each phenophase for each year was obtained by the difference from the latest and earliest phenophase dates recorded. Moreover, to quantify advances or delays of each phenophase, we computed the anomaly of the 75% quartile of each year respect to the 75% quartile of the entire monitoring period.

Growing season length (GSL) has been defined in different ways, such as the period between budburst and leaf fall (Linderholm, 2006), or the period between leaf unfolding (flushing) and the combination of leaf colouring and fall (Vitasse et al., 2009). However, in high elevation (and/or latitude) sites the greening phenological stages start in subnivean conditions with very shallow snow cover, when snow cover starts to melt (Starr & Oberbauer, 2003; Bjork & Molau, 2007). Therefore, in high elevation (and high latitude) environments it would be more correct to use snow melt (SM) to identify the onset of the growing season.

As our plots were located across an elevation gradient of 250 m, first of all we tested whether elevation could exert an impact on both SM and our phenological data. Indeed, the relation between elevation and plant phenology have been widely documented in alpine areas (e.g. Ziello et al., 2009; Cornelius et al., 2012). We thus tested by linear regression the relation between elevation and each phenophase, starting from SM to LS. We run these analyses both at inter-annual and inter-specific level as well as at the inter-annual and intra-growth forms level. According to Ziello et al. (2009) when the regression was statistically significant ($p<0.05$) we adopted the threshold value of $R^2>0.5$ t assess the occurrence of a relation. As our data indicated the poor effect of the elevation gradient, we then used our data without need for any normalization for elevation.

To assess whether SM could be used as a robust indicator of the very first onset of the growing season, we tested by linear regression the relation between a) the dates of SM and FS and b) the dates of SM and NL. According to the results of our analyses, SM was used to compute the onset of the growing season.

As a consequence, we computed the length of the pre-unfolding period (NL-SM) by computing the differences between the dates of SM and NL.

To identify the relations between phenology and climatic factors we performed general regression models (GRMs) using the backward stepwise selection. In this way the model includes from the beginning of the analysis all the variables, identifying and eliminating eventual redundancies, emphasizing only the statistically significant variables. However, to improve the robustness of our analyses and avoid any potential redundancy between the selected climatic variables, prior to GRMs we tested by linear regression the relation between each pairs of variable. We considered the two climatic variables to be correlated when $R^2>0.5$ (Ziello et al., 2009). These analyses were run at the inter-annual and inter-specific level for each specific phenophase. Once identified any redundancy, the redundant variables were excluded from the GRM.

Considering the monthly climatic dataset, we observed a redundancy ($R^2>0.5$, according to Ziello et al., 2009) between airTDD and airMEAN common for April, May, June and July (see chap. III.5.A.b). According to the results of the GRMs, the use of the airMEAN instead of the airTDD (from April to July) lead always to greater variance explained for each dataset. Moreover, since the airMEAN was related to both airTDD and airFDD, the use of airMEAN was also the best way to summarize the input of the air temperature in only one variable. On the contrary. in August we observed $R^2>0.5$ only when testing the relation between airMEAN and radTOT. In this case, we removed the radTOT to avoid redundancy in our dataset.

Considering instead the climatic parameters from the SM to the phenological events, we found for all the phenophases a strong relation ($R^2>0.5$) between radTOT and airTDD. We thus removed the radTOT to avoid redundancy with airTDD.

Other factors considered in all the GRMs were: elevation, year, SM and photoperiod (of each phenophase. The elevation in our study was not influencing directly any of the phenological stages (see chap III.5.A.a), however, our results could also be due to the restricted elevation range (only 250 m). Since the effect of the elevation on the phenology of alpine plants has been documented in several studies (e.g. Ziello et al., 2009, Cornelius et al., 2012) we considered in the GRMs also the elevation, in order to have the best descriptive model of our study area.

According to the results of the linear regressions, we then selected, for each specific phenophase, the climatic variables to be used for each GRM. For each of the analyzed phenophase, our analyses have been carried out at the inter-specific level by following two steps: I) considering only climatic factors and II) including also biotic factors (i.e. previous phenological stage).

The II approach (including biotic factors) was run only for those phenological events that could be potentially influenced by the previous phenophase: NL (vs FS), NL-SM (vs NL), FF (vs FB), MF (vs FF), SD (vs MF) and SR (vs SD). For FS, FB and LS we did not test the influence of previous phenological stages, since they have no related earlier phenological events.

The relation between related phenological events was also tested by linear regression, at the inter-annual level (both inter-specific and intra-growth forms).
Moreover, we also tested by linear regression the relation between the SM and each phenological events at the inter-annual level (both inter-specific and intra-growth forms).

All computations were performed using the software Statistica®.

III.4.B. Climatic data

Climate statistics were computed for each month, season and year for the following parameters: mean daily air temperature (airMEAN), air thawing degree days (TDD), air freezing degree days

(FDD), total daily liquid precipitation (rainTOT), global daily incoming radiation (radTOT) and wind speed (WIND).

TDD (cumulative sum of temperature above 0°C) and FDD (cumulative sum of temperature below 0°C) were calculated as these indices provide the cumulative effect of air temperature and its consequences on biota (Molau & Mølgaard, 1996; Klene et al., 2001; Cannone et al., 2006; Cannone & Guglielmin, 2009).

Moreover we calculated the climate statistics from the SM until the phenological event for each species x plot x year combination (Oberbauer et al., 2013).

Concerning SM, in order to assess the climatic representativeness of our study site at regional scale, we performed a linear regression between the 75% quartile of SM (DOY) recorded in our area (2007-2016) and those of other AWS from many locations widespread over the European Alps (Gressoney, Rabbi, Arabba, Val Noana, Pitztaler Gletscher) (Fig. V.1.a.3).

Linear regressions were run also between the SM over all our plots for each year (75% quartile) and the SM at La Foppa AWS over all the study period (2007-2016), in order to check if the long-term trend of SM recorded at the LaFoppa was representative also of our study site, and if the SM measured over the study period was representative of the long-term SM evolution.

In the alpine tundra, the photoperiod (i.e. daylight length) can be a determinant factor controlling plant phenology (e.g. Keller & Korner, 2003; Heide, 2005; Hulber et al., 2010). In order to investigate such effects we assigned the daylight length (number of hours per day) to each species x plot x year combination.

In our GRMs analyses, therefore we included the SM, photoperiod, climate statistics computed from SM to the day of phenophase and the climate factors, which could potentially interact with the studied phenological stage.

III.4.C. Ground surface temperature

The soil temperature data were elaborated to: a) analyze the changes of the mean annual ground surface temperature (MAGST) over the study period, b) estimate through different methods the presence of snow cover, c) analyze the variability of permafrost distribution, d) quantify the influence of snow cover on the GST and e) quantify the influence of the soil coverage types on the GST.

In all our further analyses, we considered only the GST recorded at 2 cm (according to Pogliotti et al., 2015).

The mean annual ground surface temperature (MAGST) was computed considering the hydrological year (1st October – 30th September) (e.g. Cannone & Guglielmin, 2009; Apaloo et al., 2012; Gruber et al., 2011; Pogliotti et al., 2015).

All the data were statistically analyzed through the following way:
a) One-way analyses of variance (ANOVA; $p<0.05$) during the entire monitoring period at inter-annual level to asses variability among years and surface types (e.g. Gubler et al., 2011; Gill et al., 2015; Rosa et al., 2015);
b) t-test to identify statistically significant differences between different years (VanVliet et al., 2014) and to identify "extreme" years;
c) Trends with time (advances or delays) were computed through linear regressions between MAGST and year only for "normal" years (Pogliotti et al., 2015).

Manually measures of snow cover were not available for each day, and when computing the start and the melt out of the snow cover, it could be unreliable, preventing us to evaluate with high accuracy the snow cover duration (SCD), which is potentially one the key factor that regulates the soil thermal regime. We then could only consider the field snow measures in order to obtain the minimum snow cover duration.

Different methods have been used by many authors to estimate the presence of snow cover using the daily GST time series obtained by temperature loggers (Taras et al., 2002; Lundquist & Lott, 2008; Gadek & Kedzia, 2008; Schmidt et al., 2009; Apaloo et al., 2012; Schmid et al., 2012; Danby & Hick, 2007; Gadek & Leszkiewicz, 2010; Staub & Delaloye, 2016). Other authors also assessed the presence/absence of snow cover by using fiber optic cable (e.g. Tyler et al., 2008; Seyfried et al., 2016), or thermal imaging system (Westermann et al., 2011; Scherrer & Korner, 2010; 2011).

In Guglielmin et al. (under preparation), relying on our dataset, we analyzed the GST patterns in relation to the field measure of snow depth, comparing the ranges of variation for the mean daily GST and its St.Dev. at 2cm, in relation to the snow thickness.

For each snow cover season, we compared our finding with the equation proposed by other authors (see above).
Since all the other methods proposed in literature were underestimating the beginning date of snow cover (BD), based on our empirical dataset we developed a new index based on daily GST and St.Dev. (Guglielmin et al., in preparation). This new method consider the soil covered by snow when one of these two conditions are satisfied: ($GST \leq 0+a$) or ($GST>0+a$ and $St.Dev.<0.1$), where "a" is the accuracy of the thermometers.

This new index were then applied to our dataset, to estimate several parameter concerning the SCD and thus the snow free period (SF):
a) the snow melt (SM), that corresponded to the complete absence of snow on the ground (Webber & Walker, 1991; Apaloo et al., 2012; Schmidt et al 2012);
b) the beginning date of snow cover (BD), that correspond to the first day of the year of the permanent winter snow cover (Gruber et al., 2011; Apaloo et al., 2012; Schmid et al., 2012).

By using the daily record of snow cover depth from La Foppa AWS, we computed the beginning date of snow cover deeper than 80 cm (BD>80) for each year of the study period, since it is assumed that over 80 cm the snow cover insulate the ground from air temperature oscillation (e.g. Haberli, 1973).

In order to assess the presence of permafrost in our monitoring sites, we calculated the conventional BTS (bottom temperature of winter snow cover) from the GST daily record, as the GST values in March (average, min, max) (Gadek & Kedzia, 2008; Gadek & Leszkievicz, 2010).

Measurement of BTS by field probing have been used as a well-established method during the past years for mapping mountain permafrost distribution in the Alps (e.g. Haeberli, 1973; Hoelzle, 1992; Guglielmin & Tellini, 1994; Isaksen et al., 2002). We compared the BTS obtained by the daily GST in March with the field BTS probe data available for the Foscagno valley.

Once identified the period of permanent snow cover (based on the new index), to quantify the insulating effect of the snow cover on GST we computed the n-factor FDD, as the ratio of the FDD in the soils to that in the air (FDD soils / FDD air), during the snow cover season (Klene et al., 2001; Cannone & Guglielmin, 2009; Zhang et al., 2005).

Once identified the length of the snow free period (SF), to quantify the influence of the vegetation cover on the soil surface energy balance, we calculated the n-factor TDD, as the proportion of TDD in the soils to that in the air (TDD soil / TDD air) during the snow free period (according to Klene et al., 2001; Cannone et al., 2006; Cannone & Guglielmin, 2009; Guglielmin et al., 2008; 2012).

III.4.D. Manipulation experiments

Phenological data were analyzed at both inter-specific and intra-growth forms levels to examine the overall (and growth forms) inter-annual variability of each phenophase and identify eventual patterns among treatments.

We used the same approach applied during the long-term phenology dataset elaboration, in order to get comparable results. In this case, we selected some qualitative and quantitative phenological data, which we identified as the most sensitive to climate and global change.

Concerning the phenological data, we selected the following phenophases:
a) MF: n=321 replicates x 2 years (2015-2016). The flowering of *Vaccinium uliginosum* was removed from our analyses since it flowered in not enough cases (<50%);
b) LS: 357 replicates x year (2015). Since the leaf senescence was still occurring when we performed our analysis, data were not available for all the species, and thus the last year (2016) was excluded from the elaborations.

Among the quantitative data, we selected for our analysis:
a) FS length (FS_beg_n): n=357 replicates x 1 year (2016). Data referred only to 2016 since in 2015 at the beginning of the experiments most species already completed their FS;
b) maximum plant height reached during the growing season (Hmax): n=357 replicates x 2 years (2015-2016);
c) maximum leaves length reached during the growing season (LLmax): n=357 replicates x 2 years (2015-2016);
d) Above ground biomass (ABG): n=42 replicates x 2 years (2015-2016).

For each phenophase (qualitative and quantitative), we run the following analyses for the selected period (see above) and at both inter-specific and intra-growth forms level:
a) Non-parametric statistics including: minimum, maximum, median, 25% and 75% quartiles, plus mean (± SE and ± 1.96 SE) (both inter-annual and intra-annual) (Maggini et al., 2011);
b) Wilcoxon test to identify statistically significant differences between each treatment and the control plots (cc) (dependent variables);
c) t-test to identify statistically significant differences between treatments (independent variables) (Smith et al., 2012).

III.5. Results

III.5.A. Preliminary analyses of the influence of the elevation gradient and of the relationships among the climatic variables

III.5.A.a. *Influence of elevation on the selected phenological events*

Since in our study we worked across an elevation gradient of 250 meters, we first assessed its potential influence on each of the phenological events selected for this study.

According to our further investigation concerning the phenophases (see chap III.5.B), we run the following analyses: I) inter-specific and inter-annual level, II) intra-growth forms and inter-annual level.

Since not all the growth forms were analyzed in all the phenophases, we here tested the relation with elevation only for the selected subgroups of species for each analyzed phenological event (see methods).

Inter-annual and inter-specific level

As tested by linear regression at the inter-annual and inter-specific level, all the phenophases and the quantitative plant traits revealed a statistically significant relation with elevation (in all cases $p<0.01$) (Table III.5.A.a.1). However, the proportion of variances of each phenophase explained by elevation were always low ($R^2<0.25$), indicating a low relevance of the elevation gradient considered in this study.

Table III.5.A.a.1. Influence of the elevation on the selected phenophases, as tested by linear regression at the inter-annual and inter-specific level.

	β	**R^2**	**p**
SM	0.13	0.25	<0.01
FS	0.14	0.25	<0.01
NL	0.12	0.21	<0.01
NL-SM	-0.01	0.02	<0.01
FB	0.08	0.11	<0.01
FF	0.09	0.11	<0.01
MF	0.09	0.10	<0.01
SD	0.09	0.08	<0.01
SR	0.01	0.00	<0.01
LS	0.04	0.02	<0.01
FS_beg_n	0.03	0.03	<0.01
Hmax	-0.41	0.13	<0.01

Deciduous dwarf shrubs

Concerning deciduous dwarf shrubs we observed a statistically significant influence of the elevation only for the greening stages (FS and NL, as well as NL-SM) and for the Hmax, as tested by linear regression at the inter-annual level ($p<0.01$). However, the proportion of explained variances were always low ($R^2<0.19$), indicating a negligible effect of the elevation. All the other phenological events did not exhibit any statistically significant effect of elevation ($p>0.05$) (Table III.5.A.a.2).

Table III.5.A.a.2. Influence of the elevation on the selected phenophases of deciduous dwarf shrubs, as tested by linear regression at the inter-annual level.

	β	**R^2**	**p**
SM	0.09	0.19	<0.01
FS	0.08	0.18	<0.01
NL	0.07	0.18	<0.01
NL-SM	-0.02	0.12	<0.01
FB	0.02	0.01	0.44
FF	0.02	0.02	0.37
MF	0.01	0.01	0.53
SD	0.01	0.00	0.66
SR	0.02	0.02	0.39
LS	0.02	0.01	0.40
FS_beg_n	0.00	0.01	0.41
Hmax	-0.04	0.09	0.03

Deciduous shrubs

In our study, the elevation did not exert any statistically significant influence on the phenology of deciduous shrubs, as tested by linear regression at the inter-annual level ($p>0.05$) (Table III.5.A.a.3).

Table III.5.A.a.3. Influence of the elevation on the selected phenophases of deciduous shrubs, as tested by linear regression at the inter-annual level.

	β	**R^2**	**p**
SM	0.07	0.01	0.60
FS	0.09	0.02	0.46
NL	-0.03	0.00	0.72
NL-SM	-0.13	0.10	0.06
FB	-0.09	0.01	0.77
FF	-0.15	0.02	0.55
MF	-0.12	0.01	0.65
LS	0.02	0.00	0.87
FS_beg_n	0.02	0.06	0.20
Hmax	-0.13	0.01	0.56

Evergreen dwarf shrubs

Also for the evergreen dwarf shrubs, all the selected phenological events were not influenced by elevation, as tested by linear regression at the inter-annual level ($p>0.05$). Only the Hmax showed a statistically significant influence ($p<0.01$) even if with low proportion of variance, indicating negligible effect of elevation (Table III.5.A.a.4).

Table III.5.A.a.4. Influence of the elevation on the selected phenophases of ev.dwarf shrubs, as tested by linear regression at the inter-annual level.

	β	**R^2**	**p**
SM	-0.03	0.01	0.30
FS	-0.02	0.01	0.44
FB	-0.01	0.00	0.75
FF	0.00	0.00	0.90
MF	-0.01	0.00	0.73
SD	0.01	0.01	0.58
SR	0.01	0.01	0.65
FS_beg_n	0.00	0.00	0.60
Hmax	-0.01	0.14	<0.01

Evergreen shrubs

As already observed for deciduous shrubs and evergreen dwarf shrubs, in our study there was no influence of the elevation on the phenology of the selected phenophases, as tested by linear regression at the inter-annual level ($p>0.05$) (Table III.5.A.a.5), except for FF, MF and SD. However, also in this case, the amount of explained variance is very low (according to R^2 values) and therefore its influence could be considered negligible.

Table III.5.A.a.5. Influence of the elevation on the selected phenophases of evergreen shrubs, as tested by linear regression at the inter-annual level.

	β	**R^2**	**p**
SM	-0.01	0.00	0.78
FS	-0.01	0.00	0.81
FB	-0.06	0.05	0.16
FF	-0.08	0.13	0.02
MF	-0.08	0.13	0.02
SD	-0.11	0.10	0.05
SR	0.02	0.01	0.68
FS_beg_n	0.02	0.01	0.42
Hmax	0.21	0.01	0.57

Forbs

The phenophases of forbs species was statistically significant affected by the elevation, only up to the flowering stage ($p<0.05$), and with higher confidence the greening stages (FS and NL), FB as well as the Hmax ($p<0.01$) (Table III.5.A.a.6). However, in all these cases the proportion of variance explained by elevation was always low ($R^2<0.17$), indicating negligible effects of elevation in our study.

Table III.5.A.a.6. Influence of the elevation on the selected phenophases of forbs, as tested by linear regression at the inter-annual level.

	β	**R²**	**p**
SM	0.15	0.17	<0.01
FS	0.15	0.16	<0.01
NL	0.14	0.17	<0.01
NL-SM	0.01	0.00	0.10
FB	0.04	0.02	<0.01
FF	0.03	0.01	0.01
MF	0.03	0.01	0.04
SD	0.03	0.01	0.08
SR	-0.01	0.00	0.63
LS	0.01	0.00	0.66
FS_beg_n	0.04	0.02	<0.01
Hmax	-0.06	0.01	0.13

Graminoids

Graminoids were probably the growth form most influenced by elevation concerning all their phenophases, as tested by linear regression at the inter-annual level ($p<0.01$). However the proportion of variance explained by elevation was always low ($R^2<0.25$), indicating again little effects from the elevation in our study (Table III.5.A.a.7).

Table III.5.A.a.7. Influence of the elevation on the selected phenophases of graminoids, as tested by linear regression at the inter-annual level.

	β	**R²**	**p**
SM	0.13	0.25	<0.01
FS	0.13	0.25	<0.01
NL	0.07	0.18	<0.01
NL-SM	-0.02	0.12	<0.01
FB	0.13	0.22	<0.01
FF	0.16	0.23	<0.01
MF	0.15	0.22	<0.01
SD	0.14	0.18	<0.01
SR	0.09	0.11	<0.01
LS	0.06	0.06	<0.01
FS_beg_n	0.02	0.01	0.07
Hmax	-0.34	0.21	<0.01

III.5.A.b. *Preliminary analyses of the relations among climatic variables*

By using data from LaFoppa AWS, we computed several meteorological variables (see methods). Therefore, in order to avoid redundancy in our dataset, we tested by linear regression the relations between the selected climatic variables.

In particular, we tested by linear regressions the relations of air temperature variables (airMEAN, airFDD, airTDD) between each other, as well as with the total incoming radiation (radTOT), as they could be potentially related. We run our analyses considering both the monthly statistics and the statistics computed from each single phenophase since SM.

This process was the starting point for the selection of the best climatic predictors that we used in the GRMs analysis (chap. III.5.B.k).
According to our further investigation provided by the GRMs (see chap III.5.B.k), we run the following analyses at inter-specific and inter-annual level, eventually separating the analysis when "extreme" years have been found concerning plant phenology (i.e. year 2007 for FS and NL-SM or year 2015 for LS).

April

All the linear regressions computed for each pair of variables in April showed high statistically significant relation ($p<0.01$). However, only the airTDD and airFDD when tested with airMEAN displayed a high R^2 (always >0.5) in both all the study period and only the normal years (Table III.5.A.b.1).

Table III.5.A.b.1. Relations between each pair of potentially related statistics computed for April, as tested by linear regression on both all the study period (2007-2016) and for the normal years of FS and NL-SM (2008-2016).

	2007-2016		**2008-2016**	
	R^2	**p**	**R^2**	**p**
airTDD_APRIL vs airMEAN_APRIL	0.78	<0.01	0.55	<0.01
airFDD_APRIL vs airMEAN_APRIL	0.87	<0.01	0.87	<0.01
airFDD_APRIL vs airTDD_APRIL	0.44	<0.01	0.21	<0.01
airFDD_APRIL vs radTOT_APRIL	0.08	<0.01	0.05	<0.01
radTOT_APRIL vs airMEAN_APRIL	0.15	<0.01	0.16	<0.01
radTOT_APRIL vs airTDD_APRIL	0.20	<0.01	0.31	<0.01

May

All the linear regressions computed for each pair of variables in May showed high statistically significant relation ($p<0.01$) (Table III.5.A.b.2). However, only the airTDD and airFDD when tested with airMEAN, and the airFDD when tested with airTDD, displayed a high R² (>0.82) in both all the study period and only the normal years (Table III.5.A.b.2).

Table III.5.A.b.2. Relations between each pair of potentially related statistics computed for May, as tested by linear regression on both all the study period (2007-2016) and only for the normal years period of FS and NL-SM (2008-2016).

	2007-2016		**2008-2016**	
	R^2	**p**	**R^2**	**p**
airTDD_MAY vs airMEAN_MAY	0.98	<0.01	0.99	<0.01
airFDD_MAY vs airMEAN_MAY	0.90	<0.01	0.90	<0.01
airFDD_MAY vs airTDD_MAY	0.82	<0.01	0.82	<0.01
airFDD_MAY vs radTOT_MAY	0.04	<0.01	0.23	<0.01
radTOT_MAY vs airMEAN_MAY	0.09	<0.01	0.37	<0.01
radTOT_MAY vs airTDD_MAY	0.11	<0.01	0.40	<0.01

June

In June, the FDD were not considered, since they showed low values and thus a very low variance over all the study period, as it could be expected due to the progress of the season.

Even if all the linear regressions computed for each pair of variables in June showed high statistically significant relation ($p<0.01$), only the airTDD, when tested again airMEAN, showed a high R² (=1.00) when considering both all the study period and only the normal years periods (Table III.5.A.b.3).

Table III.5.A.b.3. Relations between each pair of potentially related statistics computed for June, as tested by linear regression on all the study period (2007-2016) as well as for the normal years of FS and NL-SM (2008-2016), and for the normal years of LS (2007-2014).

	2007-2016		**2008-2016**		**2007-2014**	
	R^2	**p**	**R^2**	**p**	**R^2**	**p**
airTDD_JUNE vs airMEAN_JUNE	1.00	<0.01	1.00	<0.01	1.00	<0.01
radTOT_JUNE vs airMEAN_JUNE	0.03	<0.01	0.01	<0.01	0.02	<0.01
radTOT_JUNE vs airTDD_JUNE	0.11	<0.01	0.00	<0.01	0.00	<0.01

July

Also in July the FDD were not considered, since they showed values close to zero and thus low variance. All the linear regressions computed for each pair of variables in July showed high statistically significant relation ($p<0.01$) (Table III.5.A.b.4).

In this case, over the whole study period we observed also large proportion of variances explained for all the combinations of variables ($R^2>0.54$), while the radiation (radTOT) on the normal years period of LS (2007-2014) explained lower variances of both airMEAN and airTDD (Table III.5.A.b.4).

Table III.5.A.b.4. Relations between each pair of potentially related statistics computed for July, as tested by linear regression on both all the study period (2007-2016) and only for the normal years of LS (2007-2014).

	2007-2016		**2007-2014**	
	R^2	**p**	**R^2**	**p**
airTDD_JULY vs airMEAN_JULY	0.73	<0.01	0.58	<0.01
radTOT_JULY vs airMEAN_JULY	0.54	<0.01	0.34	<0.01
radTOT_JULY vs airTDD_JULY	0.54	<0.01	0.29	<0.01

August

Similarly to June and July, the FDD was not considered in August, due to their very low values and variance. Even if all the linear regressions computed for each pair of variables in August showed high statistically significant relation ($p<0.01$), only the radTOT, when tested again airMEAN, showed a high R^2 (>0.54) when considering all the study period and only the normal years periods (Table III.5.A.b.5). A high proportion of variance was also observed when testing radTOT and airTDD, but only in the normal years of LS period (2007-2014).

Table III.5.A.b.5. Relations between each pair of potentially related statistics computed for August, as tested by linear regression on both all the study period (2007-2016) and only for the normal years of LS (2007-2014).

	2007-2016		**2007-2014**	
	R^2	**p**	**R^2**	**p**
airTDD_AUG vs airMEAN_AUG	0.21	<0.01	0.19	<0.01
radTOT_AUG vs airMEAN_AUG	0.54	<0.01	0.70	<0.01
radTOT_AUG vs airTDD_AUG	0.38	<0.01	0.57	<0.01

FS-SM

In the few days occurring from SM to FS (FS-SM), the FDD showed values always close to zero and a low variance, and thus was not included in further investigations.

All the linear regressions computed for each pair of variables in the FS-SM period showed high statistically significant relation ($p<0.01$) (Table III.5.A.b.6). However, only the radTOT, when tested again airTDD, showed a high R^2 (>0.53) when considering all the study period and only the normal years period (Table III.5.A.b.6).

Table III.5.A.b.6. Relations between each pair of potentially related statistics computed for the period FS-SM, as tested by linear regression on both all the study period (2007-2016) and only for the normal years of FS and NL-SM period (2008-2016).

	2007-2016		**2008-2016**	
	R^2	**p**	**R^2**	**p**
airTDD_FS-SM vs airMEAN_FS-SM	0.41	<0.01	0.36	<0.01
radTOT_FS-SM vs airMEAN_FS-SM	0.05	<0.01	0.02	<0.01
radTOT_FS-SM vs airTDD_FS-SM	0.53	<0.01	0.53	<0.01

NL-SM

At the inter-specific level, the FDD cumulated since SM was very close to zero, showing low variance, and was thus removed from further investigations.

In the pre-unfolding period (NL-SM), the relations between each pair of variables were statistically significant ($p<0.01$) (Table III.5.A.b.7), but only the radTOT, when tested with airTDD, showed high proportion of variance explained in both all the study period and only normal years ($R^2>0.79$) (Table V.0.b.7).

Table III.5.A.b.7. Relations between each pair of potentially related statistics computed for the period NL-SM, as tested by linear regression on both all the study period (2007-2016) and only for the normal years period (2008-2016).

	2007-2016		**2008-2016**	
	R^2	**p**	**R^2**	**p**
airTDD_NL-SM vs airMEAN_NL-SM	0.05	<0.01	0.07	<0.01
radTOT_NL-SM vs airMEAN_NL-SM	0.01	0.02	0.01	0.03
radTOT_NL-SM vs airTDD_NL-SM	0.81	<0.01	0.79	<0.01

FB-SM

Also for the period FB-SM, the relations between each pair of variables were statistically significant ($p<0.01$) (Table V.0.b.8). However, only the radTOT, when tested with airTDD, showed high proportion of variance explained ($R^2=0.86$) (Table III.5.A.b.8).

Table III.5.A.b.8. Relations between each pair of potentially related statistics computed for the period FB-SM, as tested by linear regression over all the study period (2007-2016).

	2007-2016	
	R^2	**p**
airTDD_FB-SM vs airMEAN_FB-SM	0.02	<0.01
airFDD_FB-SM vs airMEAN_FB-SM	0.11	<0.01
airFDD_FB-SM vs airTDD_FB-SM	0.03	<0.01
airFDD_FB-SM vs radTOT_FB-SM	0.11	<0.01
radTOT_FB-SM vs airMEAN_FB-SM	0.01	<0.01
radTOT_FB-SM vs airTDD_FB-SM	0.86	<0.01

FF-SM

Also for the period FF-SM, the relations between each pair of variables were statistically significant ($p<0.01$) (Table III.5.A.b.9). Similarly to FB-SM, only the radTOT, when tested with airTDD, showed high proportion of variance explained ($R^2=0.86$) (Table III.5.A.b.9).

Table III.5.A.b.9. Relations between each pair of potentially related statistics computed for the period FF-SM, as tested by linear regression over all the study period (2007-2016).

	2007-2016	
	R^2	**p**
airTDD_FF-SM vs airMEAN_FF-SM	0.01	<0.01
airFDD_FF-SM vs airMEAN_FF-SM	0.01	<0.01
airFDD_FF-SM vs airTDD_FF-SM	0.03	<0.01
airFDD_FF-SM vs radTOT_FF-SM	0.11	<0.01
radTOT_FF-SM vs airMEAN_FF-SM	0.04	<0.01
radTOT_FF-SM vs airTDD_FF-SM	0.86	<0.01

MF-SM

Also in this case, even if all the relations between each pair of variables were statistically significant ($p<0.01$), only the radTOT, when tested with airTDD, showed high proportion of variance explained ($R^2=0.86$) (Table III.5.A.b.10).

Table III.5.A.b.10. Relations between each pair of potentially related statistics computed for the period MF-SM, as tested by linear regression over all the study period (2007-2016).

	2007-2016	
	R^2	**p**
airTDD_MF-SM vs airMEAN_MF-SM	0.00	<0.01
airFDD_MF-SM vs airMEAN_MF-SM	0.08	<0.01
airFDD_MF-SM vs airTDD_MF-SM	0.05	<0.01
airFDD_MF-SM vs radTOT_MF-SM	0.14	<0.01
radTOT_MF-SM vs airMEAN_MF-SM	0.05	<0.01
radTOT_MF-SM vs airTDD_MF-SM	0.85	<0.01

SD-SM

Also in this case, all the relations between each pair of variables were statistically significant ($p<0.01$), but only the radTOT, when tested with airTDD, showed high proportion of variance explained ($R^2=0.84$) (Table III.5.A.b.11).

Table III.5.A.b.11. Relations between each pair of potentially related statistics computed for the period SD-SM, as tested by linear regression over all the study period (2007-2015).

	2007-2015	
	R^2	**p**
airTDD_SD-SM vs airMEAN_SD-SM	0.01	<0.01
airFDD_SD-SM vs airMEAN_SD-SM	0.04	<0.01
airFDD_SD-SM vs airTDD_SD-SM	0.02	<0.01
airFDD_SD-SM vs radTOT_SD-SM	0.14	<0.01
radTOT_SD-SM vs airMEAN_SD-SM	0.03	<0.01
radTOT_SD-SM vs airTDD_SD-SM	0.84	<0.01

SR-SM

Similarly to the previous stages, only the radTOT, when tested with airTDD, showed high proportion of variance explained ($R^2=0.79$), even if all the relations between each pair of variables were statistically significant ($p<0.01$) (Table III.5.A.b.12).

Table III.5.A.b.12. Relations between each pair of potentially related statistics computed for the period SR-SM, as tested by linear regression over all the study period (2007-2015).

	2007-2015	
	R^2	p
airTDD_SR-SM vs airMEAN_SR-SM	0.02	<0.01
airFDD_SR-SM vs airMEAN_SR-SM	0.05	<0.01
airFDD_SR-SM vs airTDD_SR-SM	0.04	<0.01
airFDD_SR-SM vs radTOT_SR-SM	0.14	<0.01
radTOT_SR-SM vs airMEAN_SR-SM	0.15	<0.01
radTOT_SR-SM vs airTDD_SR-SM	0.79	<0.01

LS-SM

Also for the growing season period (LS-SM), only the radTOT, when tested with airTDD, showed high proportion of variance explained (R^2=0.79), even if all the relations between each pair of variables were statistically significant (p<0.01) (Table III.5.A.b.13).

Table III.5.A.b.13. Relations between each pair of potentially related statistics computed for the period LS-SM, as tested by linear regression over all the study period (2007-2015) and only for the normal years of LS (2007-2014).

	2007-2015		2007-2014	
	R^2	p	R^2	p
airTDD_LS-SM vs airMEAN_LS-SM	0.00	<0.01	0.00	<0.01
airFDD_LS-SM vs airMEAN_LS-SM	0.06	<0.01	0.12	<0.01
airFDD_LS-SM vs airTDD_LS-SM	0.05	<0.01	0.06	<0.01
airFDD_LS-SM vs radTOT_LS-SM	0.38	<0.01	0.38	<0.01
radTOT_LS-SM vs airMEAN_LS-SM	0.09	<0.01	0.18	<0.01
radTOT_LS-SM vs airTDD_LS-SM	0.79	<0.01	0.78	<0.01

III.5.B. Long-term plant phenology monitoring

III.5.B.a. *Patterns of Snow Melt (SM) and onset of the growing season*

Inter-species level

Overall the study period (2007-2016), the SM exhibited a large and statistically significant inter-annual variability, as tested by one-way ANOVA (F=78, p<0.01) (Fig. III.5.B.a.1-2).

During the entire monitoring period (2007-2016) (Table III.5.B.a.1), mean and median values of SM were coincident (169 DOY, corresponding to mid-June) and its 75% quartile occurred 11 days later (180 DOY, which correspond to the end of June).

Table III.5.B.a.1. Non-parametric statistics of snow melt (SM) computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	130	150	135	135	153	161	174	14.5
2008	120	176	158	168	175	182	204	10.4
2009	128	181	165	170	177	188	216	12.6
2010	133	178	160	166	178	186	206	12.2
2011	133	160	143	146	158	169	181	12.4
2012	133	161	144	147	162	171	184	12.4
2013	133	181	161	168	182	192	217	16.0
2014	131	175	147	161	171	189	221	16.8
2015	133	161	127	152	158	173	206	15.5
2016	131	166	145	159	172	175	181	11.3
2007-2016	1305	169	127	158	169	180	221	16.8

Analyzing each year separately (Table III.5.B.a.1), the beginning of SM was recorded between early May (127 DOY, in 2015) and mid-June (165 DOY, in 2009), while the SM completion ranged from late June (174 DOY, in 2007) to early August (221 DOY, in 2014).

The total duration of the SM showed a large variability, ranging from 36 days (occurred last year, in 2016) up to 79 days (in 2015), while the SM peak duration showed a lower variability, ranging from 2 weeks (14 days, in 2008) up to almost one month (28 days, in 2014).

It is significant the large SM advance of 2007 respect to all the other years. According to the 75% quartile anomalies, in this year the SM occurred 19 days earlier, while on the opposite, the latest SM occurred in 2013, with a delay of 12 days (Fig. III.5.B.a.2).

Figure III.5.B.a.1. Example of SM (complete absence of snow cover) in plot G2.

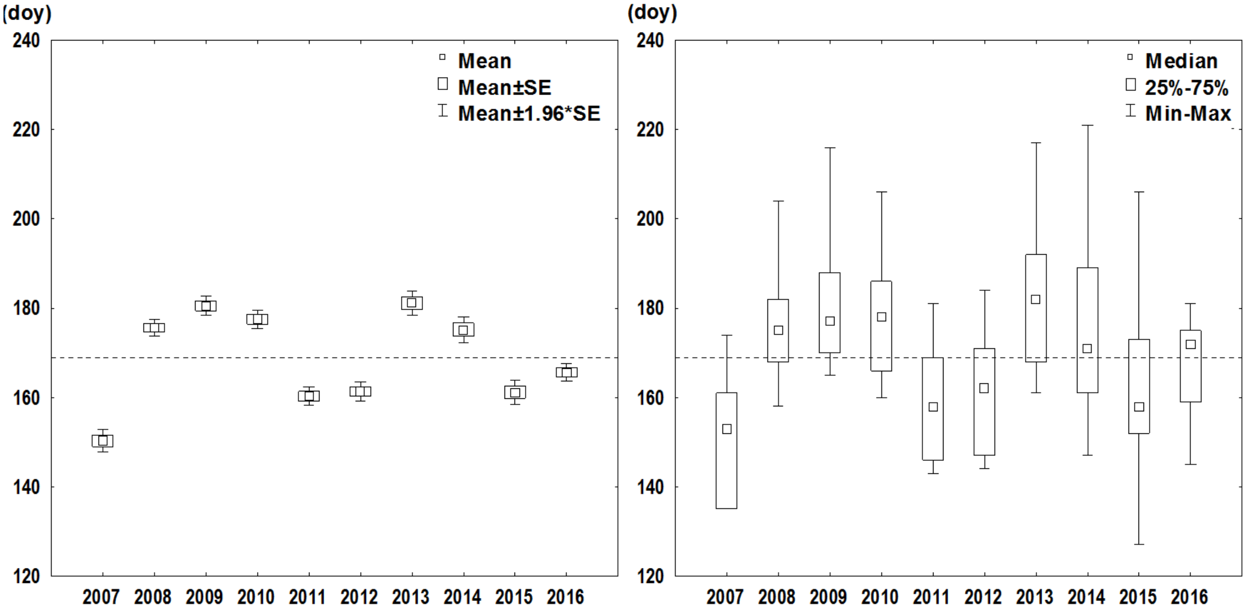


Figure III.5.B.a.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (SM) from 2007 to 2016. The dotted black line represents the mean value for the whole period.

The year 2007 was the only one identifiable as “extreme”, as tested by t-test ($p<0.05$). We then excluded this year when computing temporal trend analysis, in order to incorporate only the background variation of “normal” years (2008-2016).

We did not find statistically significant trend of SM with time. However, the beginning of SM (given by the earliest SM date) exhibited a statistically significant advance of -2.9 days/year (R^2=0.43, p=0.05) (Fig. III.5.B.a.3).

As tested by linear regression (Table III.5.B.a.2) our SM data were representative for the European Alps (Fig. III.5.B.a.4). In particular, the extreme early SM of 2007 was identified for all the Alps, with a significant SM advance.

According to the long-term snow record from LaFoppa AWS, this year corresponded to the earliest SM since at least the last two decades (1996-2016) (Fig. III.5.B.a.3).

Table III.5.B.a.2. Elevation of the AWS from different locations of the European Alps used for the snow melt comparison with our study area (75% quartile) and their statistical significance as tested by linear regression with La Foppa AWS (2650 m a.s.l.).

AWS	**Elevation (m a.s.l.)**	**R^2**	**p**
Gressoney-La Trinité	2379	0.85	< 0.01
Rabbi	1335	0.80	0.02
Arabba	2265	0.90	< 0.01
Val Noana	1020	0.83	< 0.01
Pitztaler	2850	0.97	0.02

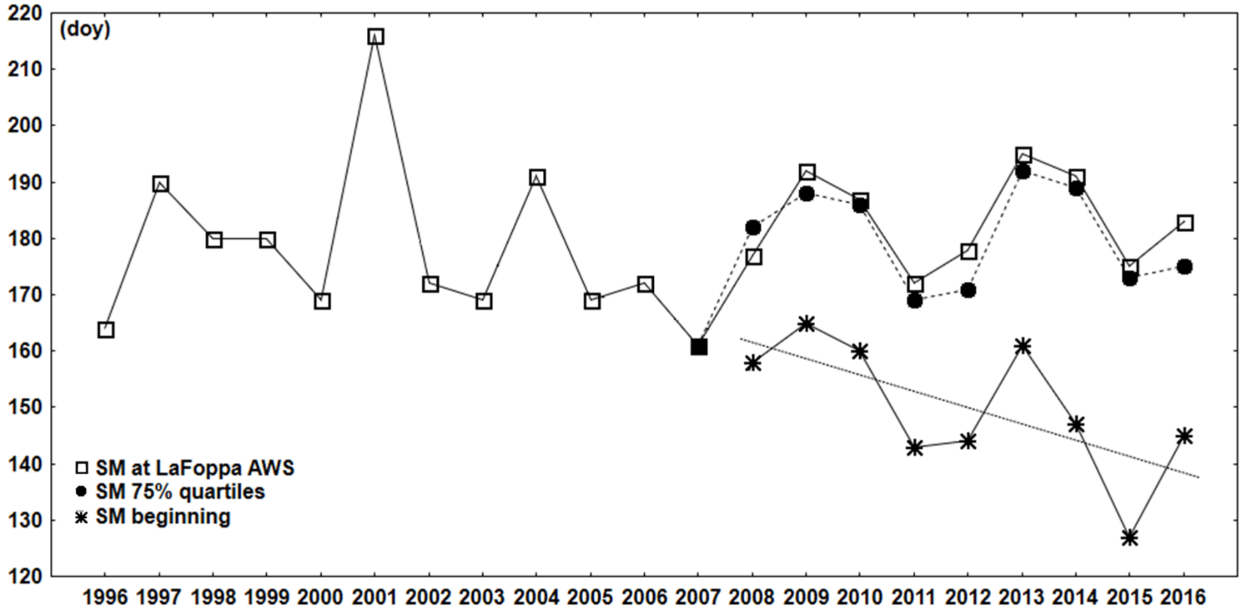
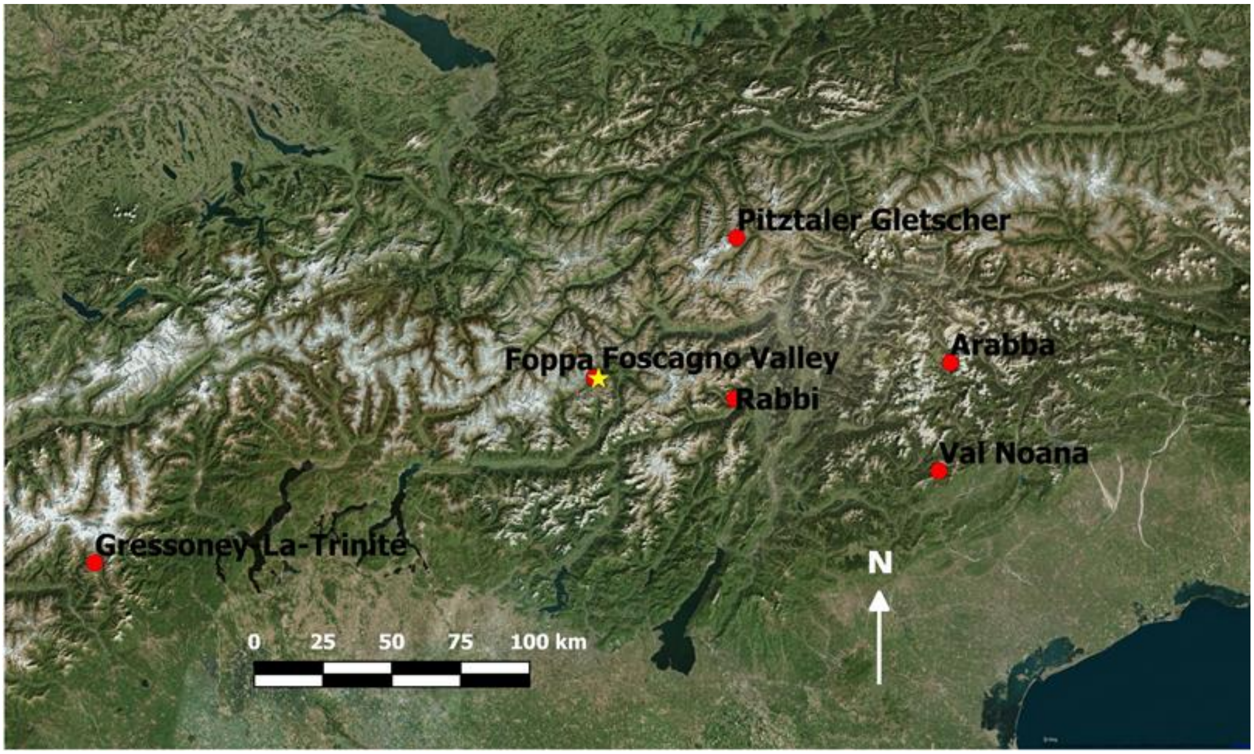


Figure III.5.B.a.3. Trends with time of the SM at La Foppa AWS (white quadrats) and for the SM at our studied plots: 75% quartiles (black dots) and earliest SM of "normal years" (stars). Statistical significance coefficients of the earliest SM with time as tested by linear regression: β=-2.9, R^2=0.43, p=0.05.

Figure III.5.B.a.4. Location of the Automatic Weather Stations (AWS, red dots) used to assess the representativeness of the snow melt data from our study site (yellow star, Foscagno valley).



Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the SM of deciduous dwarf shrubs (i.e. *Salix herbacea*) exhibited statistically significant differences among years (F=4, p<0.01) (Fig III.5.B.a.5).

Over the study period (2007-2016), according to the mean and median values, the SM occurred at mid-June (170 DOY), or in early July (183 DOY) considering the 75% quartile (Table III.5.B.a.3).

Analyzing each single year, the earliest onset of SM (135 DOY, mid-May) was recorded in 2007, while the latest in 2009 (170 DOY, mid-June). The latest SM completion showed an even larger variability, ranging from mid-June (170 DOY, in 2007) to late July (217 DOY, in 2013) (Table III.5.B.a.3).

The total duration and the peak duration of SM showed a great variability. The total duration ranged from 24 days (in 2009) to 53 days (in 2013), while the peak duration spanned from only 7 days (in 2008) to 35 days (in 2007) (Fig. III.5.B.a.5).

Considering the anomalies of the 75% quartiles referred to the whole period, the SM showed comparable advances in 2007, 2011, 2012 ad 2015, although not statistically significant, as tested by t-test (p>0.05).

Considering thus the whole period (2007-2016) the analysis of SM with time did not reveal any statistically significant trend, as tested by linear regression (p>0.05).

Table III.5.B.a.3. Non-parametric statistics of snow melt (SM) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	7	151	135	135	138	170	170	17.9
2008	5	175	158	168	175	175	197	14.3
2009	6	185	170	177	188	194	194	9.9
2010	7	181	161	166	183	189	199	13.1
2011	7	163	146	149	169	169	181	12.5
2012	7	165	147	150	168	171	184	12.9
2013	7	183	164	164	185	192	217	19.3
2014	7	175	161	161	182	189	189	13.6
2015	7	161	146	146	166	169	180	12.9
2016	7	167	149	153	175	175	181	12.7
2007-2016	67	170	135	161	170	183	217	16.9

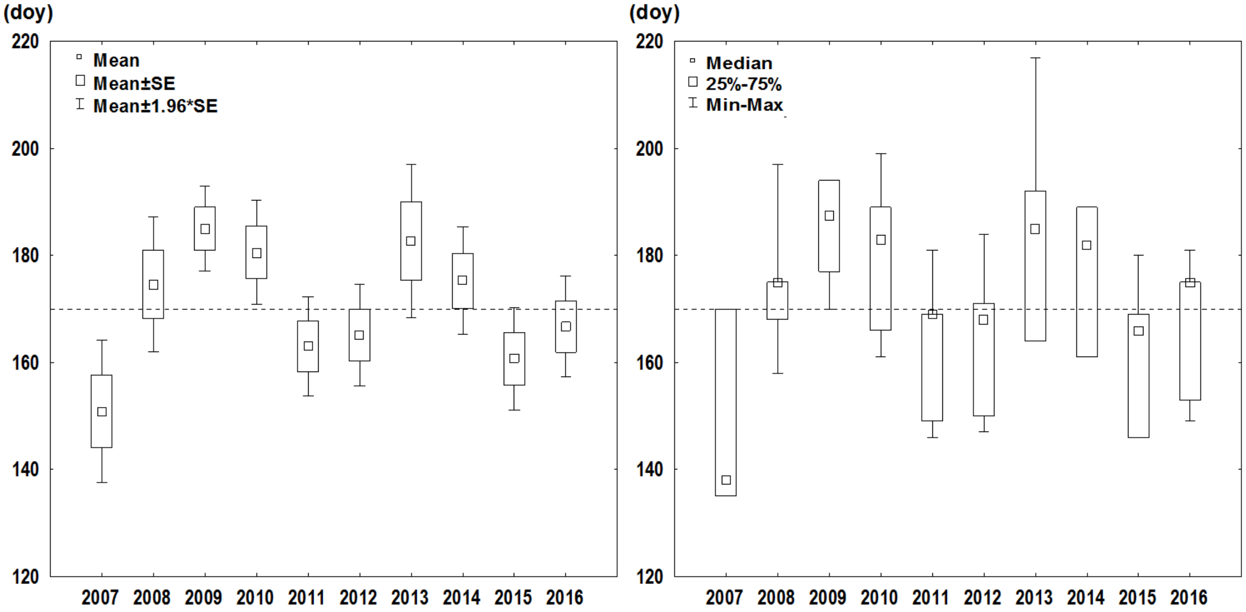


Figure III.5.B.a.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (SM) for deciduous dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Deciduous shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the SM of deciduous shrubs (i.e. *Vaccinium uliginosum*) exhibited statistically significant differences among years (F=4, p<0.01) (Fig. III.5.B.a.5).

Over the study period (2007-2016), the SM exhibited mean and median values at the beginning of June (respectively 157 and 159 DOY), while the 75% quartile occurred at mid-June (165 DOY) (Table III.5.B.a.4).

Table III.5.B.a.4. Non-parametric statistics of snow melt (SM) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	4	155	135	135	155	174	174	22.5
2008	2	168	168	168	168	168	168	-
2009	4	178	165	171	177	186	194	11.9
2010	4	163	160	160	161	167	172	5.9
2011	4	150	146	146	148	154	158	5.7
2012	4	149	144	146	149	152	154	4.3
2013	4	164	161	161	163	166	168	3.3
2014	4	155	147	149	156	161	161	7.3
2015	4	141	127	130	139	152	158	14.0
2016	4	152	145	147	151	156	159	6.0
2007-2016	38	157	127	147	159	165	194	13.9

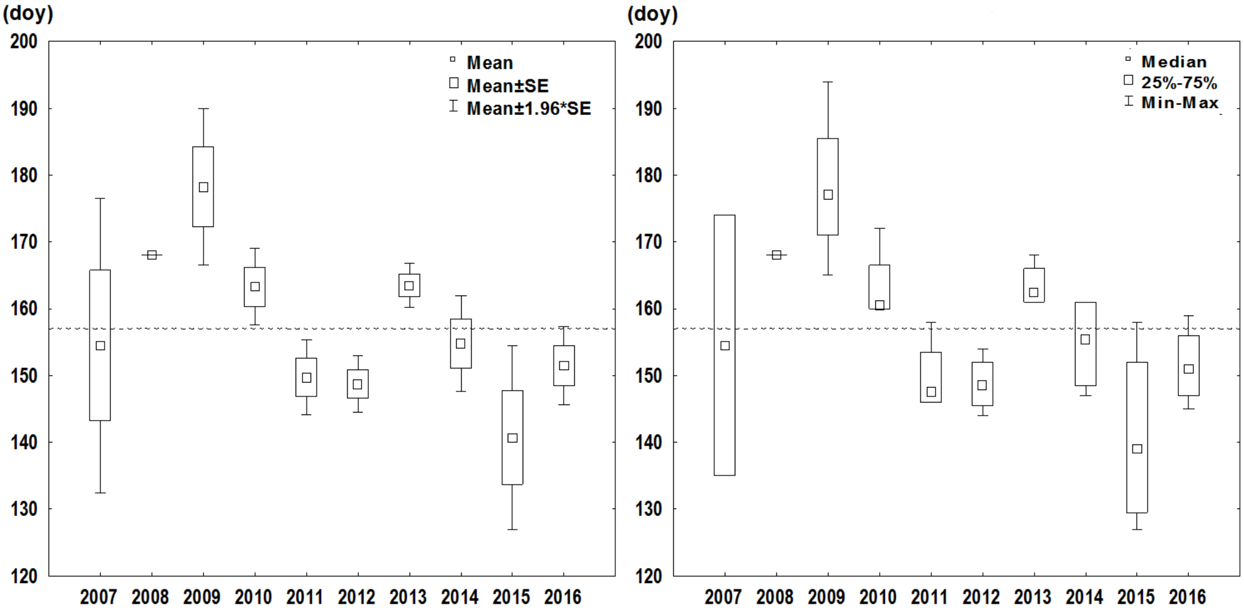


Figure III.5.B.a.6. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (SM) for deciduous shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering the intra-annual variability, the earliest onset of SM (127 DOY, early May) was recorded in 2015, while the latest in 2008 (168 DOY, mid-June) (Table III.5.B.a.4). The SM completion ranged from early June (154 DOY, in 2012) to mid-July (194 DOY, in 2009).

In 2008, for logistical constraints, the field monitoring started when the snow melting at these plots was almost completed. For this reason, snow cover was recorded only in 50% of the deciduous shrubs plots and lasted very few days. Therefore, the SM data collected for this growth form in 2008 were characterized by lack of variance. Indeed, this year all the statistics occurred at 168 DOY (Table III.5.B.a.4). All the other years, the total duration of SM for deciduous shrubs ranged from only one week (in 2013) to 39 days (in 2007). Similarly, the SM peak duration was concentrated from 5 days only (in 2013) to 39 days maximum (in 2007) (Fig. III.5.B.a.6).

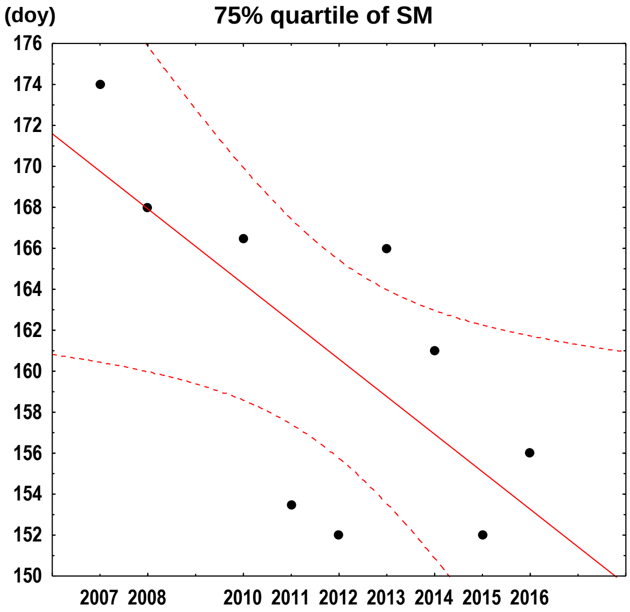


Figure III.5.B.a.7. Trend with time of the 75% quartiles of SM (β=-1.8, R^2=0.5, $p<0.05$) for deciduous shrubs, as tested by linear regression.

According to the anomalies of the 75% quartiles, the SM showed a statistically significant delay in 2009 (+21 days), as tested by t-test (Fig. III.5.B.a.5). We thus removed this year for further analysis of trend of SM with time.

Analyzing thus only the “normal” years (excluding 2009 as “extreme” year of SM), we did not find statistically significant trend of SM with time. However, we observed a statistically significant advance of the 75% quartiles (i.e. ¾ of the population data) of SM with a rate of -1.8 days/year (R^2=0.50, $p<0.05$) (Fig III.5.B.a.7).

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the SM of evergreen dwarf shrubs (i.e. *Empetrum hermaphroditum* and *Kalmia procumbens*) exhibited statistically significant differences among years (F=30, p<0.01) (Fig III.5.B.a.8).

Table III.5.B.a.5. Non-parametric statistics of snow melt (SM) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	9	136	135	135	135	135	138	1.3
2008	8	170	158	168	172	175	175	6.0
2009	8	170	165	165	170	174	177	5.0
2010	9	168	160	166	166	172	172	4.4
2011	9	148	143	146	146	149	158	5.8
2012	9	151	144	147	147	154	162	6.7
2013	9	167	161	164	168	168	172	4.1
2014	9	162	147	161	161	164	171	7.2
2015	9	152	132	146	158	158	158	9.1
2016	9	156	145	149	159	159	166	7.5
2007-2016	88	158	132	147	160	168	177	12.2

Over all the study period (2007-2016), the mean and median values of SM coincided with the beginning of June (respectively 158-160 DOY), while the 75% quartile occurred in mid-June (168 DOY) (Table III.5.B.a.5).

Considering the intra-annual variability, the earliest onset of SM (135 DOY, mid-May) was recorded in 2007, while the latest in 2009 (165 DOY, mid-June) (Table III.5.B.a.5). The SM completion ranged from mid-May (138 DOY, in 2007) to late-June (177 DOY, in 2009).

In 2007, our data showed a very low variance, probably due to the scarcity of snow cover during this anomalous year. However, to avoid underestimation we did not consider such data to extrapolate information about the range and peak of SM (Table III.5.B.a.5). Thus, the total duration of SM for evergreen dwarf shrubs ranged from 12 days (in 2009 and 2010) to 26 days (in 2015), while the SM peak duration was concentrated to only 3 days (in 2011 and 2014) or to 12 days maximum (in 2015) (Fig. III.5.B.a.8).

According to the anomalies of the 75% quartiles, the SM showed the largest advance in 2007 (-33 days), which was the only one year with a statistically significant advance, as tested by t-test (p<0.01), and was thus identified as “extreme” year (Fig. III.5.B.a.8).

Considering only “normal” years (2008-2016), we did not find any trend of SM with time. However we observed a statistically significant advance of the earliest SM of -2.7 days/year, as tested by linear regression (R2=0.4, p=0.05) (Fig. III.5.B.a.9).

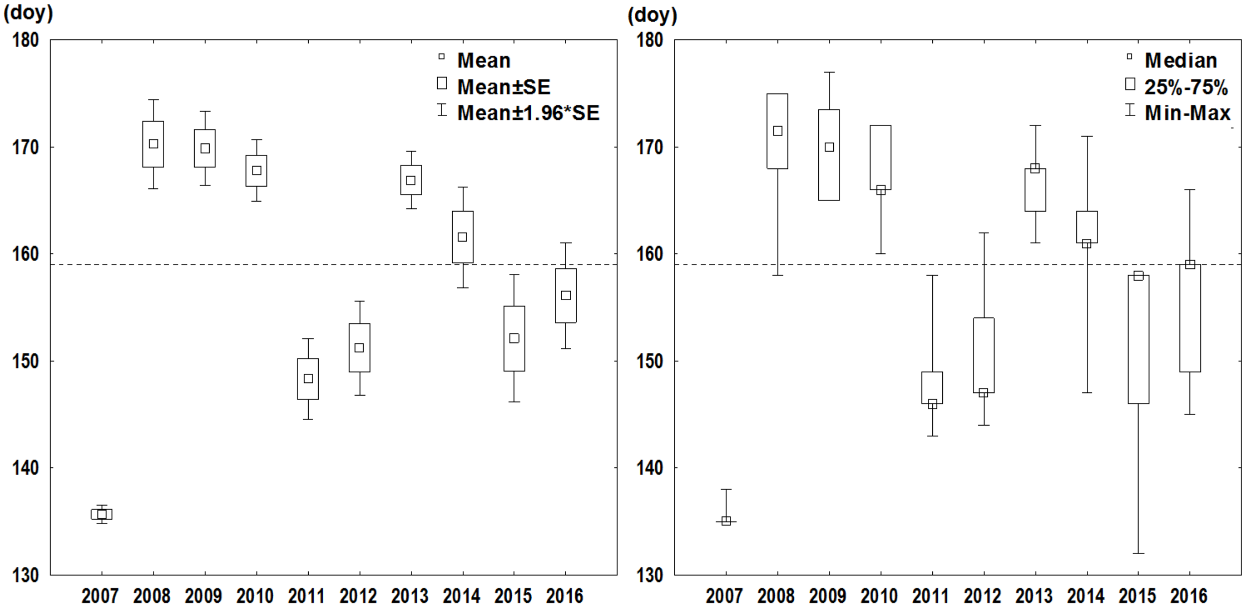


Figure III.5.B.a.8. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (SM) for evergreen dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

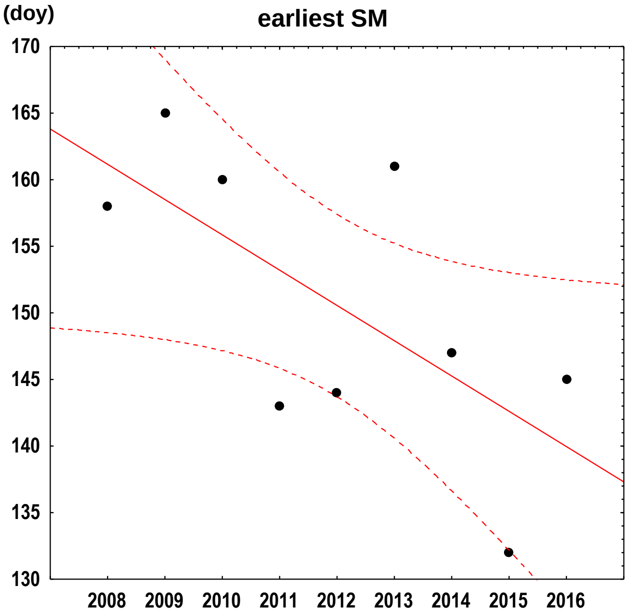


Figure III.5.B.a.9. Trend with time of the earliest SM (β=-2.7, R^2=0.4, p=0.05) for the evergreen dwarf shrubs, as tested by linear regression.

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the SM of evergreen shrubs (i.e. *Rhododendron ferrugineum* and *Juniperus communis*) exhibited statistically significant differences among years (F=16, p<0.01) (Fig III.5.B.a.10).

Table III.5.B.a.6. Non-parametric statistics of snow melt (SM) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev.**
2007	8	140	135	135	135	137	170	12.3
2008	6	165	158	158	165	168	175	6.8
2009	8	170	165	165	168	177	177	5.9
2010	8	164	160	160	163	166	172	4.3
2011	8	148	146	146	146	146	158	4.2
2012	8	148	144	144	147	149	162	6.0
2013	8	164	161	161	164	164	172	3.6
2014	8	158	147	154	157	161	171	7.3
2015	8	144	127	137	144	151	158	10.2
2016	8	151	145	147	149	151	166	6.7
2007-2016	78	155	127	146	157	164	177	12.0

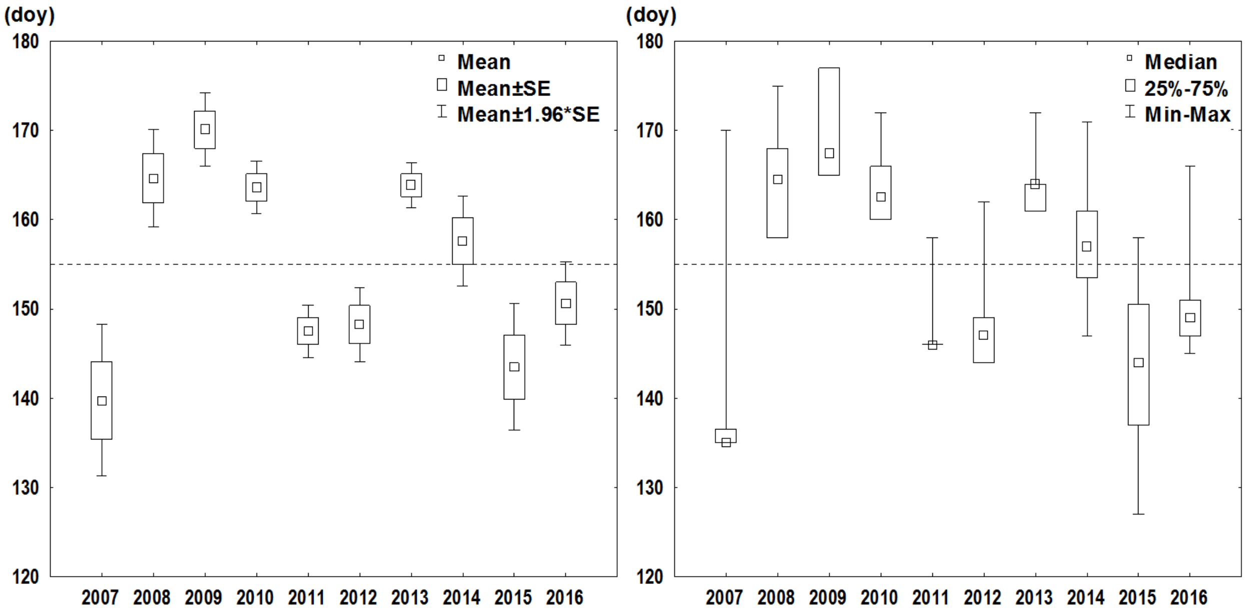


Figure III.5.B.a.10. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (SM) for evergreen shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Over all the study period (2007-2016), the SM occurred at the beginning of June, according to its mean and median values (respectively 155-157 DOY), while the 75% quartile occurred at mid-June (164 DOY) (Table III.5.B.a.6).

The onset of SM ranged between early May (127 DOY in 2015), and mid-June (165 DOY, in 2009) (Table III.5.B.a.6). The SM completion was achieved between the beginning of June (158 DOY, in 2011 and 2015) and late June (177 DOY, in 2009).

The total duration of SM for the evergreen shrubs ranged from 11 days (in 2013) to 35 days (in 2007), while the SM peak duration ranged from 0 to 14 days (respectively in 2011 and 2015) (Fig. III.5.B.a.10).

According to the anomalies of the 75% quartiles, the SM showed the largest advance in 2007 (-28 days), although not statistically significant tested by t-test ($p>0.05$) (Fig. III.5.B.a.10).

Considering thus all the study period (2007-2016) we did not find statistically significant trend of the SM with time for evergreen shrubs, as tested by linear regression ($p>0.05$).

Forbs

Over all the study period, also forbs exhibited statistically significance differences among years, as tested by one-way ANOVA (F=48, $p<0.01$) (Fig III.5.B.a.11).

The mean and median value for the SM over the whole period (2007-2016) occurred in late June (respectively 174 and 175 DOY), while the 75% at the beginning of July (184 DOY) (Table III.5.B.a.7).

Table III.5.B.a.7. Non-parametric statistics of snow melt (SM) for forbs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	64	155	135	138	161	166	174	12.8
2008	63	179	158	175	175	182	204	9.7
2009	65	184	165	177	181	194	216	12.6
2010	67	183	160	175	186	189	206	10.9
2011	67	166	143	158	169	173	181	10.8
2012	67	166	147	158	171	174	184	10.9
2013	67	188	161	179	189	196	217	14.5
2014	66	182	150	171	184	189	221	15.5
2015	67	167	127	155	169	176	206	14.9
2016	66	171	149	166	172	175	181	8.9
2007-2016	659	174	127	165	175	184	221	15.8

The onset of SM was documented between early May (127 DOY, in 2015) up to mid-June (165 DOY, in 2009), while the SM completion ranged from 174 DOY (in 2007) to 221 DOY (in 2014). The total duration of SM ranged from 37 days (in 2012) up to 79 days (in 2015), while the peak SM duration spanned over only one week (in 2008) to 27 days maximum (in 2007) (Table III.5.B.a.7).

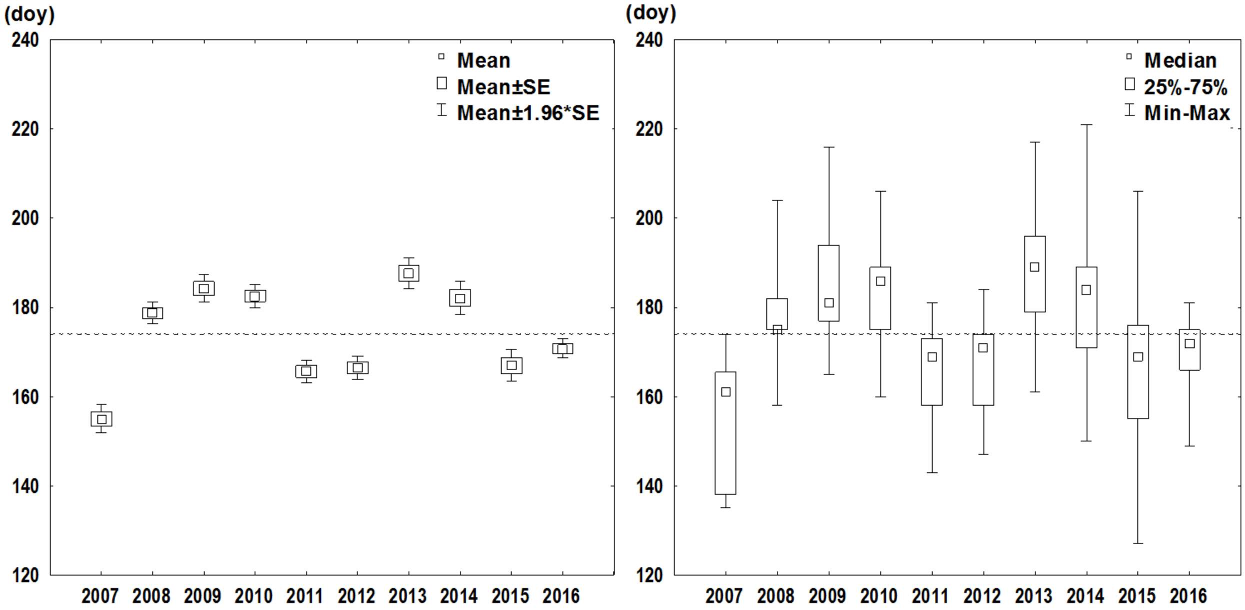


Figure III.5.B.a.11. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (SM) for forbs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

According to the 75% quartiles, forbs recorded the earliest and “extreme” SM in 2007, showing a statistically significant advance (-19 days), as tested by t-test ($p<0.05$). The most delayed SM occurred in 2013, with a delay of 12 days, although not statistically significant ($p>0.05$) (Fig. III.5.B.a.11). We thus removed 2007 from further analysis of SM trend with time.

Considering only the “normal” years (2008-2016), we did not find any statistically significant trend of SM with time, as tested by linear regression ($p>0.05$).

Graminoids

As tested by one-way ANOVA, overall the study period (2007-2016) the SM of graminoids exhibited statistically significant differences among years (F=25, $p<0.01$) (Fig. III.5.B.a.12).

Over the study period (2007-2016), according to the mean and median values, the SM occurred at mid-June (166 DOY), while the 75% quartile occurred at late-June (175 DOY) (Table III.5.B.a.8).

Table III.5.B.a.8. Non-parametric statistics of snow melt (SM) for graminoids computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	38	147	135	135	138	161	174	14.6
2008	36	174	158	168	175	182	197	10.7
2009	37	178	165	170	177	181	205	12.8
2010	38	175	160	166	172	186	199	11.6
2011	38	157	143	146	158	169	181	12.3
2012	38	158	144	147	152	171	184	12.3
2013	38	178	164	164	170	189	217	15.4
2014	37	172	157	161	164	184	221	16.5
2015	38	159	132	146	157	169	199	13.6
2016	37	163	145	153	159	172	181	10.8
2007-2016	375	166	132	157	166	175	221	16.5

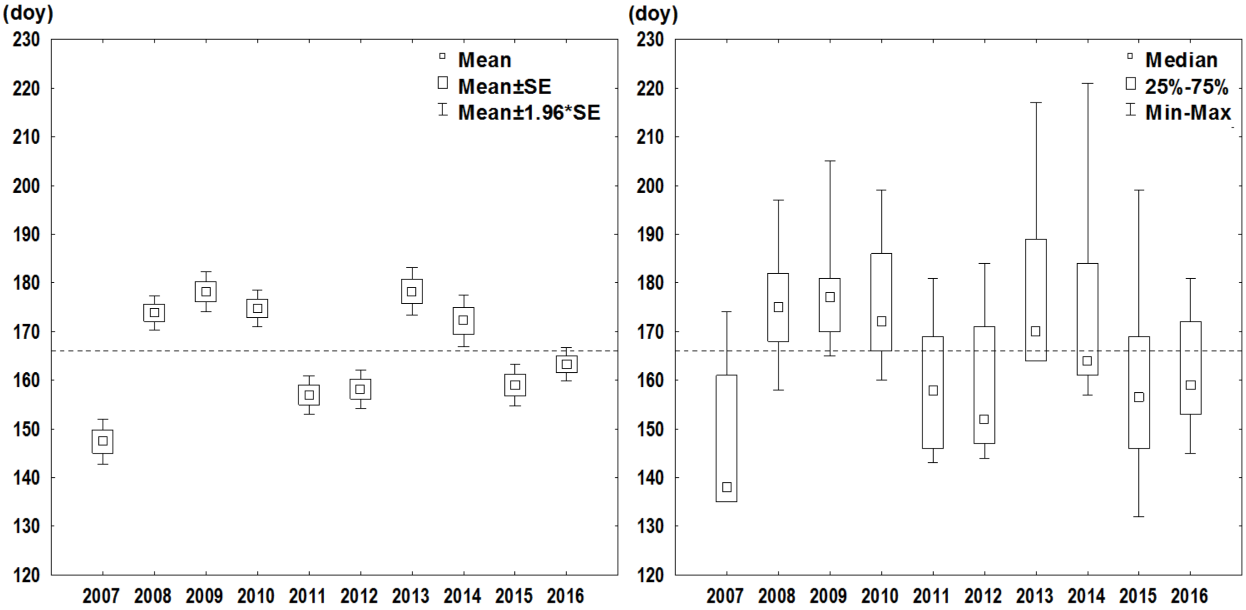


Figure III.5.B.a.12. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (SM) for graminoids from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering each single year, the earliest onset of SM (132 DOY, mid-May) was recorded in 2015, while the latest in 2009 (165 DOY, mid-June). The SM completion showed a larger variability, ranging from late June (174 DOY, in 2007) to early August (221 DOY, in 2014) (Table III.5.B.a.8).

For graminoids, the total duration of SM ranged from 36 days (in 2016) to 67 days maximum (in 2015), while, the peak duration of SM was concentrated to 11 days only (in 2009) or 26 days maximum (in 2007) (Fig. III.5.B.a.12).

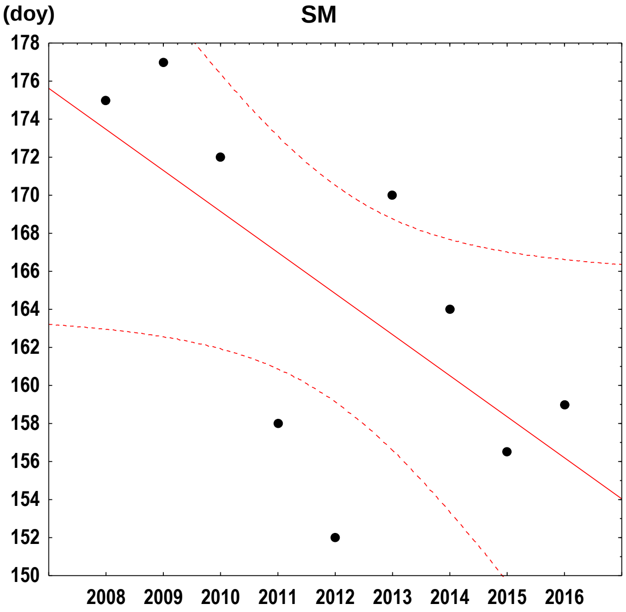


Figure III.5.B.a.13. Trend of SM with time (β=-2.1, R^2=0.40, p=0.05) for the graminoids, as tested by linear regression.

Considering the anomalies of the 75% quartiles referred to the whole study period, the graminoids showed the greatest SM advance in 2007 (-14 days), while in 2013 the greatest delay (+14 days), even if in both cases not statistically significant, as tested by t-test (p>0.05).

However we found a statistically significant advance of SM in 2007 tested by t-test (p<0.01). Thus, considering only the "normal years" there was a statistically significant advance of the SM, as tested by linear regression (β=-2.1 days/year, R^2=0.40, p=0.05) (Fig. III.5.B.a.13).

Comparison of trends among growth forms

Considering all the study period (2007-2015) the trends of SM analyzed comparing the different growth forms (deciduous dwarf shrubs, deciduous shrubs, evergreen dwarf shrubs, evergreen shrubs, forbs, and graminoids) showed a large and statistically significant variability (Fig. III.5.B.a.14), as tested by one-way ANOVA (F=43, p<0.01).

Deciduous shrubs, evergreen dwarf shrubs and evergreen shrubs showed the earliest SM respect the other growth forms (Fig. III.5.B.a.14). According to the 75% quartiles the SM for these growth forms occurred respectively 15, 12 and 16 days before the 75% quartile referred to the whole dataset, even if not statistically significant when tested by t-test (p>0.05).

The SM completion (provided by its maximum value) for the evergreen shrubs and evergreen dwarf shrubs was the earliest, while the latest SM occurred for deciduous dwarf shrubs, forbs and graminoids, even if these differences were not statistically significant as tested by t-test (p>0.05). The total duration of the SM (provided by its range) showed also a large variability. It spanned over almost 3 months for forbs, graminoids and deciduous dwarf shrubs, or less than two months for deciduous shrubs, evergreen dwarf shrubs and evergreen shrubs.

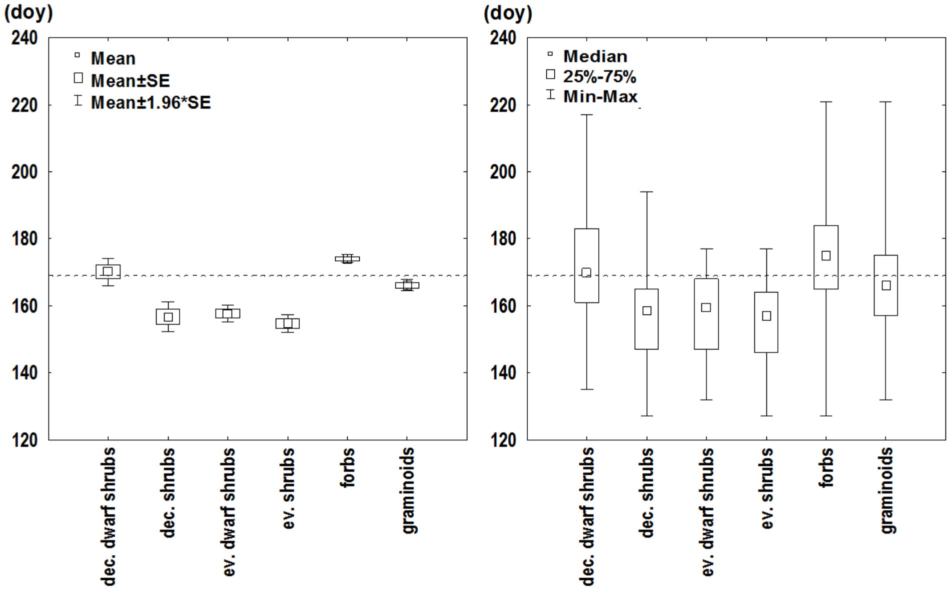


Figure III.5.B.a.14. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (SM) between different growth forms over the period 2007-2016. The dotted black line represents the mean value for the whole period.

The comparison of the trends of SM with time among growth forms emphasized different potential responses to climate, according to the growth form types.

Graminoids were the only growth form showing a statistically significant advance of SM, and could be thus identified as the most potentially susceptible species to climate warming if they will not be able to cope with these advances.

However, we documented other trends with time regarding the SM population data. The evergreen dwarf shrubs displayed an advance of the earliest SM, thus resembling the pattern observed at the inter-specific level. Simultaneously, deciduous shrubs exhibited a SM advance when analyzing the trends of their 75% quartiles (instead of their median) over the study period, which correspond to a shift of a large part of the population.

Therefore, graminoids, deciduous shrubs and evergreen dwarf shrubs could be identified as the most sensitive growth forms to climate warming, displaying rapid changing of the pattern of SM. We could thus hypothesize that, in a warmer scenario with earlier snow melting, such species could start their growing season earlier, with either potential benefits (e.g. growing season lengthening) or risks (e.g. cold slash and frost event) depending on their capability to adapt to the observed abiotic changes.

III.5.B.b. *Patterns of First Shoot (FS) and onset of plant growth*

Analogously to the other phenophases, our analyses have been carried out following two steps: I) inter-species level; II) intra-growth form level.

Inter-specific level

Similarly to what observed for the SM, overall the study period (2007-2016) at inter-specific level FS exhibited a large inter-annual variability, exhibiting statistically significant differences, as tested by one-way ANOVA (F=76, p<0.01) (Fig. III.5.B.b.1).

During the entire monitoring period (2007-2016) (Table III.5.B.b.1), mean and median values of FS were almost coincident (173 and 174 DOY, corresponding to late June) and its 75% quartile occurred at 184 DOY, which correspond to the beginning of July.

Table III.5.B.b.1. Non parametric statistics of first shoot (FS) computed for each single year, as well as for the entire monitoring period (2007-2016), at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	128	154	138	138	157	165	179	14.8
2008	103	183	161	175	182	189	211	11.6
2009	119	186	170	177	181	191	223	13.2
2010	133	181	161	169	180	189	210	12.4
2011	133	165	148	149	163	175	187	13.1
2012	133	166	147	154	165	174	186	11.0
2013	132	185	164	172	185	196	220	15.8
2014	130	180	150	164	173	197	233	18.5
2015	131	165	132	152	162	176	209	15.6
2016	131	170	149	162	175	179	189	11.5
2007-2016	1273	173	132	162	174	184	233	17.3

Analyzing each year separately (Table III.5.B.b.1), the beginning of FS ranged between mid-May (132 DOY, in 2015) and mid-June (170 DOY, in 2009), while the end of FS ranged from late June (179 DOY, in 2007) to mid-August (233 DOY, in 2014).

The longest duration of FS was recorded in 2014 (83 days), while the shortest in 2011 and 2012 (in both cases 39 days). The longest FS peak duration was recorded in 2014 (33 days) and the shortest in 2008 and 2009 (14 days).

Analogously to what observed for the SM, the earliest FS was recorded in 2007 (-19 days) and the latest in 2012 and 2013 (respectively +12 and +13 days), according to the anomalies of the 75% quartiles. Also in this case, the FS advance of 2007 was identified as statistically significant and "extreme" year, as tested by t-test (p=0.05) (Fig. III.5.B.b.1).

We did not find statistically significant trend of FS with time, investigating the "normal" years (2008-2016). However, we observed a statistically significant advance of the earliest onset of FS (-2.8 days/year, likewise SM), as tested by linear regression (R2=0.44, p=0.05) (Fig. III.5.B.b.2).

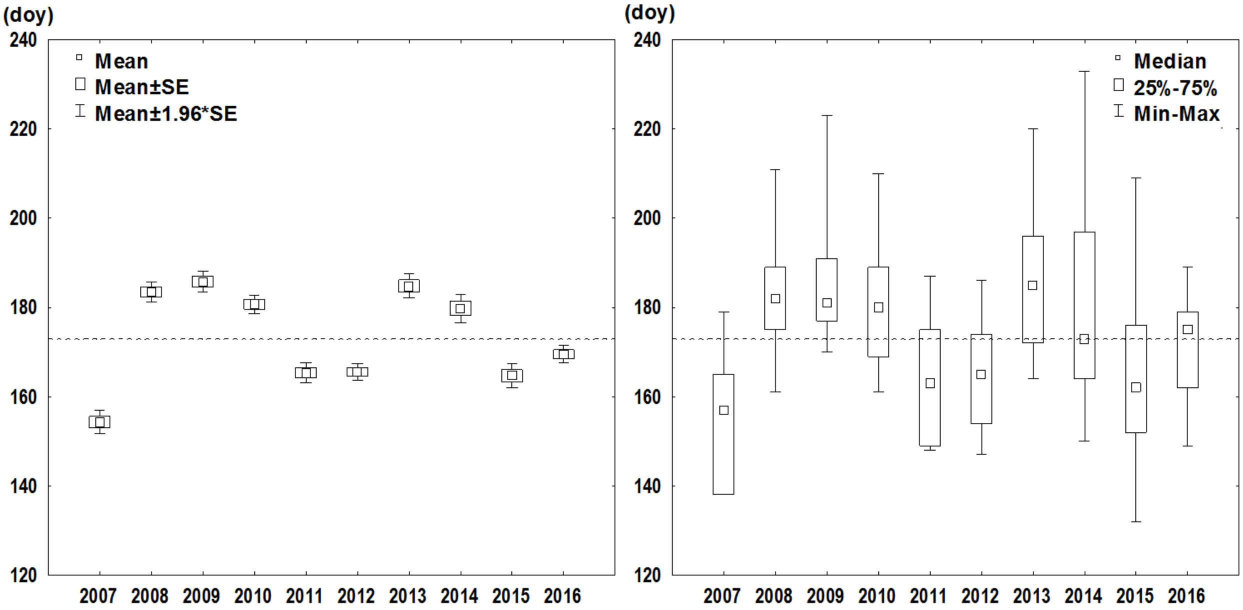


Figure III.5.B.b.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of onset of first shoot (FS) from 2007 to 2016 at the inter-specific level. The dotted black line represents the mean value for the whole period.

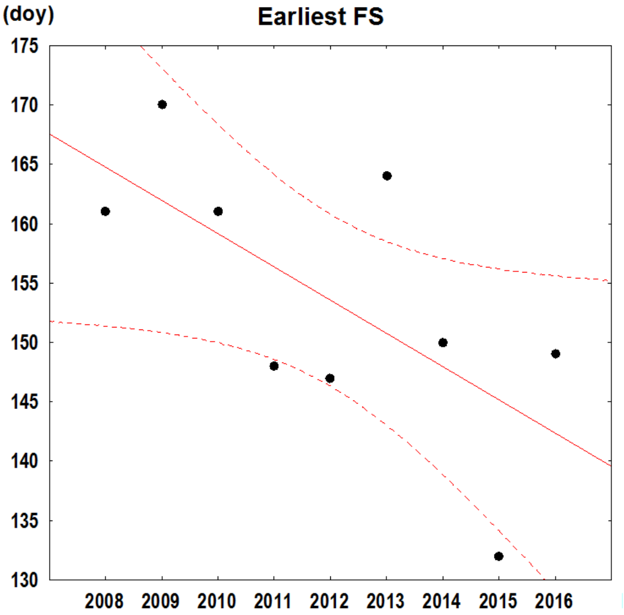


Figure III.5.B.b.2: Trend with time of the earliest FS (β=-2.8, R^2=0.44, p=0.05) at the inter-specific level, as tested by linear regression on the "normal" years period (2008-2016).

The timing of SM was the main factor influencing FS, as tested by linear regression at inter-annual level (Fig. III.5.B.b.3), thus confirming the important role of SM as signal for the start of the growing season.

The observed advance of the earliest FS allows to hypothesize that in a warmer scenario, plants could be able to profit of an earlier SM, starting earlier their development and potentially lengthening their growing season.

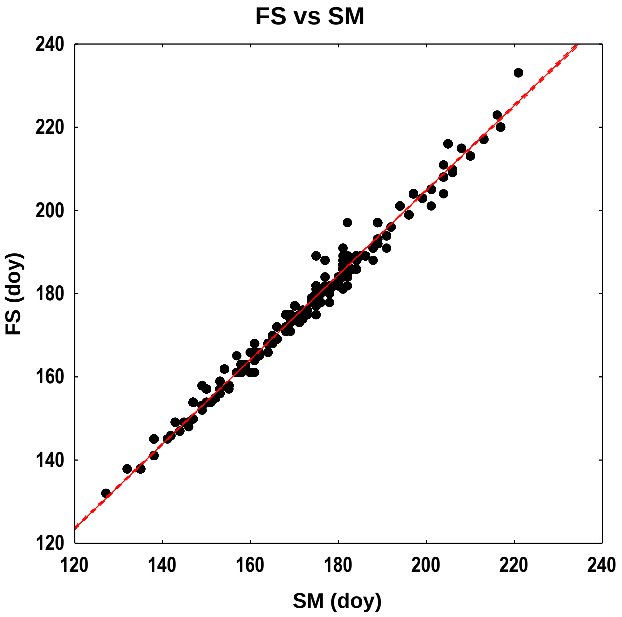


Figure III.5.B.b.3: Relation between FS and SM at intra-annual and inter-specific level, as tested by linear regression (β=1.0, R^2=0.98, p<0.01).

Intra-growth form level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FS of deciduous dwarf shrubs (i.e. *Salix herbacea*) (Fig. III.5.B.b.4) exhibited statistically significant differences among years (F=4, p<0.01) (Fig. III.5.B.b.5).

Over the study period (2007-2016), according to the mean and median values, the FS occurred at late June (respectively 175 and 174 DOY), while the 75% quartile coincided with early July (187 DOY, only 4 days later respect the 75% quartile of SM) (Table III.5.B.b.2).

Figure III.5.B.b.4. Example of FS on *Salix herbacea.*

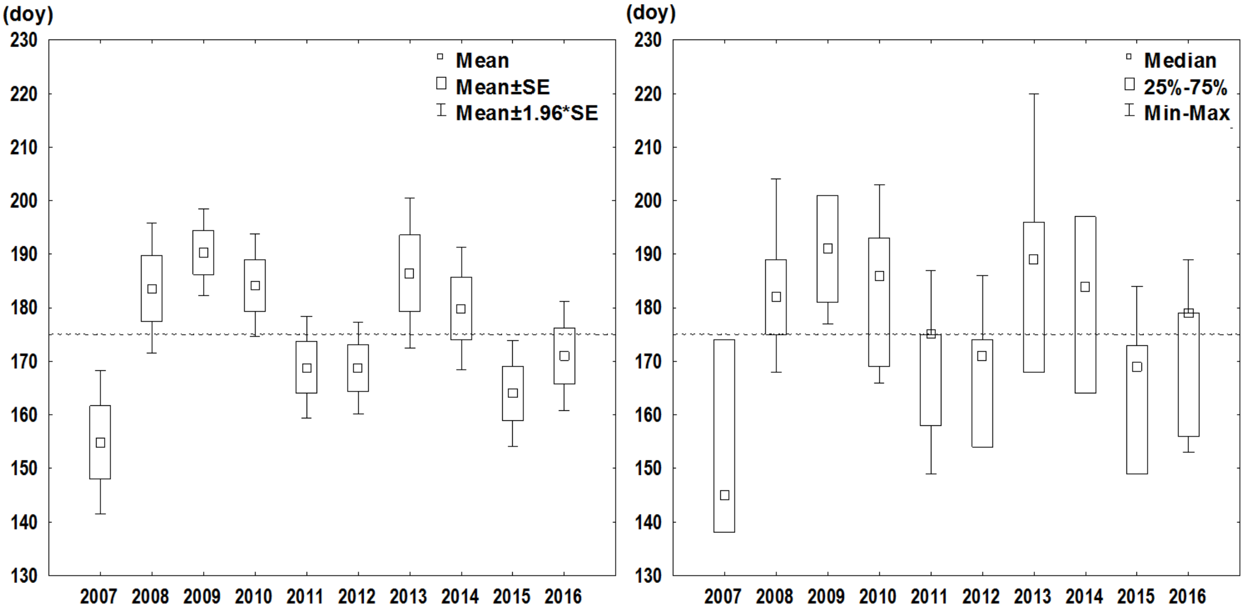


Figure III.5.B.b.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot (FS) for deciduous dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering the intra-annual variability, the earliest onset of FS (138 DOY, mid-May) was recorded in 2007, while the latest in 2009 (177 DOY, late June) (Table III.5.B.b.2). The FS completion was achieved from late June (174 DOY, in 2007) to early August (220 DOY, in 2013).

For this growth form, the total duration of FS ranged from 24 days (in 2009) to 52 days (in 2013), while the duration of the FS peak lasted from 14 days (in 2008) to 36 days (in 2007) (Table III.5.B.b.2).

Considering the anomalies of the 75% quartiles over the whole study period, the FS showed a large variability, with comparable advances of their 75% in 2007, 2011, 2012 and 2015, all without statistically significance, as tested by t-test (p>0.05).

Table III.5.B.b.2. Non-parametric statistics of first shoot (FS) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	7	155	138	138	145	174	174	18.1
2008	5	184	168	175	182	189	204	13.8
2009	6	190	177	181	191	201	201	10.1
2010	7	184	166	169	186	193	203	12.9
2011	7	169	149	158	175	175	187	12.8
2012	7	169	154	154	171	174	186	11.5
2013	7	186	168	168	189	196	220	18.9
2014	7	180	164	164	184	197	197	15.5
2015	7	164	149	149	169	173	184	13.3
2016	7	171	153	156	179	179	189	13.8
2007-2016	67	175	138	164	174	187	220	17.2

Considering thus the whole period (2007-2016) the analysis of FS with time did not reveal any statistically significant trend, as tested by linear regression (p>0.05).

However, as tested by linear regression, at the inter-annual level we found a statistically significant relation between FS and SM (β=1.0, R2=0.99, p<0.01).

Deciduous shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FS of deciduous shrubs (i.e. *Vaccinium uliginosum*) (Fig. III.5.B.b.6) exhibited statistically significant differences among years (F=4, p<0.01) (Fig. III.5.B.b.7).

Table III.5.B.b.3. Non-parametric statistics of first shoot (FS) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	4	159	138	138	159	179	179	23.7
2008	2	175	175	175	175	175	175	
2009	4	183	170	176	181	191	201	12.9
2010	4	166	161	161	164	171	175	6.6
2011	4	155	149	149	154	161	163	6.9
2012	4	154	147	151	154	158	162	6.1
2013	4	167	164	164	166	170	172	3.8
2014	4	159	150	154	161	164	164	6.7
2015	4	145	132	135	144	156	162	13.2
2016	4	155	149	151	155	159	162	5.5
2007-2016	38	161	132	150	162	170	201	14.2

Over the study period (2007-2016), according to the mean and median values, the FS occurred at early June (respectively 161 and 162 DOY), while its 75% quartile coincided to mid-June (170 DOY) (Table III.5.B.b.3).

Considering the intra-annual variability, the earliest onset of FS (132 DOY, mid-May) was recorded in 2015, while the latest in 2008 (175 DOY, late-June). The FS completion showed a comparable variability, with a range of variation of 39 days, from mid-June (162 DOY, in 2012, 2015 and 2016) to mid-July (201 DOY, in 2009) (Table III.5.B.b.3).

In 2008 only 50% of the data were collected which resulted in absence of variances of the data (due to the problem of the lepidopter masting, see methods): this year all the statistics occurred at 175 DOY (Table III.5.B.b.3), therefore we did not consider this year for the analysis of range and peak duration.

The total duration of FS for deciduous shrubs ranged from only 8 days (in 2013) to 41 days (in 2007). Similarly, the FS peak lasted from only 6 days (in 2013) up to 41 days (in 2007) (Fig. III.5.B.b.7).

Figure III.5.B.b.6. Example of FS on *Vaccinium uliginosum.*

Considering the anomalies of the 75% quartiles, the FS showed the largest delay in 2009 (+21 days), and the greatest advance in 2015 (-15 days) (Fig. III.5.B.a.7). As tested by t-test, the delay of 2009 was identified as statistically significant ($p<0.01$), and we thus removed this year from trend of FS with time.

Analyzing only the “normal” years (excluding 2009 as “extreme” year) we did not find any statistically significant trend of FS with time, as tested by linear regression ($p>0.05$).
The patterns of FS also for deciduous shrubs were related to those of SM. Tested by linear regression at the inter-annual level, we found a statistically significant relation between FS and SM ($\beta=1.0$, $R^2=0.98$, $p<0.01$).

According to the relation between FS and SM, and considering that the 75% quartiles of SM exhibited statistically significant trends with time, we then tested whether analyzing the 75% quartiles any trend could be identified. We observed a statistically significant advance of the 75% quartiles of FS (β=-2.1 days/year, $R^2=0.59$, $p=0.03$), likewise SM (Fig III.5.B.b.8).

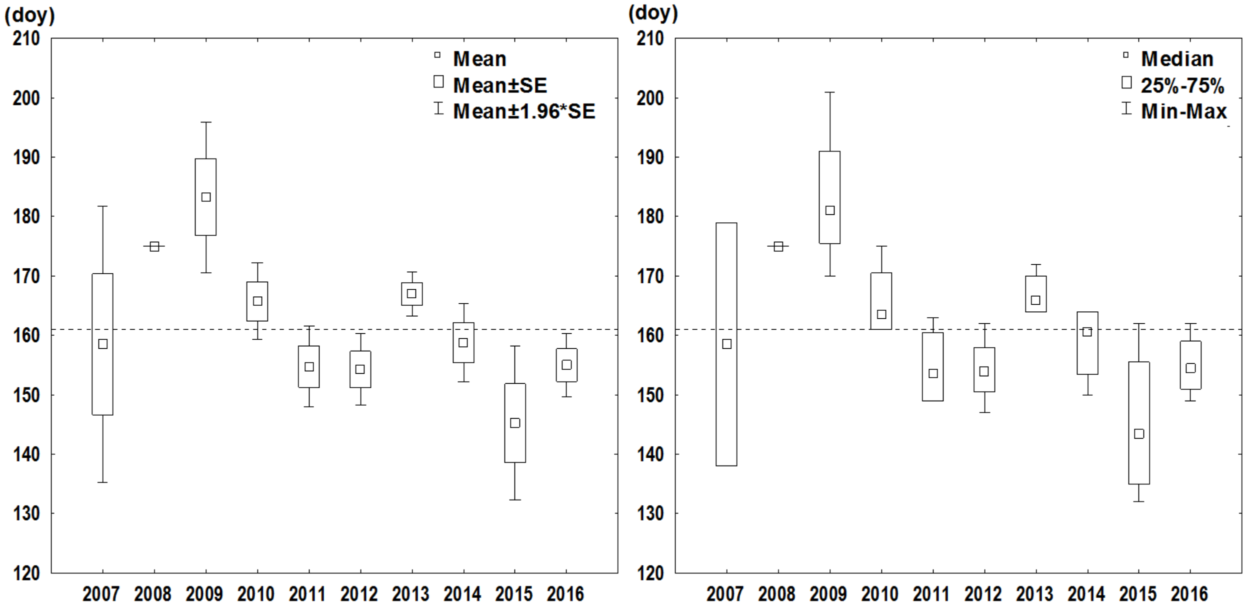


Figure III.5.B.b.7. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot (FS) for deciduous shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

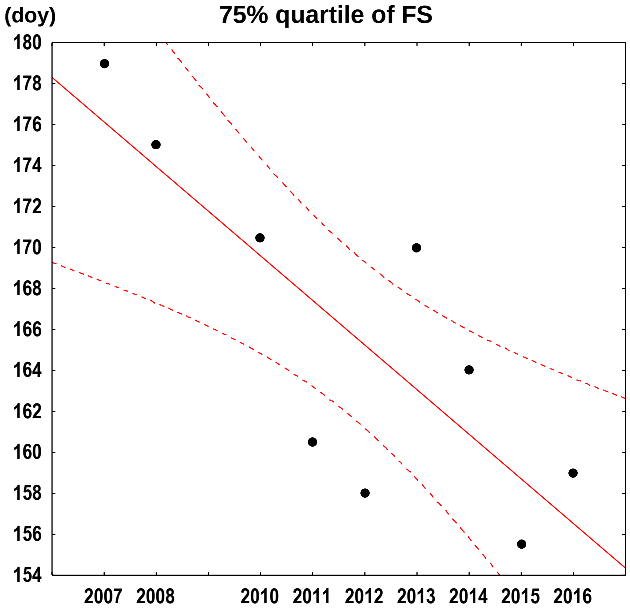


Figure III.5.B.b.8. Trend with time of the 75% quartiles FS (β=-2.1, $R^2=0.59$, $p=0.03$) for deciduous shrubs, as tested by linear regression on normal years.

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FS of evergreen dwarf shrubs (i.e. *Empetrum hermaphroditum* and *Kalmia procumbens*) (Fig. III.5.B.b.9) exhibited statistically significant differences among years (F=28, p<0.01) (Fig. III.5.B.b.10).

Over all the study period (2007-2016), according to the mean and median values, the FS of the evergreen dwarf shrubs occurred at mid-June (respectively 161 and 163 DOY), and one week later was recorded the 75% quartile (170 DOY) (Table III.5.B.b.4).

Table III.5.B.b.4. Non-parametric statistics of first shoot (FS) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev..**
2007	8	138	138	138	138	138	141	1.1
2008	5	181	164	182	184	184	189	9.6
2009	6	174	170	170	174	177	181	4.8
2010	9	170	161	169	169	175	175	4.9
2011	9	153	149	149	149	153	163	6.1
2012	9	157	147	154	154	162	165	6.1
2013	9	171	164	168	172	172	176	4.5
2014	9	165	150	164	164	168	173	7.0
2015	9	156	138	149	162	162	162	8.7
2016	9	160	149	153	162	163	169	7.2
2007-2016	82	161	138	153	163	170	189	12.5

Photo III.5.B.b.9. Example of FS on a) *Kalmia procumbens* and b) *Empetrum hermaphroditum.*

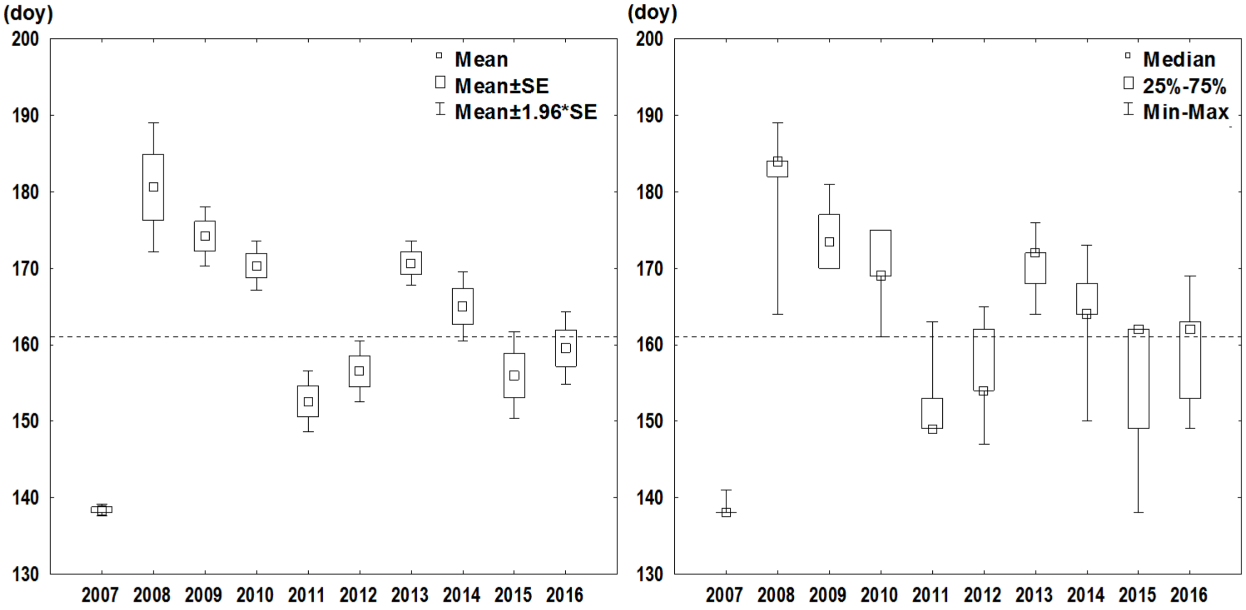


Figure III.5.B.b.10. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot (FS) for evergreen dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering the intra-annual variability, the earliest onset of FS (138 DOY, mid-May) was recorded in 2007 and 2015, while the latest in 2009 (170 DOY, mid-June) (Table III.5.B.b.4). The FS completion showed a range of variation of 48 days, from late May (141 DOY, in 2007) to early July (189 DOY, in 2008).

Similarly to SM, in 2007 our FS data showed a very low variance, possibly due to the scarcity of snow cover during this anomalous year (according to the t-test results reported below). However to avoid underestimation we did not consider such data to extrapolate information about the range and peak duration of FS (Table III.5.B.b.4).

Therefore, without considering 2007, the total duration of FS for evergreen dwarf shrubs ranged from 11 days (in 2009) to 24 days (in 2015), thus showing a variability of almost two weeks. The FS peak duration was concentrated to only 2 days (in 2008) or to 13 days maximum (in 2015) (Fig. III.5.B.b.10).

Analyzing the anomalies of the 75% quartiles, FS showed the largest advance in 2007 (-32 days) (Fig. III.5.B.b.10). Indeed, 2007 was the only year with a statistically significant advance according to the t-test ($p<0.01$) and was thus identified as “extreme” year (Fig. III.5.B.b.10).

Considering only “normal” years (2008-2016) the evergreen dwarf shrubs did not show any statistically significant trend of the FS with time ($p>0.05$).

However, they showed a high statistically significant relation between FS and SM, as tested by linear regression at inter-annual level ($\beta=1.0$, $R^2=0.99$, $p<0.01$). Therefore, considering the statistically significant advance of the earliest onset of SM, also in this case we tested by linear regression the existence of eventual trends of FS with time detectable at different levels of our population data. Our analyses indicated a statistically significant advance of the earliest FS (β=-2.7, R^2=0.51, p=0.03) (Fig. III.5.B.b.11).

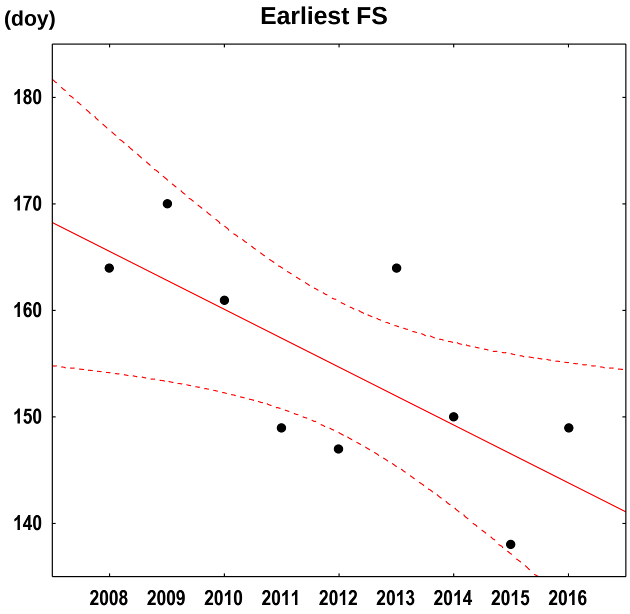


Figure III.5.B.b.11. Trend with time of the earliest FS (β=-2.7, R^2=0.51, p=0.03) for the evergreen dwarf shrubs, as tested by linear regression on the "normal" years.

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FS of evergreen shrubs (i.e. *Rhododendron ferrugineum* and *Juniperus communis*) (Fig. III.5.B.b.12) exhibited statistically significant differences among years (F=18, p<0.01) (Fig. III.5.B.b.13).

Table III.5.B.b.5. Non-parametric statistics of first shoot (FS) for evergreen shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	8	143	138	138	138	140	174	12.6
2008	6	177	168	168	177	182	188	8.5
2009	7	175	170	170	170	181	181	5.9
2010	8	166	161	161	166	169	174	4.7
2011	8	151	148	149	149	149	163	5.0
2012	8	153	147	147	154	154	165	6.0
2013	8	168	164	164	168	168	176	4.0
2014	8	161	150	159	161	164	173	6.5
2015	8	148	132	142	148	154	162	9.4
2016	8	154	149	151	153	155	169	6.3
2007-2016	77	159	132	149	161	168	188	12.8

Figure III.5.B.b.12. Example of FS on a) *Juniperus nana* and b) *Rhododendron ferrugineum.*

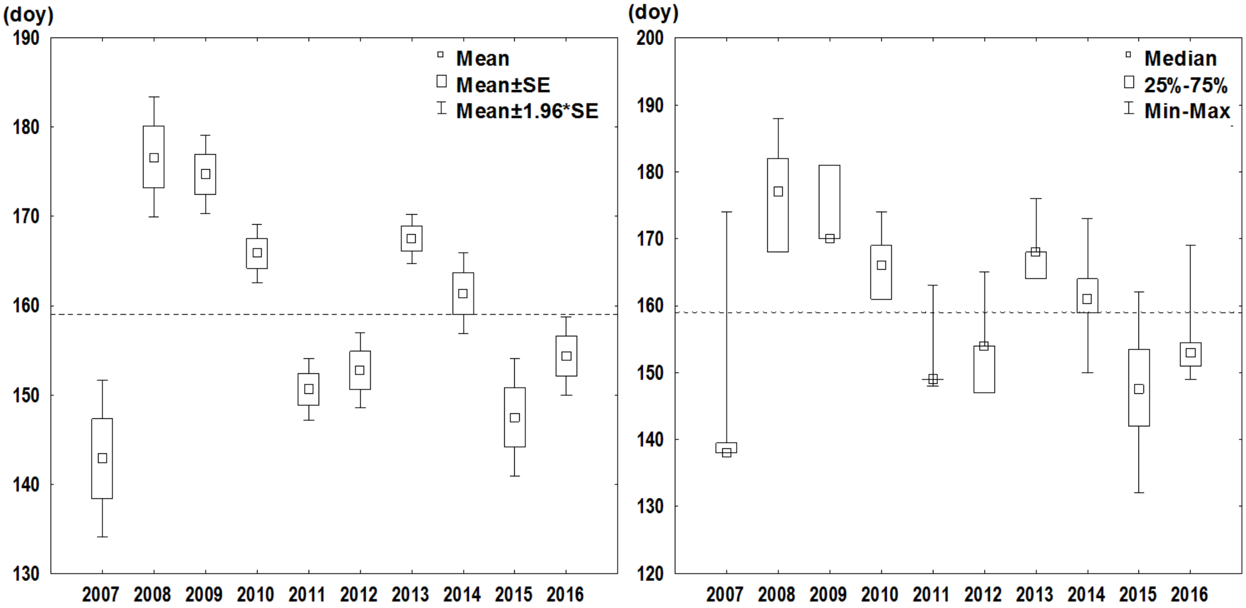


Figure III.5.B.b.13. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot (FS) for evergreen shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Over all the study period (2007-2016), according to the mean and median values, the FS for the evergreen shrubs occurred at the beginning of June (respectively 159 and 161 DOY), while the 75% corresponded to mid-June (168 DOY) (Table III.5.B.b.5).

Considering each single year, the earliest onset of FS (132 DOY, mid-May) was recorded in 2015, while the latest in 2009 (170 DOY, mid-June) (Table III.5.B.b.5). The FS completion ranged from mid- June (162 DOY, in 2015) to the beginning of August (188 DOY, in 2008).

The total duration of FS for the evergreen shrubs ranged from 11 days (in 2009) to 36 days (in 2007). The duration of the FS peak ranged from 0 to 12 days maximum (respectively in 2011 and 2015), showing thus a very similar pattern to SM (Fig. III.5.B.b.13).

Considering the anomalies of the 75% quartiles, the FS showed the largest advance in 2007 (-29 days), even without any statistically significance, according to t-test ($p>0.05$) (Fig. III.5.B.b.13).
Analyzing thus all the study period (2007-2016) we did not find any statistically significant trend of the FS with time for evergreen shrubs, as tested by linear regression ($p>0.05$), similarly to what found for the SM.
However, as tested by linear regression at inter-annual level, FS and SM showed a statistically significant relation also for the evergreen shrubs ($\beta=1.0$, $R^2=0.99$, $p<0.01$).

Figure III.5.B.b.14. Example of FS on a) *Senecio carniolicus* and b) *Geum reptans.*

Forbs

Considering all the study period, also forbs exhibited statistically significant differences among years, as tested by one-way ANOVA ($F=47$, $p<0.01$) (Fig. III.5.B.b.14-15).

The mean and median values of FS over the whole period (2007-2016) were coincident corresponding to late-June (178 DOY), while the 75% quartile of the FS occurred at early July (189 DOY) (Table III.5.B.b.6).

The beginning of FS occurred since mid-May (132 DOY, in 2015) up to mid-June (170 DOY, in 2009), while the end of FS ranged from late June (179 DOY, in 2007) to late August (233 DOY, in 2014) (Table III.5.B.b.6).

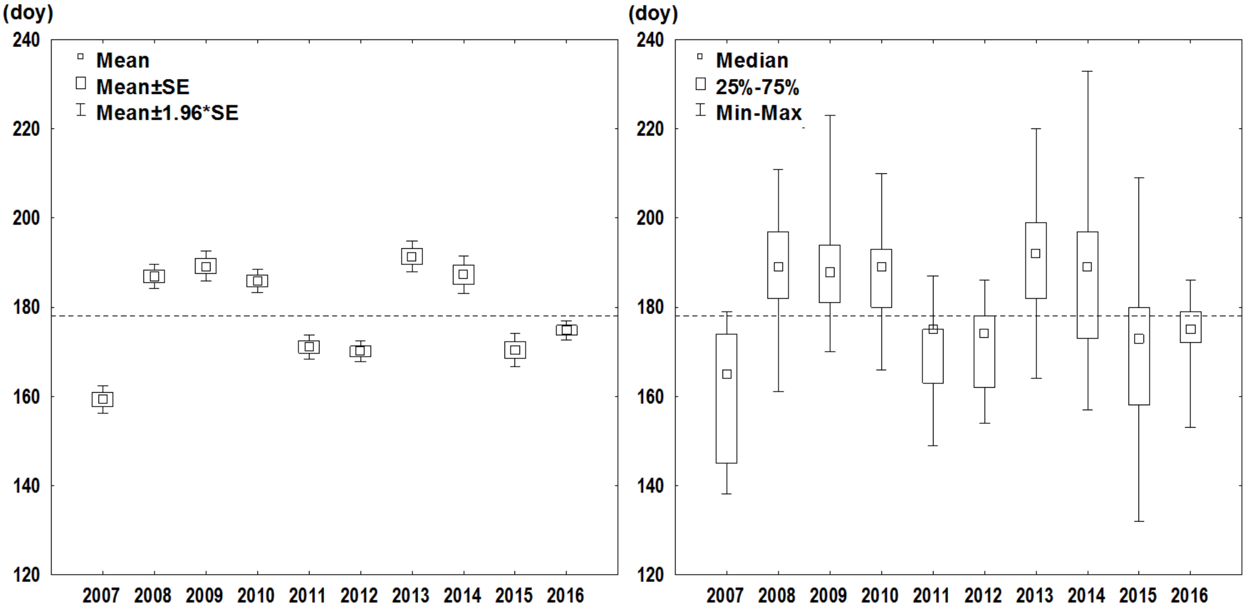


Figure III.5.B.b.15. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot (FS) for forbs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

The length of FS lasted from 32 days (in 2012) to a maximum of 77 days (in 2015), while the duration of the FS peak ranged from only 7 days (in 2016) to 29 days (in 2007) (Table III.5.B.b.6).

Comparing the 75% anomalies, forbs showed comparable advances in 2007 and 2011 (-15 and -14 days), while the largest delay was recorded in 2013 (+10 days). However, as tested by t-test, the differences among years were not statistically significant (Fig III.5.B.b.15).

Table III.5.B.b.6. Non-parametric statistics of first shoot (FS) for forbs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	159	138	145	165	174	179	12.6
2008	54	187	161	182	189	197	211	10.4
2009	62	189	170	181	188	194	223	13.4
2010	67	186	166	180	189	193	210	11.0
2011	67	171	149	163	175	175	187	11.3
2012	67	170	154	162	174	178	186	9.6
2013	66	191	164	182	192	199	220	14.2
2014	65	187	157	173	189	197	233	17.4
2015	66	170	132	158	173	180	209	15.2
2016	66	175	153	172	175	179	186	9.1
2007-2016	643	178	132	168	178	189	233	16.3

Similarly to SM, we did not observe any statistically significant trend with time for the forbs FS, considering the whole period (2007-2016), as tested by linear regression (p>0.05).

However, tested by linear regression at inter-annual level, FS and SM showed a statistically significant relation also for forbs (β=1.0, R2=0.98, p<0.01).

Graminoids

As tested by one-way ANOVA, overall the study period (2007-2016) the FS of graminoids (Fig. III.5.B.b.16) exhibited statistically significant differences among years (F=23, p<0.01) (Fig. III.5.B.b.17).

Over the study period (2007-2016), according to the mean and median values, the FS occurred at mid-June (respectively 170 and 169 DOY), while at the end of June (180 DOY) the 75% of the graminoids started FS (Table III.5.B.b.7).

Table III.5.B.b.7. Non-parametric statistics of first shoot (FS) for graminoids computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	38	151	138	138	145	165	179	15.0
2008	31	180	161	175	175	189	204	12.7
2009	34	183	170	177	181	188	216	13.1
2010	38	178	161	169	175	189	203	11.7
2011	38	162	149	149	163	175	187	13.0
2012	38	163	147	154	158	174	186	10.7
2013	38	182	168	168	174	192	220	15.1
2014	37	176	161	164	168	189	233	18.2
2015	37	162	138	149	158	173	203	13.8
2016	37	167	149	159	162	175	186	10.7
2007-2016	366	170	138	161	169	180	233	16.9

Figure III.5.B.b.16. Example of FS on a) *Carex curvula* and b) *Luzula alpinopilosa*.

Considering the intra-annual variability, the earliest onset of FS occurred between mid-May (138 DOY, in 2007 and 2015) and mid-June (170 DOY, in 2009) (Table III.5.B.b.7), while the latest FS was recorded from late June (179 DOY, in 2007) to mid-August (233 DOY, in 2014).

For graminoids, the total duration of FS ranged from 37 days (in 2016) to 72 days the year before (in 2014). On the contrary, the peak duration of FS was concentrated to 11 days only (in 2009) or to 27 days maximum (in 2007) (Fig. III.5.B.b.17).

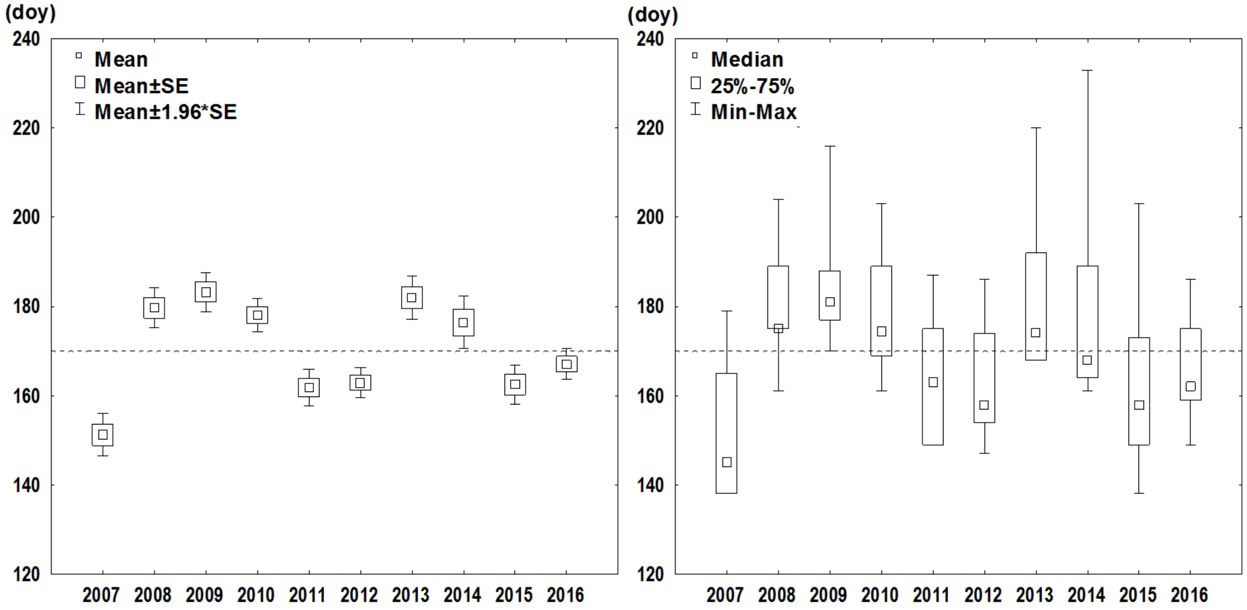


Figure III.5.B.b.17. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot (FS) for graminoids from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering the anomalies of the 75% quartiles, in 2007 the FS advanced of 15 days, while in 2013 it delayed of 12 days, although in both cases without statistically significance, as tested by t-test ($p>0.05$).

As tested by linear regression at the inter-annual level, we found also for graminoids a high statistically significant relation between FS and SM ($\beta=1.0$, $R^2=0.99$, $p<0.01$).

Likewise SM, also FS showed a statistically significant advance in 2007, as tested by t-test ($p<0.01$). Considering thus only the “normal” years period (2008-2016) we observed a statistically significant advance of the FS with time, as tested by linear regression ($\beta=-2.1$, $R^2=0.45$, $p=0.05$) (Fig. III.5.B.b.18).

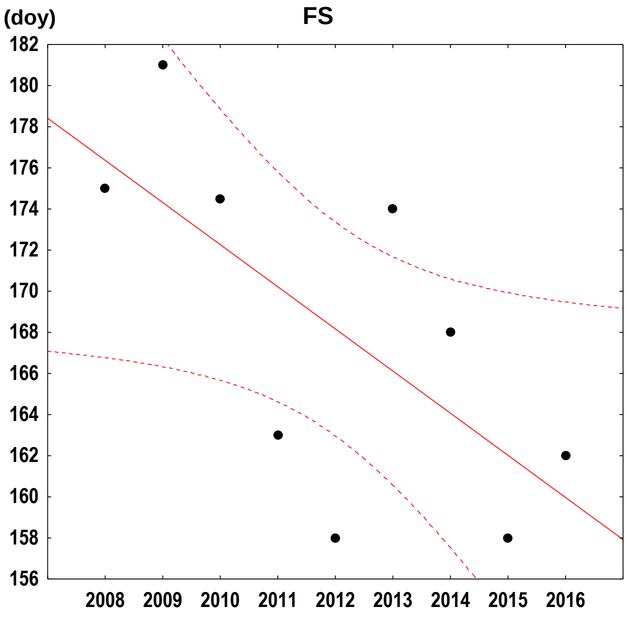


Figure III.5.B.b.18. Trend with time of the FS (β=-2.1, R^2=0.45, p=0.05) for graminoids, as tested by linear regression on the "normal" years period.

Comparison of trends among growth forms

Analogously to SM, when analyzing the trends of FS for all the study period (2007-2016) comparing the different growth forms, there was a large and statistically significant variability (Fig. III.5.B.b.19), as tested by one-way ANOVA (F=42, p<0.01).

Deciduous shrubs, evergreen dwarf shrubs and evergreen shrubs showed earlier FS respect the other growth forms (Fig. III.5.B.b.19). Indeed, according to the 75% quartiles, the FS for these growth forms occurred respectively -14, -14 and -16 days before the 75% referred to the whole dataset, although these differences were not statistically significant, as tested by t-test (p>0.05).

The patterns of FS among growth forms were comparable with those of SM. Therefore, as for the SM, the completion of FS occurred earlier for the evergreen shrubs and evergreen dwarf shrubs, while the latest FS occurred for forbs and graminoids. However, also in this case the observed differences were not statistically significant, as tested by t-test (p>0.05).
Considering the herbaceous growth forms, interestingly forbs showed the latest FS (+5 days according to 75% quartiles anomalies), which corresponded to 9 days later respect graminoids.

The total duration of FS (provided by its range) showed also a wide range of variability, with forbs, graminoids and deciduous dwarf shrubs completing this phenophase within almost 3 months, while deciduous shrubs, evergreen dwarf shrubs and evergreen shrubs needed a shorter time (approximately 2 months).

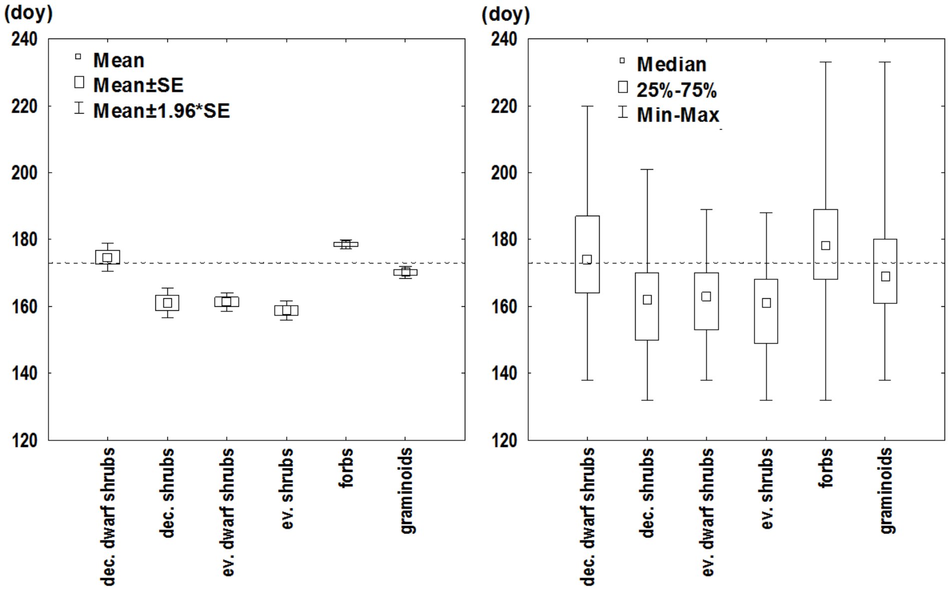


Figure III.5.B.b.19. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot (FS) between different growth forms over the period 2007-2016. The dotted black line represents the mean value for the whole period.

Similarly to SM, also the earliest onset of FS exhibited an advance at the inter-specific level over the study period. The selected growth forms displayed great differences considering their FS trends with time.

FS patterns always exhibited a statistically significant relation with SM both at inter-specific level (Fig. III.5.B.b.3) as well as when analyzing each single growth form, highlighting that, despite our observed trend of SM with time over the study period was not statistically significant for all the growth forms, more significant changes in SM pattern could impact FS stages.

Our findings emphasized that deciduous dwarf shrubs, evergreen shrubs and forbs did not advance their FS, highlighting that they were the growth forms less sensitive towards an earlier start of the growing season.

Conversely, deciduous shrubs, evergreen dwarf shrubs and graminoids showed a statistically significant advance of FS (likewise SM) over the study period, even if with different slope coefficients and population size parameters. Graminoids advanced their FS (median) at the same rate of the advance of the 75% quartile (thus a larger part of the population data) of deciduous shrubs. Evergreen dwarf shrubs advanced their onset of FS at faster rate (comparable to the trend for all the dataset).

III.5.B.c. *Patterns of New Leaf unfolding*

As for the other phenophases, our analyses have been carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2007-2016), NL exhibited a large inter-annual variability, with statistically significant differences, as tested by one-way ANOVA (F=53, $p<0.01$) (Fig. III.5.B.c.1).

The mean and median values of onset of NL were coincident at the end of June (179 DOY) while its 75% quartile occurred c.10 days later (Table III.5.B.c.1).

Table III.5.B.c.1. Non parametric statistics of new leaf (NL) for deciduous growth forms (i.e. deciduous dwarf shrubs, deciduous shrubs, forbs, graminoids) computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev.**
2007	109	167	138	157	174	179	193	14.9
2008	90	190	168	182	189	197	217	11.1
2009	106	189	170	181	188	201	223	13.0
2010	116	186	166	180	186	193	218	11.2
2011	116	169	149	163	169	178	197	12.7
2012	116	170	147	162	171	178	197	11.1
2013	115	188	164	172	189	199	227	15.4
2014	113	184	157	168	177	197	233	17.6
2015	114	171	138	162	169	180	212	14.5
2016	114	177	153	172	179	181	195	8.4
2007-2016	1109	179	138	168	179	189	233	15.8

Considering each single year, the earliest NL unfolding was recorded in 2007 and 2015 in mid-May (138 DOY), while the latest in 2009 corresponded to almost one month later (170 DOY). The completion of NL formation was recorded between early July (193 DOY, in 2007) and mid-August (233 DOY, in 2014) (Table III.5.B.c.1).

According to the 75% quartile, the t-test did not identify years with statistically significant differences ($p>0.05$). Thus analyzing the whole dataset, we did not find any statistically significant trend with time, tested by linear regression ($p>0.05$).

As already emphasized for FS, also NL exhibited important relations with SM. Indeed, as tested by linear regression at inter-annual level, there was a statistically significant relation between SM and NL ($\beta=0.9$, $R^2=0.88$, $p<0.01$; Fig. III.5.B.c.2).

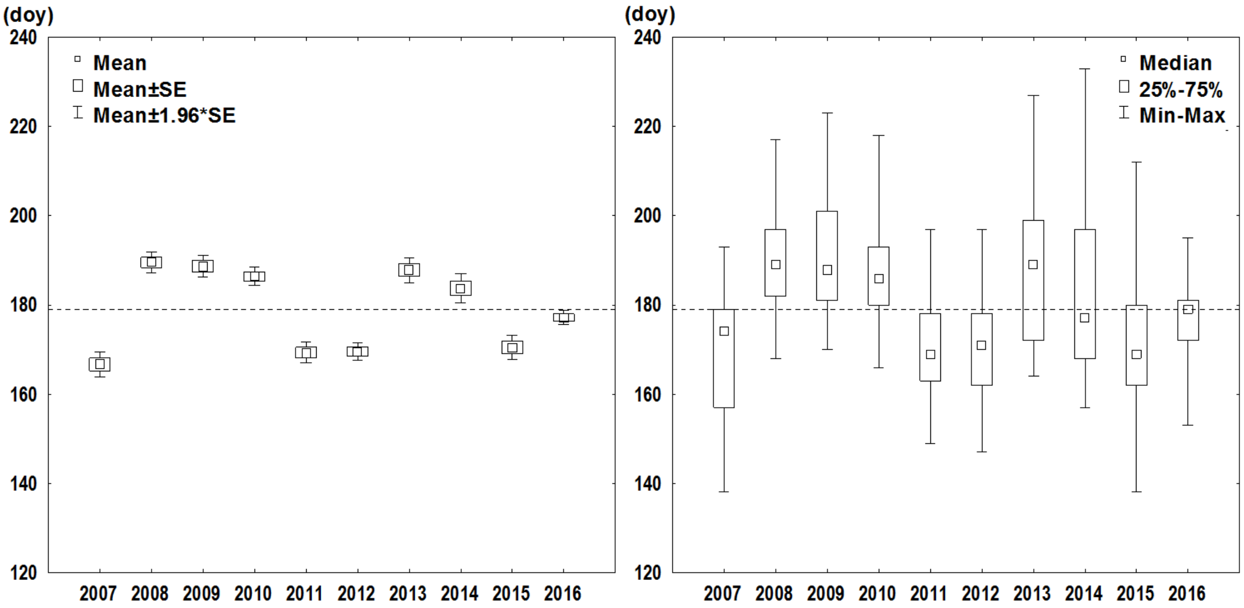


Figure III.5.B.c.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of new leaf (NL) for deciduous species (i.e. deciduous dwarf shrubs, deciduous shrubs, forbs, graminoids) from 2007 to 2016. The dotted black line represents the mean value for the whole period.

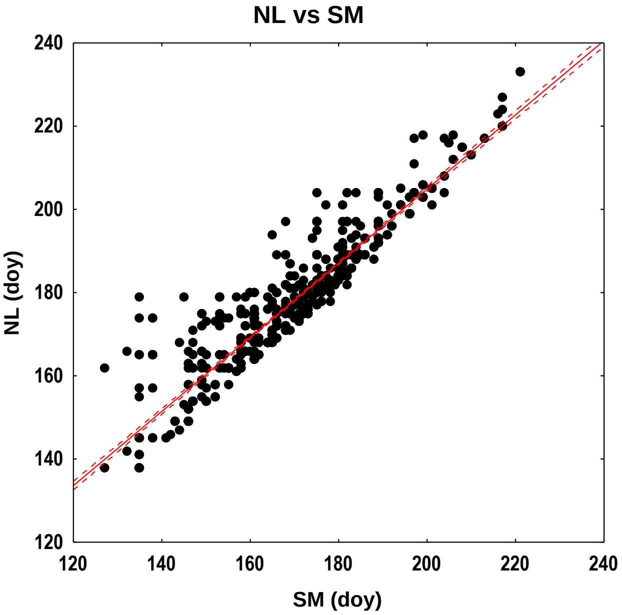


Figure III.5.B.c.2: Relation between NL (DOY) and SM (DOY) for the deciduous growth forms, at inter-annual and inter-species level, as tested by linear regression (β=0.9, R^2=0.88, p<0.01).

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the NL of deciduous dwarf shrubs (i.e. *Salix herbacea*) (Fig. III.5.B.c.3) exhibited statistically significant differences among years (F=3, p<0.01) (Fig. III.5.B.c.4).

Table III.5.B.c.2. Non-parametric statistics of new leaf (NL) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev.**
2007	6	169	145	157	177	179	179	14.5
2008	5	188	175	182	182	197	204	12.0
2009	6	194	181	184	198	201	205	9.9
2010	7	194	180	180	193	203	218	13.2
2011	7	180	163	163	187	187	197	13.2
2012	7	178	165	168	178	182	197	10.4
2013	7	193	176	176	196	199	227	18.2
2014	7	188	173	175	189	204	204	13.9
2015	7	175	162	162	176	184	191	10.8
2016	7	183	172	172	186	195	195	10.3
2007-2016	66	184	145	175	182	195	227	14.5

Figure III.5.B.c.3. Example of NL for a) *Vaccinium uliginosum* and b) *Salix herbacea.*

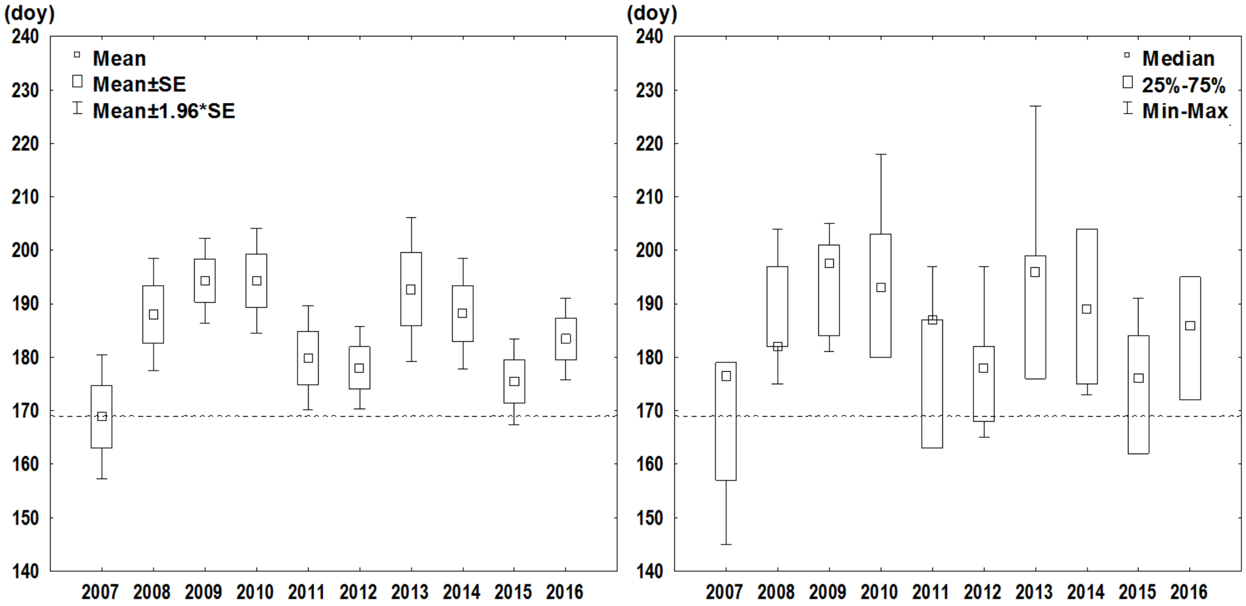


Figure III.5.B.c.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of new leaf (NL) for deciduous dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Over the study period (2007-2016), according to the mean and median values, the NL occurred at early July (respectively 184 and 182 DOY), while the 75% quartiles corresponded to mid-July (195 DOY, 12 days later than the 75% quartile of FS) (Fig. III.5.B.c.4).

Considering the intra-annual variability, the earliest NL onset (145 DOY, late May) was recorded in 2007, while the latest (181 DOY, end of June) in 2009. The NL completion ranged from late June (179 DOY, in 2007) to mid-August (227 DOY, in 2013) (Table III.5.B.c.2).

For this growth form, the total duration of NL ranged from 23 days (in 2016) to 51 days (in 2013), while the NL peak duration ranged from 14 days (in 2012) to 29 days maximum (in 2014) (Table III.5.B.c.2).

According to the anomalies of the 75% quartiles over the whole period (2007-2016), the greatest advance of NL was recorded in 2007 (-16 days). However we did not identify any extreme years, as tested by t-test ($p>0.05$).

Considering thus the whole period (2007-2016), the analysis of NL with time did not reveal any statistically significant trend, as tested by linear regression.
However, when considering the linear regression between NL and SM at inter-annual level, we found a high statistically significant relation ($\beta=0.8$, $R^2=0.99$, $p<0.01$).

Deciduous shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the NL of deciduous shrubs (i.e. *Vaccinium uliginosum*) (Fig. III.5.B.c.3) exhibited statistically significant differences among years (F=8, p<0.01) (Fig III.5.B.c.5).

Table III.5.B.c.3. Non-parametric statistics of new leaf (NL) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	3	188	179	179	193	193	193	8.1
2008	2	182	182	182	182	182	182	-
2009	4	193	181	183	193	203	205	12.0
2010	4	182	180	180	180	183	186	3.0
2011	4	169	163	163	169	175	175	6.9
2012	4	168	165	165	167	171	174	4.2
2013	4	175	172	174	176	176	176	2.0
2014	4	174	171	172	174	175	175	1.9
2015	4	168	162	164	166	171	176	6.0
2016	4	178	175	177	179	179	179	2.0
2007-2016	37	177	162	172	176	180	205	9.8

Over the study period (2007-2016), according to the mean and median values, the NL occurred in late June (respectively 177 and 176 DOY), and the 75% quartile occurred few days later (180 DOY) (Fig. III.5.B.c.4).

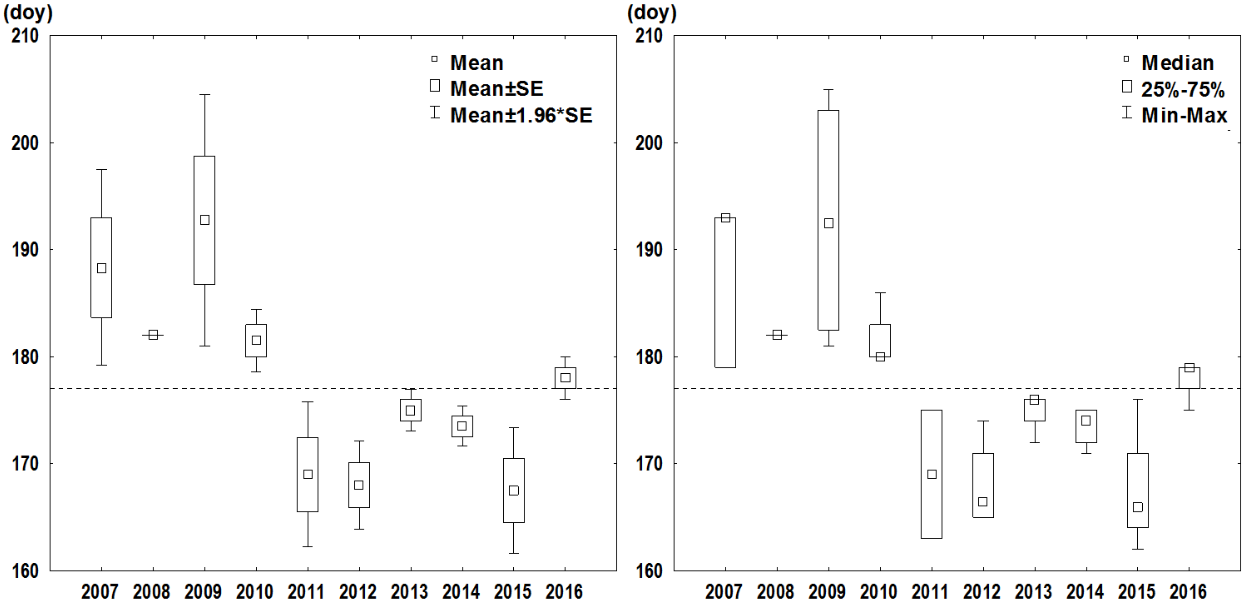


Figure III.5.B.c.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of new leaf (NL) for deciduous shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

The earliest onset of NL (162 DOY, mid-June) was recorded in 2015, while the latest in 2008 (182 DOY, beginning of July), while the latest NL completion spanned from late June (174 DOY, in 2012) to late July (205 DOY, in 2009) (Table III.5.B.c.3).

Similarly to FS, also for NL in 2008 few data were collected (only 50%), due to the impacts of the masting event of a defoliator lepidopter (see method) (Fig. III.5.B.c.6), which resulted in absence of NL variance for this year (Table III.5.B.c.3). For this reason, we did not consider this year for the analysis of range and peak duration.

Figure III.5.B.c.6. Effects of grazing on *Vaccinium uliginosum* of the lepidopter *Zygena alpina*.

The total duration of NL for deciduous shrubs extended from only 4 days (in 2013, 2014 and 2016) to 24 days (in 2009). Similarly, the NL peak duration ranged from only 2 days (in 2013 and 2016) up to 21 days maximum (in 2009) (Fig. III.5.B.c.5).

Considering the anomalies of the 75% quartiles, the NL showed the largest delay in 2009 (+23 days), which was also the only one year identified as statistically significant different, tested by t-test ($p<0.01$).
A largest and statistically significant delay in 2009 was recorded also for FS (Fig. III.5.B.b.7). Possibly the observed delay of the greening development (FS and NL) detected in this year could be attributable to the "extreme" delay of SM in 2009 recorded for deciduous shrubs (Fig. III.5.B.a.6). Indeed, considering all the dataset (2007-2016) we found a statistically significant relation between NL and SM at inter-annual level, as tested by linear regression ($\beta=0.8$, $R^2=0.67$, $p<0.01$).

Therefore, we evaluated NL trend with time only for "normal" years (thus removing 2009, identified as "extreme"). We did not find a statistically significant trend of NL with time, as tested by linear regression (p>0.05). However, we observed a statistically significant advance when considering the 75% quartile of NL (β=-1.6, R^2=0.51, p=0.03), as in this case the trend became evident when considering a larger part of the population data (Fig III.5.B.c.7).

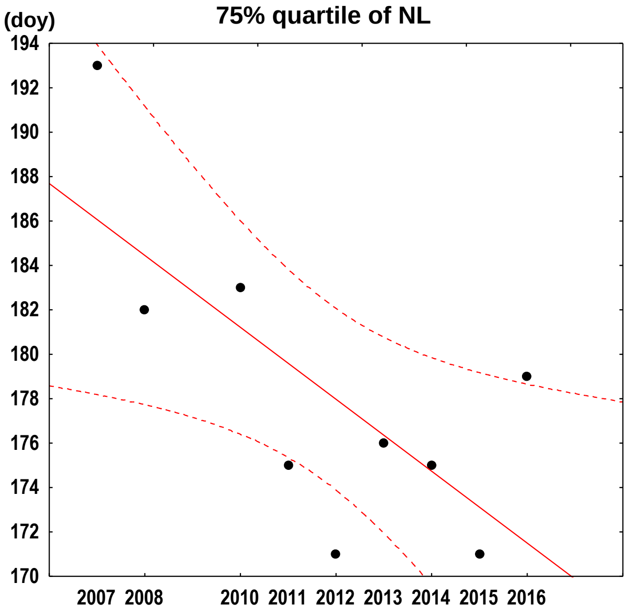


Figure III.5.B.c.7. Trend with time of the 75% quartiles of NL (β=-1.6, R^2=0.51, p=0.03) for deciduous shrubs, as tested by linear regression.

Forbs

Over the period 2007-2016, NL showed a large and statistically significant variability, according to one-way ANOVA (F=35, p<0.01) (Fig. III.5.B.c.7-8).

Table III.5.B.c.4. Non-parametric statistics of NL for forbs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	170	138	165	174	174	193	11.2
2008	52	192	168	182	189	201	217	10.7
2009	62	190	170	181	188	194	223	12.7
2010	67	188	166	180	189	193	218	10.7
2011	67	172	149	163	175	181	192	11.3
2012	67	172	154	165	174	178	190	10.0
2013	66	191	164	182	192	199	224	14.4
2014	65	188	157	175	189	197	233	16.8
2015	66	173	138	162	176	184	212	14.8
2016	66	179	159	175	179	181	189	7.6
2007-2016	641	181	138	174	181	189	233	14.9

Figure III.5.B.c.7. Example of NL in *Leucanthemopsis alpina.*

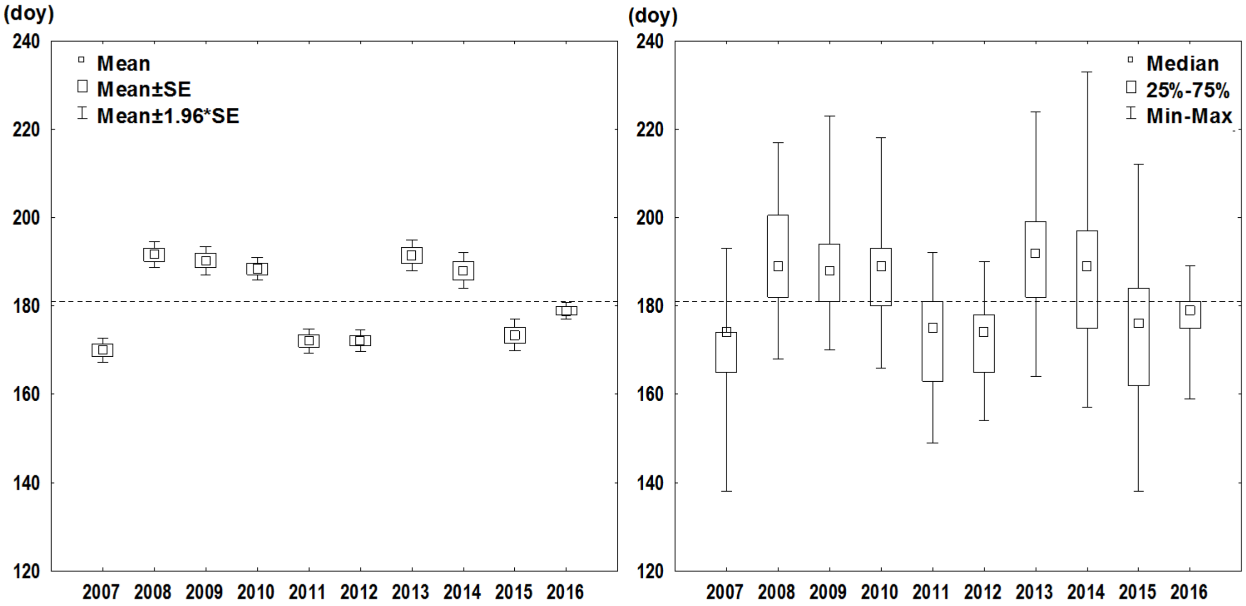


Figure III.5.B.c.8. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of NL for forbs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

According to mean and median values, NL occurred at the end of June (181 DOY), while the 75% corresponded to early July (189 DOY) (Table III.5.B.c.4).

The earliest NL onset was recorded in 2007 and 2015 (138 DOY, mid-May), while the latest in 2009 (170 DOY, mid-June) (Table III.5.B.c.4). The NL completion showed a large variability ranging between early July (189 DOY in 2016) and late August (233 DOY in 2014).

The total duration of NL ranged from a minimum of 30 days (in 2016) up to 76 (in 2014), while the NL peak duration lasted from only 6 days (in 2016) to 22 days in 2014 (Fig. III.5.B.c.8).

According to the 75% quartiles anomalies over the whole period, in 2007 NL advanced of 15 days, while in 2008 it was delayed of 12 days, although without statistically significant differences, as tested by t-test ($p>0.05$) (Fig. III.5.B.c.8).
Considering thus the whole dataset (2007-2016), we did not find any statistically significant trend with time, as tested by linear regression ($p>0.05$).
However, as confirmed by linear regression, we found a statically significant relation between NL and SM for forbs at inter-annual level ($\beta=0.9$, $R^2=0.90$, $p<0.01$).

Graminoids

As tested by one-way ANOVA, the NL inter-annual variability was statistically significant ($F=21$, $p<0.01$) (Fig. III.5.B.c.8-9).

Over the period 2007-2016, NL occurred towards late-June (173 DOY), according to mean and median values, while the 75% quartile occurred at the beginning of July (182 DOY) (Table III.5.B.c.5).

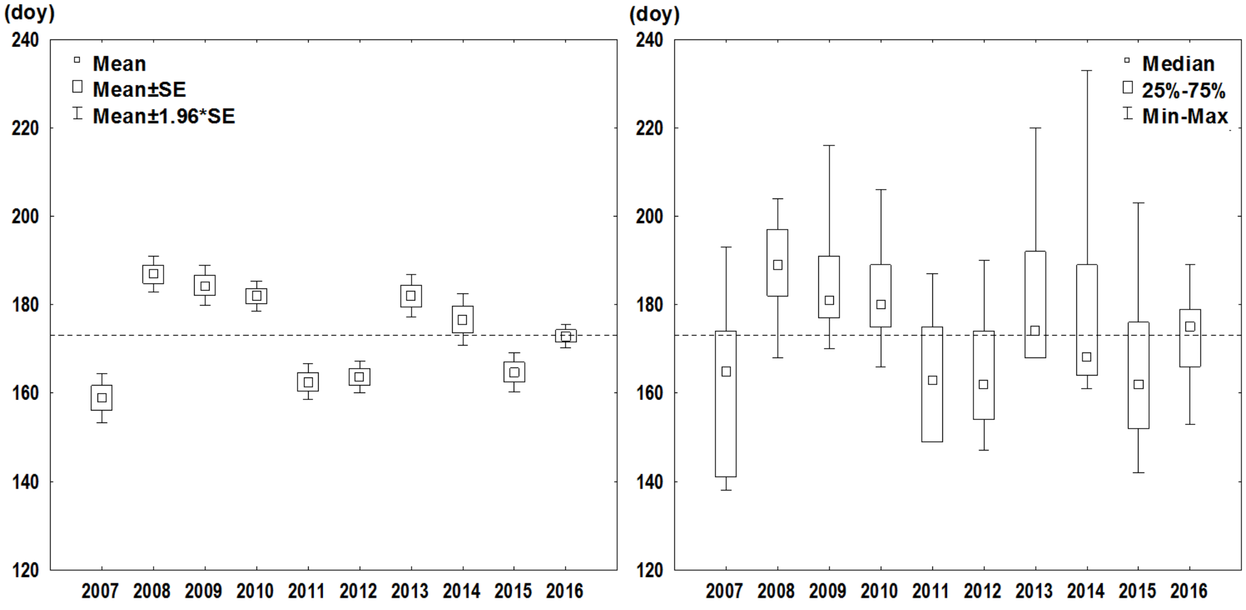


Figure III.5.B.c.8. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of NL for graminoids from 2007 to 2016. The dotted black line represents the mean value for the whole period.

The NL onset ranged between mid-May in 2007 (138 DOY) and mid-June in 2009 (170 DOY) (Table III.5.B.c.5). The NL completion ranged between early July (187 DOY in 2011) and late August (233 DOY, in 2014).

The duration of this phenophase exhibited a large variability, ranging from 36 days (in 2016) to 72 days (in 2014). The NL peak duration showed less variability, from 13 days (in 2016) to 33 days (in 2007) (Fig. III.5.B.c.8).

Table III.5.B.c.5. Non-parametric statistics of NL for forbs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	37	159	138	141	165	174	193	17.3
2008	31	187	168	182	189	197	204	11.5
2009	34	184	170	177	181	191	216	13.5
2010	38	182	166	175	180	189	206	10.6
2011	38	163	149	149	163	175	187	12.8
2012	38	164	147	154	162	174	190	11.3
2013	38	182	168	168	174	192	220	15.1
2014	37	177	161	164	168	189	233	18.2
2015	37	165	142	152	162	176	203	13.8
2016	37	173	153	166	175	179	189	8.2
2007-2016	365	173	138	163	173	182	233	16.5

Figure III.5.B.c.9. Example of NL in *Anthoxanthum alpinum.*

According to the 75% quartiles anomalies, the earliest NL occurred in 2007 and 2012 (advance of only -8 days) and the latest in 2008, with a delay of 15 days, although all without statistically significant differences, as tested by t-test ($p>0.05$).
Analyzing the whole study period, we did not find any statistically significant trend with time, as tested by linear regression ($p>0.05$).

However, also for graminoids, we found a statically significant relation between NL and SM at inter-annual level, as tested by linear regression ($\beta=1.0$, $R^2=0.91$, $p<0.01$). Since graminoids displayed a statistically significant advance of the SM over the period 2008-2016, we removed

2007 from analysis of NL. However, also on this period we did not find statistically significant trend of NL with time, tested by linear regression (p>0.05). This result emphasized differences of NL and FS trends of graminoids (see chapter III.5.B.b. and Fig. III.5.B.b.18).

Comparison of trends among growth forms

Considering all the study period (2007-2016) the patterns of NL showed statistically significant differences between deciduous growth forms, as tested by one-way ANOVA (F=26, p<0.01) (Fig. III.5.B.c.10).

According to the 75% quartiles, graminoids and deciduous shrubs started earlier the NL formation (respectively -9 and -7 days) while deciduous dwarf shrubs (i.e. *S.herbacea*) was the latest (+6 days), although this delay was not statistically significant, as tested by t-test (p>0.05).

Deciduous shrubs (i.e. *V.uliginosum*) displayed the shortest range compared to the other growth forms (Fig. III.5.B.c.10): the earliest NL started almost one month later, and conversely the latest NL occurred almost one month before the other considered growth forms, and in both cases the observed differences were statistically significant as tested by t-test (p<0.05).

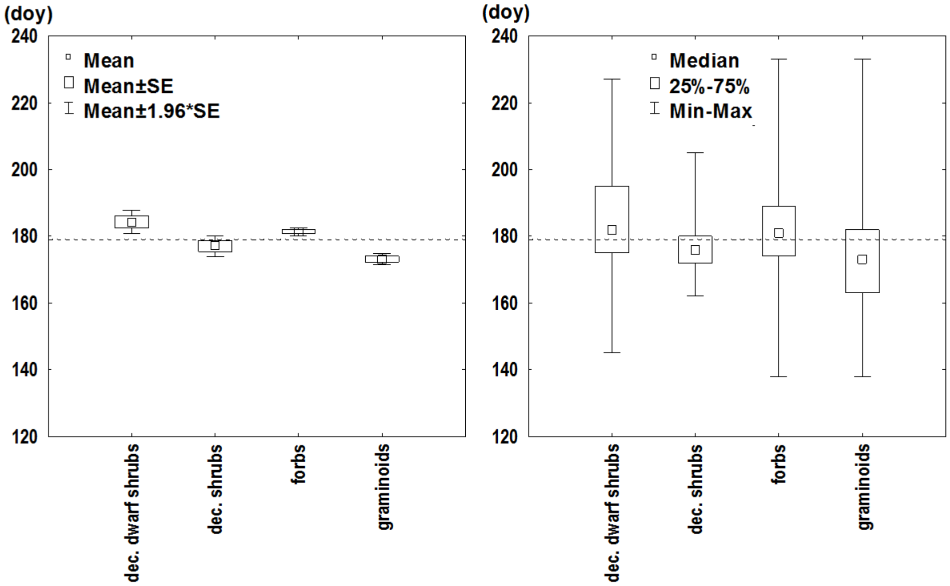


Figure III.5.B.c.10. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of new leaf (NL) between deciduous growth forms over the period 2007-2016. The dotted black line represents the mean value for the whole dataset.

NL did not display an advance trend over the study period at the inter-specific level, contrary to SM and FS. However, we found great differences when comparing the selected growth forms. Deciduous shrubs were the most reactive growth form (largest advance of NL with time), able to

shift their NL in response to earlier SM (see chap. III.5.B.a and Fig. III.5.B.a.7). Moreover, deciduous shrubs also showed the advance of FS of the largest part (75%) of the population (compared to trend of the whole dataset) (see chap III.5.B.b and Fig. III.5.B.b.8).
Conversely, graminoids, which showed an advance of the onset of growing season (see chap. III.5.B.a.), did not show a statistically significant advance of NL, indicating that leaves unfolding is for this species a less plastic phenological stage.

NL patterns always exhibited a statistically significant relation with SM at inter-specific level (Fig. III.5.B.c.8), and since all the selected deciduous growth forms showed high statistically significant relation between NL and SM, we could hypothesize that with an earlier SM scenario all these species could react.

III.5.B.d. *Length of the pre-unfolding period (NL-SM)*

Following the analysis of NL, we focused on the following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Over the study period (2007-2016) the pre-unfolding period length (NL-SM) displayed statistically significant differences among years, as tested by one-way ANOVA (F=39, p<0.01) (Fig. III.5.B.d.1).

The NL occurred one week after SM, according to mean and median values, or 10 days later, according to the 75% quartile (Table III.5.B.d.1).

The shortest NL-SM ranged from 0 days (in 2012 and 2009) to 7 days (in 2008), while the longest NL-SM ranged from 15 (in 2013) to 44 days (in 2007) (Table III.5.B.d.1), but with a large variation depending on the growth forms, as explained below.

Table III.5.B.d.1. Non parametric statistics of the pre-unfolding period length (NL-SM) at inter-specific level, computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev.**
2007	109	14	3	9	13	21	44	8.9
2008	90	13	7	7	14	15	29	5.4
2009	106	7	0	4	5	10	29	4.4
2010	116	7	2	4	7	8	23	4.4
2011	116	7	2	5	6	8	26	4.3
2012	116	7	0	3	6	7	24	4.1
2013	115	4	3	3	4	4	15	2.3
2014	113	6	2	3	5	8	24	4.1
2015	114	7	3	6	7	8	35	4.9
2016	114	10	3	7	8	10	34	5.6
2007-2016	1109	8	0	4	7	10	44	5.8

According to the 75% quartiles, the NL-SM duration showed the largest delay in 2007 (+11 days), and the shortest in 2013 (-6 days). As tested by t-test, 2007 was identified as statistically significant different (p<0.01), and was thus considered as “extreme” year concerning NL-SM (Fig. III.5.B.d.1).

As tested by linear regression over the “normal” years (2008-2016), we did not find any statistically significant trend with time (p<0.05).

The “extreme” SM of 2007 (see chap. III.5.B.a) thus implied a statistically significant lengthening of NL-SM, highlighting that the earlier and extreme SM did not correspond to an anticipation of

NL, indicating potentially a) conservative strategies or b) influencing of other climatic factors occurred in the period of leaves unfolding in this year.
Similarly, 2013, which was the year with the latest SM (see chap. III.5.B.a), induced a NL advance, shortening the NL-SM duration, indicating that plant became active earlier without losing valuable time for photosynthetic activity.

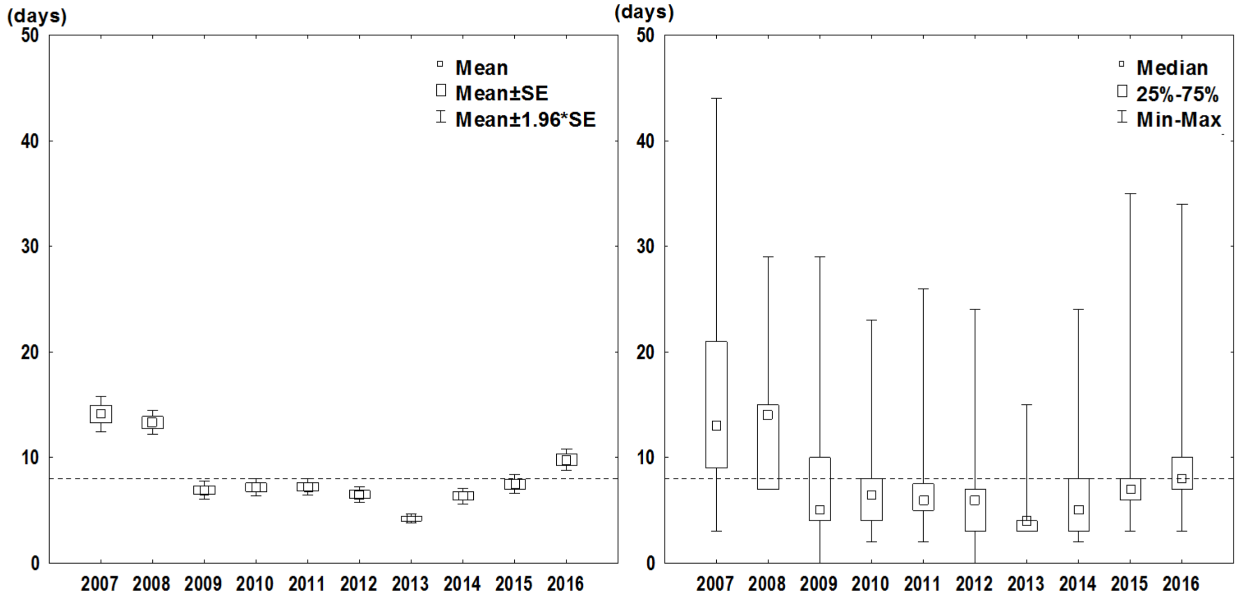


Figure III.5.B.d.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of the pre-unfolding period (NL-SM) at inter-specific level, from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Intra-growth forms level

Deciduous dwarf shrubs

Over the study period (2007-2016) the duration of NL-SM for deciduous dwarf shrubs showed statistically significant differences, as tested by one-way ANOVA (F=2, p<0.01) (Fig. III.5.B.d.2).

The NL occurred almost two weeks after SM, according to mean and median values (respectively 13 and 14 days), or 16 days later, according to the 75% quartile (Table III.5.B.d.2).

The earliest NL-SM ranged from 7 days (in 2008, 2012, 2013 and 2014) up to 14 days (in 2011), while the latest NL-SM spanned from 14 days (in 2009) to 39 days (in 2007) (Table III.5.B.d.2)

The 75% quartile anomalies showed that the shortest NL-SM occurred in 2009 (-5 days), while the longest occurred in 2016 (+4 days), although all without statistically significant differences (p>0.05).

Considering the whole study period, we did not identify any statistically significant trend with time, as tested by linear regression (p>0.05).

Table III.5.B.d.2. Non parametric statistics of the pre-unfolding period length (NL-SM) of deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	6	16	9	9	10	19	39	12.0
2008	5	13	7	7	14	17	22	6.5
2009	6	9	4	7	10	11	14	3.4
2010	7	14	10	10	14	19	19	4.0
2011	7	17	14	16	17	18	18	1.5
2012	7	13	7	10	13	15	21	4.4
2013	7	10	7	7	10	12	15	2.9
2014	7	13	7	8	14	15	20	4.4
2015	7	15	10	11	15	16	21	3.6
2016	7	17	11	14	16	20	23	4.2
2007-2016	66	13	0	10	14	16	39	5.8

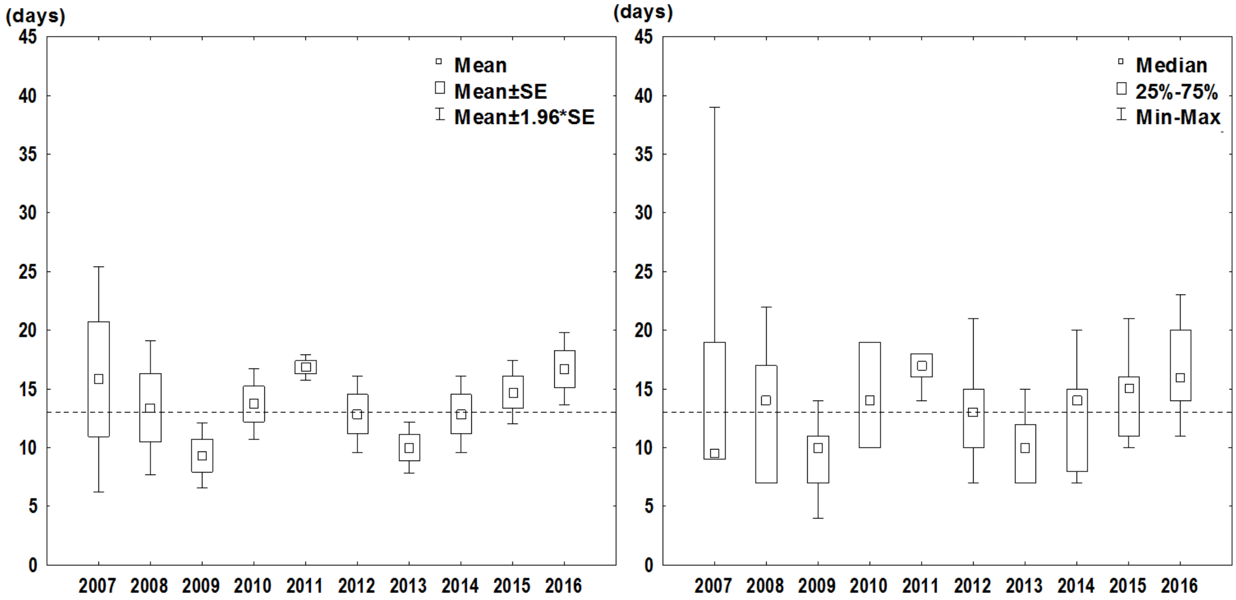


Figure III.5.B.d.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of the pre-unfolding period (NL-SM) for deciduous dwarf shrubs, from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Deciduous shrubs

Over the study period (2007-2016) the duration of NL-SM for deciduous shrubs showed statistically significant differences, as tested by one-way ANOVA (F=3, p<0.01) (Fig. III.5.B.d.3). Mean and median values of NL-SM were coincident, and indicated that NL occurred 19 days after SM, while according to the 75% quartile it occurred 24 days after SM (Table III.5.B.d.3).

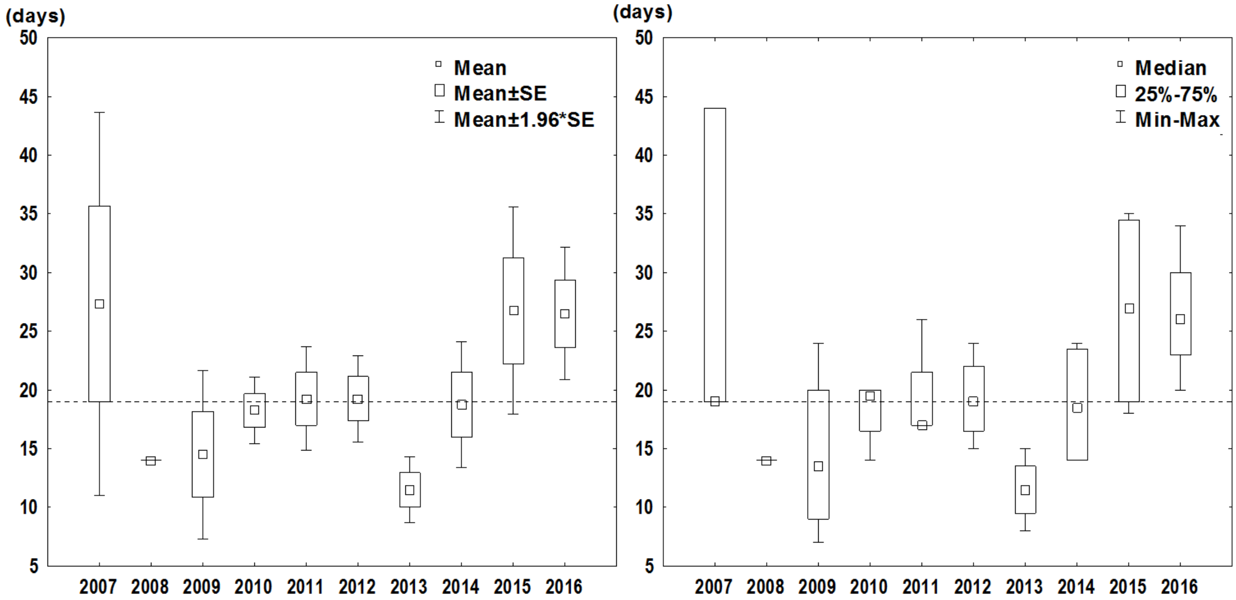


Figure III.5.B.d.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of the pre-unfolding period (NL-SM) for deciduous shrubs, from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Table III.5.B.d.3. Non parametric statistics of the pre-unfolding period length (NL-SM) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	3	27	19	19	19	44	44	14.4
2008	2	14	14	14	14	14	14	-
2009	4	15	7	9	14	20	24	7.3
2010	4	18	14	17	20	20	20	2.9
2011	4	19	17	17	17	22	26	4.5
2012	4	19	15	17	19	22	24	3.8
2013	4	12	8	10	12	14	15	2.9
2014	4	19	14	14	19	24	24	5.5
2015	4	27	18	19	27	35	35	9.0
2016	4	27	20	23	26	30	34	5.7
2007-2016	37	19	7	14	19	24	44	8.2

The earliest NL-SM ranged from 7 days (in 2009) to 20 days (in 2016), while the latest NL-SM spanned from 14 days (in 2008) to 44 days (in 2007) (Table III.5.B.d.3).

In 2008 we documented a very low variance in our dataset, due to the lepidopter masting event that characterized this year (see methods), thus we excluded 2008 from further analysis of NL-SM.

The 75% quartile anomalies documented that the shortest NL-SM occurred in 2013 (-11 days), while the longest occurred in 2007 (+20 days), thus in coincidence of the earliest and “extreme”

SM (see chap III.5.B.a). Also concerning NL-SM, the 2007 was identified as statistically significant different (t-test, p<0.05), and was thus classified as an "extreme" year.

Considering thus only the "normal" years of NL-SM (2009-2016, removing 2007 as "extreme NL-SM, and 2008 for the reason explained above), we did not identify any statistically significant trend with time, as tested by linear regression (p>0.05).

Forbs

NL-SM of forbs showed statistically significant variability between years, as tested by one-way ANOVA (F=51, p<0.01) (Fig. III.5.B.d.4).

Considering all the study period, forbs required one week since SM for the NL formation, according to mean and median values (7 days), and to the 75% quartile (8 days) (Table III.5.B.d.4).

Table III.5.B.d.4. Non parametric statistics of new leaves (NL) of forbs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	15	3	9	13	21	36	8.2
2008	52	13	7	7	14	15	29	5.7
2009	62	6	0	4	4	10	29	4.3
2010	67	6	2	3	6	7	14	2.8
2011	67	6	2	5	6	6	14	2.6
2012	67	6	0	3	6	7	15	2.9
2013	66	3	3	3	3	4	7	0.7
2014	65	6	2	4	7	8	14	2.6
2015	66	7	3	6	7	8	12	2.0
2016	66	8	6	7	7	9	19	2.6
2007-2016	641	7	0	4	7	8	36	5.1

As observed for graminoids (see following paragraphs), the earliest onset of NL was very close to the SM (normally ranging from 0 to 3 days), and only in 2008 and 2016 NL required a longer time after SM (c. one week) (Table III.5.B.d.4). On the contrary, the latest NL-SM spanned from 7 days (in 2013) to 36 days (in 2007).

Analyzing the 75% quartiles, the NL-SM anomalies ranged from a shortening of 4 days (in 2013) to a lengthening of 21 days (in 2007). The longest pre-unfolding period of 2007, was the only one identified as "extreme" according to the t-test (p<0.01) (Fig. III.5.B.d.4).

Considering thus only the period 2008-2016, we did not observe statistically significant temporal trends of NL-SM with time, as tested by linear regression (p>0.05).

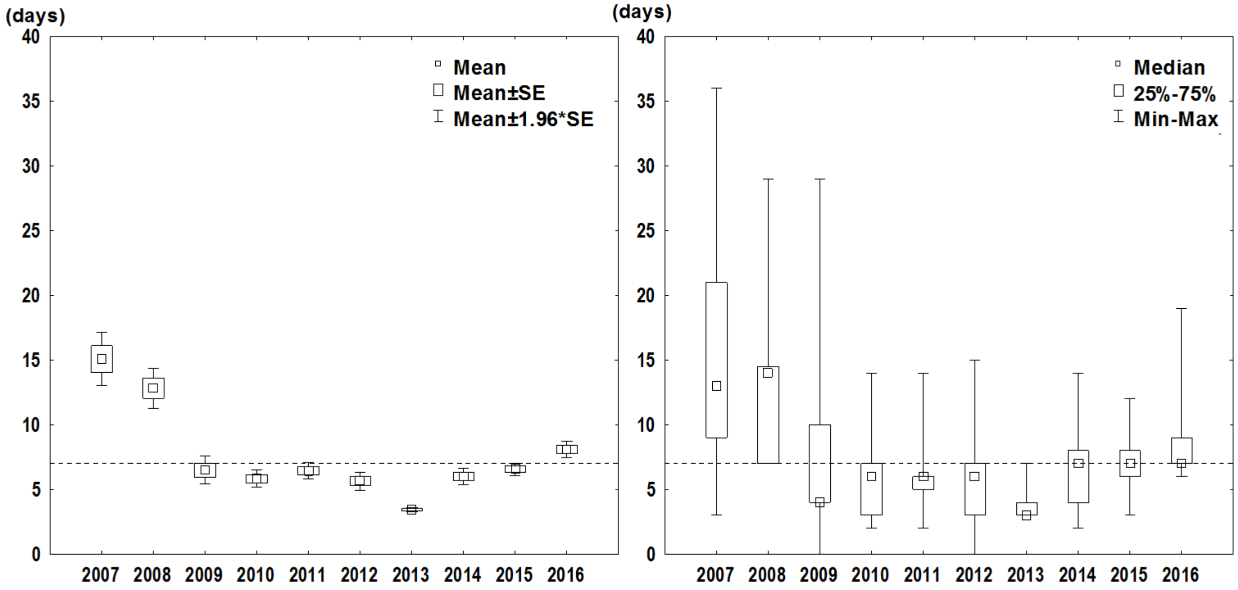


Figure III.5.B.d.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of pre-unfolding period (NL-SM) of forbs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Graminoids

As tested by one-way ANOVA, the NL-SM of graminoids showed statistically significant differences between different years over the period 2007-2016 (F=22, p<0.01) (Fig. III.5.B.d.5). Over the whole study period, mean and median values of NL-SM were similar to those of forbs (respectively 7 and 6 days) and also the 75% quartile (8 days) (Table III.5.B.d.5).

Graminoids started NL formation soon after the SM; after 2 or 3 days depending on the year and only in 2008 the beginning of NL required one week after SM. The latest NL completion occurred from only 4 days (in 2013) to 30 days after SM (Table III.5.B.d.5).

Table III.5.B.d.5. Non parametric statistics of new leaves (NL) of graminoids computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	37	11	3	5	10	13	30	7.9
2008	31	14	7	10	14	17	22	4.8
2009	34	6	3	4	5	7	20	3.4
2010	38	7	3	5	7	9	23	4.3
2011	38	6	2	3	5	6	12	2.6
2012	38	6	2	3	6	7	15	2.5
2013	38	4	3	3	4	4	4	0.5
2014	37	4	2	3	4	5	12	2.2
2015	37	6	3	4	6	7	10	1.9
2016	37	10	3	7	7	13	26	5.9
2007-2016	365	7	2	4	6	8	30	5.1

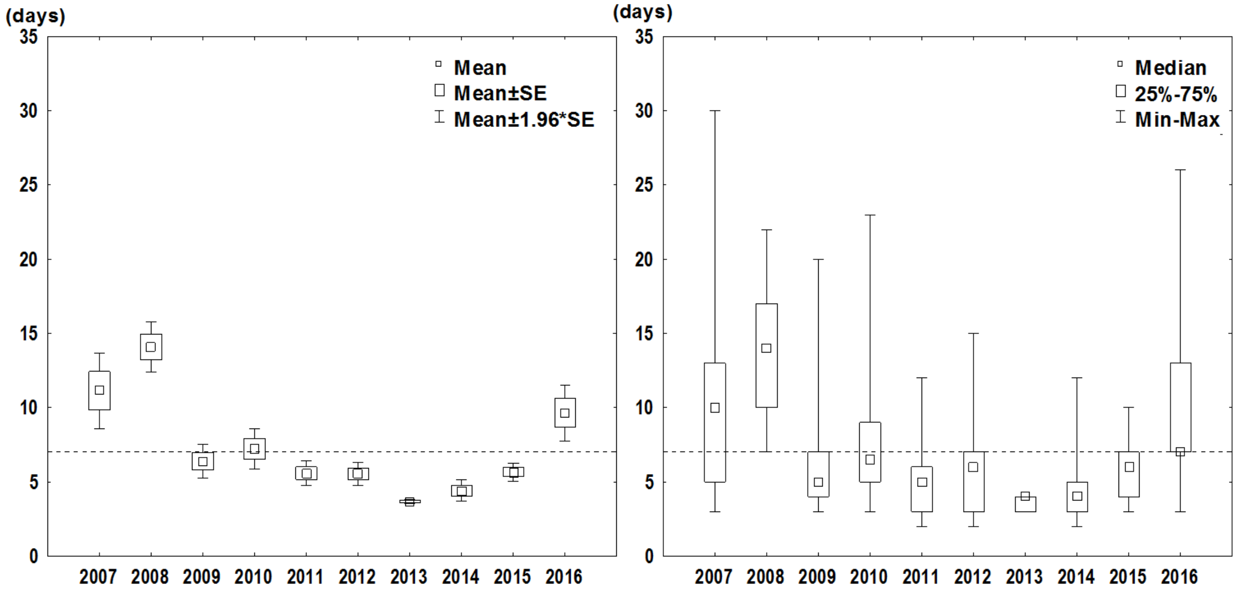


Figure III.5.B.d.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of pre-unfolding period (NL-SM) for graminoids from 2007 to 2016. The dotted black line represents the mean value for the whole period.

According to the 75% quartiles anomalies, the longest NL-SM occurred in 2008 (+9 days), which was the only one year with a statically significant difference respect others, tested by t-test ($p=0.03$).

As tested by linear regression, we did not find any statistically significant trend of NL-SM with time (excluding 2008 as “extreme” year). However, since graminoids displayed a statistically significant relation between NL and SM (see chap III.5.B.c.), and they showed a statistically significant advance of the SM over the period 2008-2016, we tested if any trend with time could be apparent when removing also 2007 from NL-SM, as “extreme” year of SM.
Also in this case we did not find any statistically significant trend of NL-SM with time, as tested by linear regression ($p>0.05$).

Comparison of NL-SM trends among growth forms

Considering all the study period (2007-2015) the duration of NL-SM exhibited statistically significant differences among the selected growth forms, as tested by one-way ANOVA ($F=83$, $p<0.01$) (Fig. III.5.B.d.6).

Comparing the median values of NL-SM, both graminoids and forbs started the development of NL soon after SM (c. one week), while the longest duration of NL-SM was found for the deciduous shrubs, which unfolded their leaves 19 days after SM.
This was confirmed also by the earliest NL-SM trends, which was delayed of almost one week for deciduous shrubs, identified as statistically significant different, as tested by t-test ($p<0.01$).

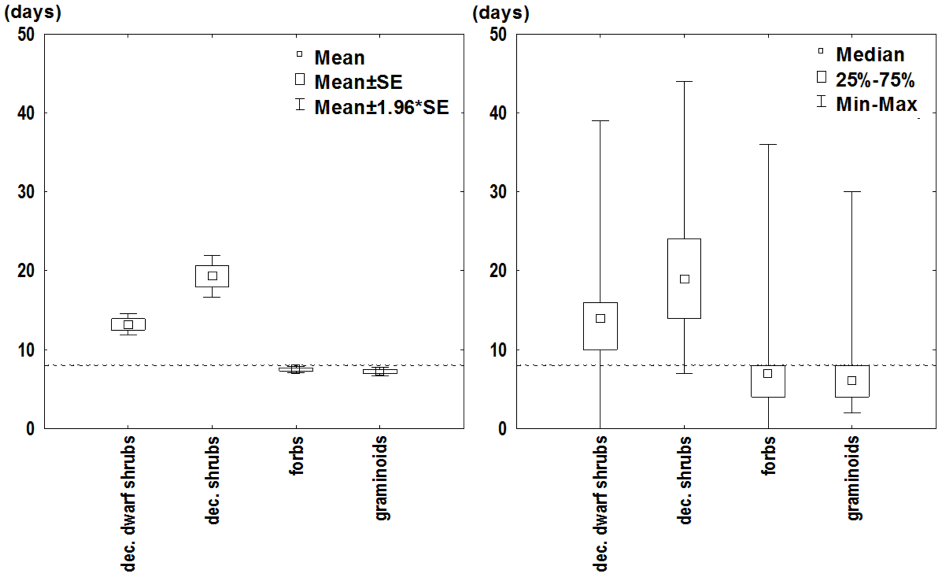


Figure III.5.B.d.6. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of length of pre-unfolding season (NL-SM) between the selected growth forms over the period 2007-2016. The dotted black line represents the mean value for the whole period.

We observed opposite trends when comparing among growth forms the patterns of SM (chap. III.5.B.a) with the duration of NL-SM: the earlier is the SM, the longer is NL-SM and vice versa. Indeed, graminoids and forbs showed the latest SM, although they started NL formation soon after the snow melting, while deciduous shrubs, which showed the earliest SM, displayed also the longest NL-SM.

All the selected growth forms did not show NL-SM trends with time, thus highlighting the high relation between NL and SM (see also chap. III.5.B.c and III.5.B.k), even when the NL onset does not occur soon after SM (e.g. deciduous shrubs). This strong relation could allow to identify the high capability of alpine plants of exploiting earlier SM and onset of growing season, in particular for graminoids and forbs.

Moreover, we observed differences among growth forms in their response to the earlier and extreme SM of 2007. Indeed, deciduous shrubs and forbs showed a statistically significant lengthening of NL-SM in this year, resembling the pattern observed at the inter-specific level, and thus indicating possible conservative strategy or dependency from other climatic factors occurred in that year (see chap. III.5.B.k).
Conversely, deciduous dwarf shrubs and graminoids, did not exhibit a delay of NL in 2007, indicating their high potential of exploiting earlier onset of growing season.

III.5.B.e. *Patterns of Flower bud appearance (FB)*

Analogously to the other phenophases, our analyses have been carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2007-2016), the FB exhibited statistically significant inter-annual variability, as tested by one-way ANOVA ($F=49$, $p<0.01$) (Fig. III.5.B.e.1).
The mean and median values of FB were coincident, and occurred at mid-July (193 DOY), while the 75% one week later (201 DOY) (Table III.5.B.e.1).

Table III.5.B.e.1. Non-parametric statistics of onset of flower bud (FB) computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	116	187	145	179	193	193	210	11.9
2008	95	206	175	197	204	211	238	12.9
2009	108	203	170	191	201	216	237	15.4
2010	118	196	172	189	196	206	221	12.4
2011	120	187	149	175	187	197	213	12.8
2012	122	185	154	178	186	190	208	10.5
2013	113	198	168	189	196	206	248	16.5
2014	116	197	164	182	197	208	255	18.7
2015	120	179	149	169	180	188	232	12.7
2016	108	188	153	179	189	195	209	11.0
2007-2016	1136	192	145	181	192	201	255	15.8

Considering each single year (Table III.5.B.e.1), the onset of FB was observed between late May (145 DOY, in 2007) and late June (175 DOY, in 2008), while the FB completion was documented between late July (208 DOY, in 2012) and mid-September (255 DOY, in 2014).

The total duration of FB lasted from 49 days (in 2010) to 91 days (in 2014), while the FB peak lasted from only 12 days (in 2012) to 26 days (in 2014).

According to the 75% quartiles anomalies referred to all the period 2007-2016, in 2015 the FB showed the largest advance (-15 days) opposite to 2009 which revealed the largest delay (+13 days) (Fig. III.5.B.e.1), although in both cases it was not statistically significant, as tested by t-test ($p>0.05$).

Moreover, as tested by linear regression on the whole study period (2007-2016), we did not find any statistically significant trend of FB with time ($p>0.05$).
We found instead a statistically significant relation between FB and SM, as tested by linear regression at the inter-annual level, even if SM explained a small proportion of the variance of FB

(β=0.6, R^2=0.45, p<0.01) (Fig. III.5.B.e.2), highlighting that other factors could contribute in shaping FB responses (see chap III.5.B.k).

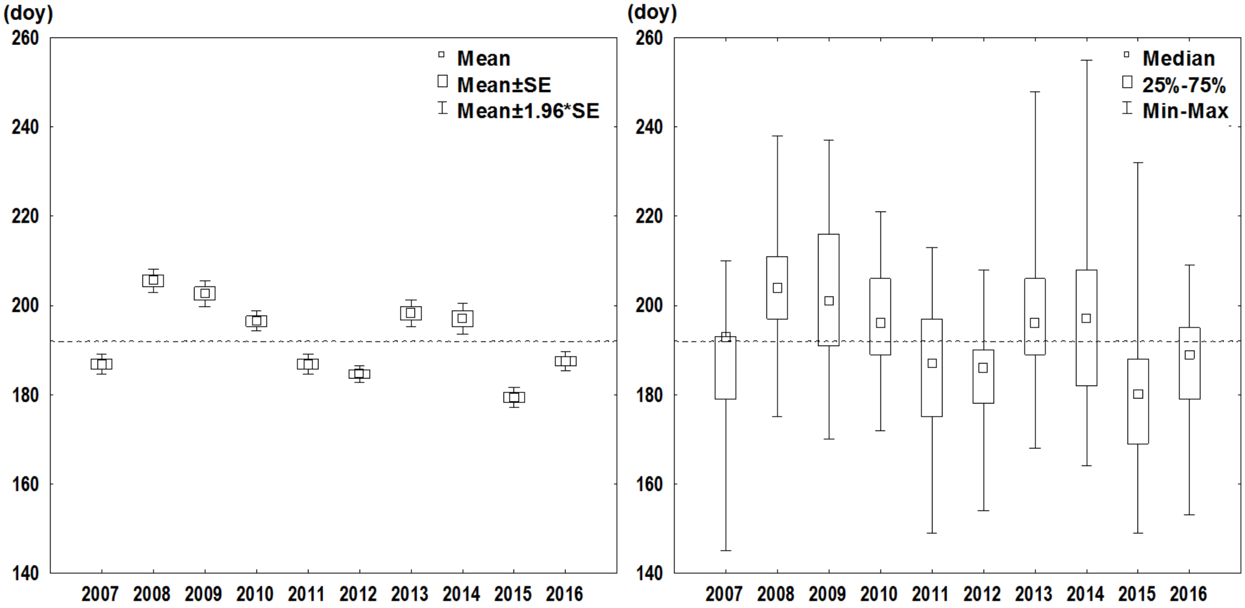


Figure III.5.B.e.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of onset of flower bud (FB) from 2007 to 2016. The dotted black line represents the mean value for the whole period.

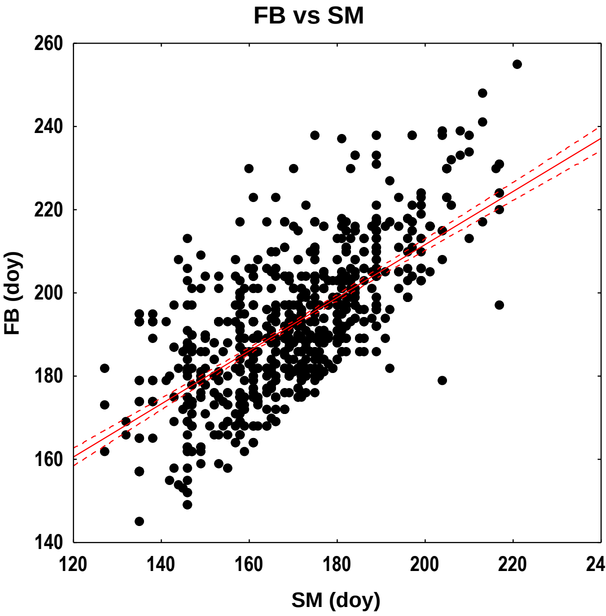


Figure III.5.B.e.2: Relation between FB and SM at inter-specific and inter-annual level, as tested by linear regression (β=0.6, R^2=0.45, p<0.01).

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FB of deciduous dwarf shrubs (i.e. *Salix herbacea*) (Fig. III.5.B.e.3) exhibited statistically significant differences among years (F=6, p<0.01) (Fig. III.5.B.e.4).

Over the study period (2007-2016), according to the mean and median values, the FB occurred at mid-July (respectively 195 and 193 DOY), or few days later (199 DOY) according to 75% quartile (Table III.5.B.e.2).

Table III.5.B.e.2. Non-parametric statistics of flower bud (FB) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev.**
2007	6	190	179	186	193	193	193	5.9
2008	5	200	189	197	197	204	211	8.3
2009	5	220	201	223	223	223	230	11.0
2010	6	195	180	186	191	206	218	14.1
2011	5	193	187	192	192	192	200	4.7
2012	6	187	182	182	186	190	197	5.7
2013	6	199	185	185	198	199	231	16.9
2014	5	197	184	197	197	204	204	8.2
2015	5	181	173	176	180	184	191	7.0
2016	7	188	175	181	189	195	195	7.8
2007-2016	56	195	173	186	193	199	231	13.3

Figure III.5.B.e.3. Example of flower buds on a) *Vaccinium uliginosum* and b) *Salix herbacea.*

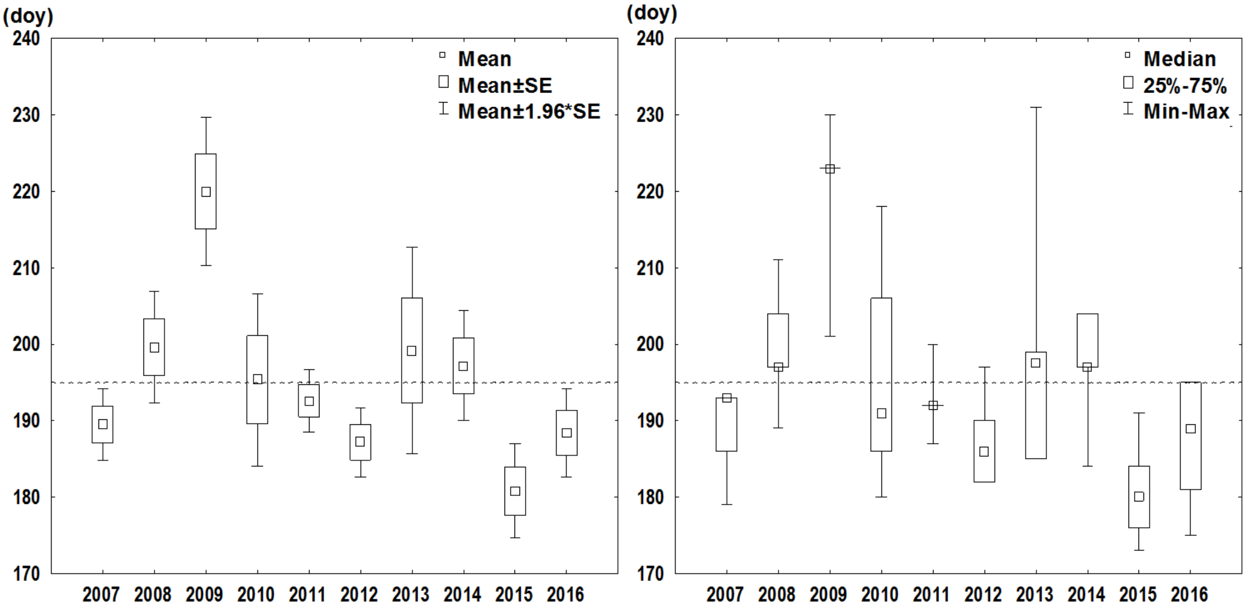


Figure III.5.B.e.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of flower bud (FB) for deciduous dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering the intra-annual variability, the earliest onset of FB was recorded from late June (173 DOY, in 2015) to mid-July (201 DOY, in 2009) (Table III.5.B.e.2). The FB completion was achieved from mid-July (191 DOY, in 2015) to mid-August (231 DOY, in 2013).

For deciduous dwarf shrubs, the total duration of FB ranged from 13 days (in 2011) to 46 days (in 2013), while the FB peak duration ranged from 0 days (in 2009 and 2011) to 20 days maximum (in 2010) (Table III.5.B.e.2).

Analyzing the anomalies of the 75% quartiles, the FB showed a large variability, with the largest advance in 2015 (-15 days) and the greatest delay in 2009 (+24 days). As tested by t-test, 2009 was the only one year that showed statistically significant differences and was thus identifiable as “extreme” concerning its FB ($p<0.01$) (Fig. III.5.B.e.4).
Considering thus only the “normal” years (excluding 2009 as “extreme” year of FB), we did not find any statistically significant trend, as tested by linear regression.

Deciduous shrubs

The FB for deciduous shrubs (i.e. *Vaccinium uliginosum*) (Fig. III.5.B.e.3) was observed only in 7 years as in 2007, 2011 and 2013 no flowering was observed. As tested by one-way ANOVA, over the years with available data, the FB exhibited statistically significant differences among years ($F=35$, $p<0.01$) (Fig III.5.B.e.5).

Over the study period (2007-2016), according to the mean and median values, the FB occurred at early/mid-July (respectively 192 and 186 DOY), while the 75% quartile occurred in late-July (208 DOY) (Fig. III.5.B.e.5).

Considering the intra-annual variability, the earliest onset of FB (162 DOY, mid-June) was recorded in 2015, while the latest in 2009 (223 DOY, mid-August). The FB completion ranged from mid-June (176 DOY, in, 2015) to mid-July (238 DOY, in 2008) (Table III.5.B.e.3).
The total duration of FB for deciduous shrubs lasted from 0 to 21 days (respectively in 2016 and 2008), and also the FB peak duration followed the same pattern (Table III.5.B.e.3).

Table III.5.B.e.3. Non-parametric statistics of flower bud (FB) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	0							
2008	2	228	217	217	228	238	238	14.8
2009	2	227	223	223	227	230	230	4.9
2010	2	196	193	193	196	199	199	4.2
2011	0							
2012	1	208	208	208	208	208	208	-
2013	0							
2014	4	179	173	175	180	182	182	4.4
2015	4	168	162	164	168	173	176	5.9
2016	3	186	186	186	186	186	186	-
2007-2016	18	192	162	176	186	208	238	22.6

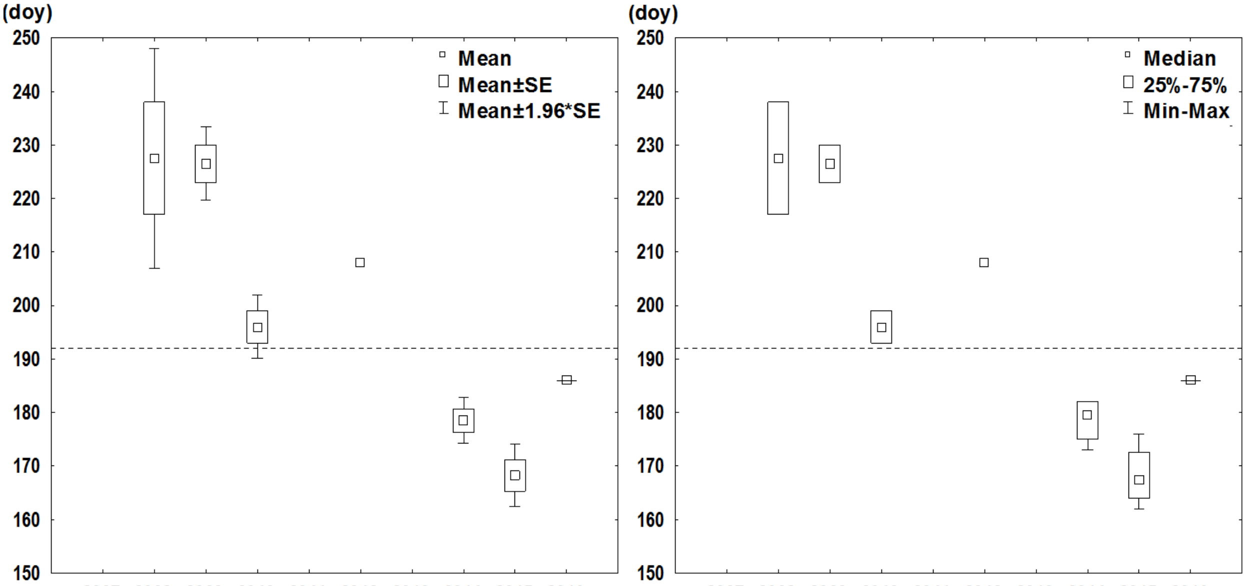


Figure III.5.B.e.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of flower bud (FB) for deciduous shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering the anomalies of the 75% quartiles, the FB showed the largest delay in 2008 (+30 days), and the largest advances in 2015 (-36 days) (Fig. III.5.B.e.5), although without statistically significance, as tested by t-test (p>0.05).

Analyzing thus the whole dataset, we found a statistically significant advance of FB over the study period (β=-6.5, R^2=0.76, p=0.01) (Fig. III.5.B.e.6).

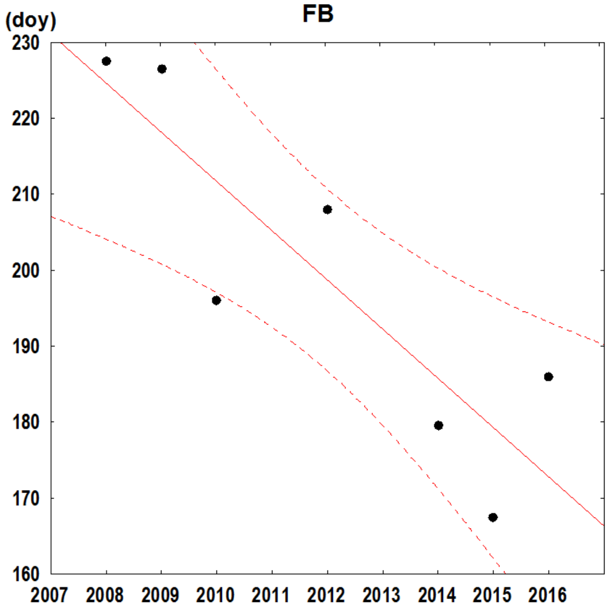


Figure III.5.B.e.6. Trend of FB with time (β=-6.5, R^2=0.76, p=0.01) for deciduous shrubs, as tested by linear regression.

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FB of evergreen dwarf shrubs (i.e. *Kalmia procumbens*) (Fig. III.5.B.e.7) exhibited statistically significant differences among years (F=14, p<0.01) (Fig III.5.B.e.8).

Table III.5.B.e.4. Non-parametric statistics of flower bud (FB) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev..**
2007	6	160	157	157	157	165	165	4.1
2008	3	194	182	182	189	211	211	15.1
2009	4	185	181	181	185	188	188	4.0
2010	6	183	175	180	183	186	189	4.8
2011	6	166	158	163	163	169	181	8.1
2012	6	170	168	168	168	174	174	3.1
2013	6	184	176	182	184	189	192	5.7
2014	6	167	164	164	166	168	175	4.3
2015	6	165	155	162	168	169	169	5.6
2016	6	175	175	175	175	175	175	-
2007-2016	55	173	155	165	174	182	211	11.1

Over all the study period (2007-2016), according to the mean and median values, the FB for the evergreen dwarf shrubs occurred at mid-June (respectively 173 and 169 DOY) and at the beginning of July (182 DOY) according to 75% quartile (Table III.5.B.e.4).

Figure III.5.B.e.7. Example of flower buds on *Kalmia procumbens* and *Rhododendron ferrugineum.*

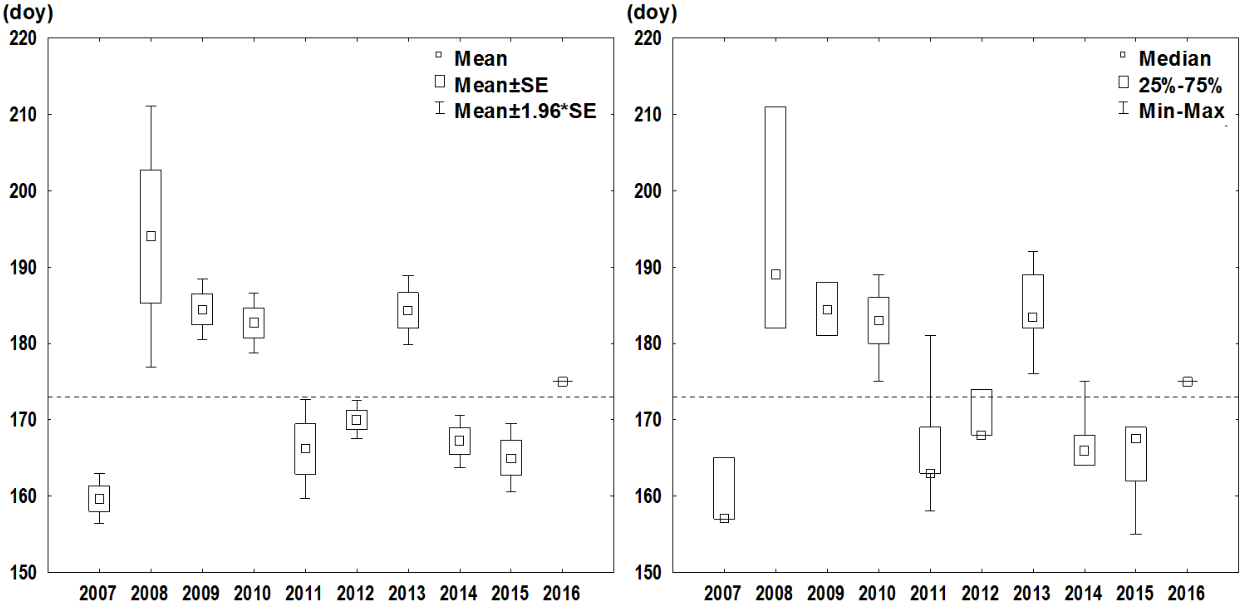


Figure III.5.B.e.8. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of flower bud (FB) for evergreen dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering the intra-annual variability, the earliest onset of FB (155 DOY, early June) was recorded in 2015, while the latest in 2008 (182 DOY, beginning of July). The latest FB spanned from mid-June (165 DOY, in 2007) to the beginning of August (211 DOY, in 2008) (Table III.5.B.e.4).

The total duration of FB for evergreen dwarf shrubs ranged from 0 days (in 2016) to 29 days (in 2008), while the FB peak duration ranged from 0 days (in 2016) to 29 days (in 2008). However, without considering 2008 (see following sentences), the maximum total duration of FB was of 16 days (in 2013) and its peak ranged up to 8 days (in 2007).

Considering the anomalies of the 75% quartiles, the FB showed the largest advance in 2007 (-17 days), and the largest delay in 2008 (+29 days). FB recorded in 2008 was the only one identified as "extreme", as tested by t-test ($p<0.01$).
Considering thus only "normal" years for the FB (removing 2008), we did not find any statistically significant trend with time, as tested by linear regression ($p>0.05$).

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FB of evergreen shrubs (i.e. *Rhododendron ferrugineum*) (Fig. III.5.B.e.7) exhibited statistically significant differences among years ($F=4$, $p<0.01$) (Fig. III.5.B.e.9).

Over all the study period (2007-2016), mean and median values of FB for the evergreen shrubs were coincident, and occurred at the beginning of July (187 DOY), while the 75% occurred at mid-July (193 DOY) (Table III.5.B.e.5).

The earliest onset of FB (162 DOY, mid-June) was recorded in 2015, while the latest (189 DOY, early July) in 2008, 2013 and 2014. The FB completion ranged from the beginning of July (186 DOY, in 2012 and 2016) to end of July (211 DOY, in 2008). (Table III.5.B.e.5).

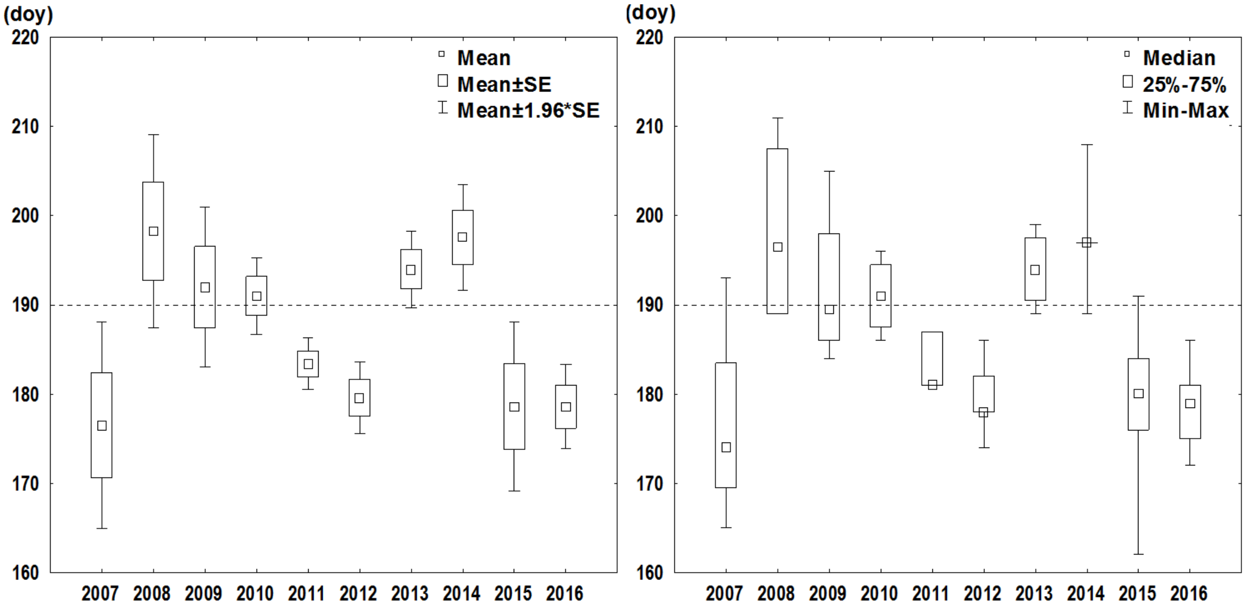


Figure III.5.B.e.9. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of flower bud (FB) for evergreen shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Table III.5.B.e.5. Non-parametric statistics of flower bud (FB) for evergreen shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	4	177	165	170	174	184	193	11.8
2008	4	198	189	189	197	208	211	11.1
2009	4	192	184	186	190	198	205	9.1
2010	4	191	186	188	191	195	196	4.4
2011	5	183	181	181	181	187	187	3.3
2012	5	180	174	178	178	182	186	4.6
2013	4	194	189	191	194	198	199	4.4
2014	5	198	189	197	197	197	208	6.8
2015	5	179	162	176	180	184	191	10.8
2016	5	179	172	175	179	181	186	5.4
2007-2016	45	187	162	180	187	193	211	10.6

The total duration of FB for the evergreen shrubs ranged from 6 days (in 2011) to 29 days (in 2015), while the FB peak duration ranged from 0 to 19 days (respectively in 2008 and 2014) (Fig. III.5.B.e.9).

Considering the anomalies of the 75% quartiles, the FB showed the largest advance in 2016 (-12 days), and the largest delay in 2008 (+15 days). Tested by t-test, the delay of 2008 was identified as statistically significant (p=0.04), and was thus excluded by further analysis of trend with time. Analyzing thus only the “normal” years (excluding 2008, “extreme” year of FB) we did not find any statistically significant trend of FB with time for evergreen shrubs, as tested by linear regression (p>0.05).

Forbs

Considering all the study period, FB of forbs (Fig. III.5.B.e.10) exhibited statistically significant differences among years, as tested by one-way ANOVA (F=30, p<0.01) (Fig III.5.B.e.11).

Table III.5.B.e.6. Non-parametric statistics of flower bud (FB) for forbs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	190	174	193	193	193	201	6.6
2008	50	206	175	197	204	217	238	12.8
2009	59	204	177	194	201	216	237	13.5
2010	63	200	180	189	199	210	221	10.7
2011	66	190	163	181	192	197	213	10.4
2012	66	187	171	182	186	190	208	8.1
2013	60	200	172	192	199	208	248	15.1
2014	61	202	175	197	204	208	255	16.0
2015	64	182	162	173	180	188	232	12.0
2016	56	190	175	186	189	195	204	8.0
2007-2016	608	195	162	186	193	203	255	13.9

The mean and median value for the FB over the whole period (2007-2016) were almost coincident (195 and 193 DOY, mid-July), while the 75% occurred at late July (203 DOY) (Table III.5.B.e.6).

Figure III.5.B.e.10. Example of flower bud on *Leucanthemopsis alpina.*

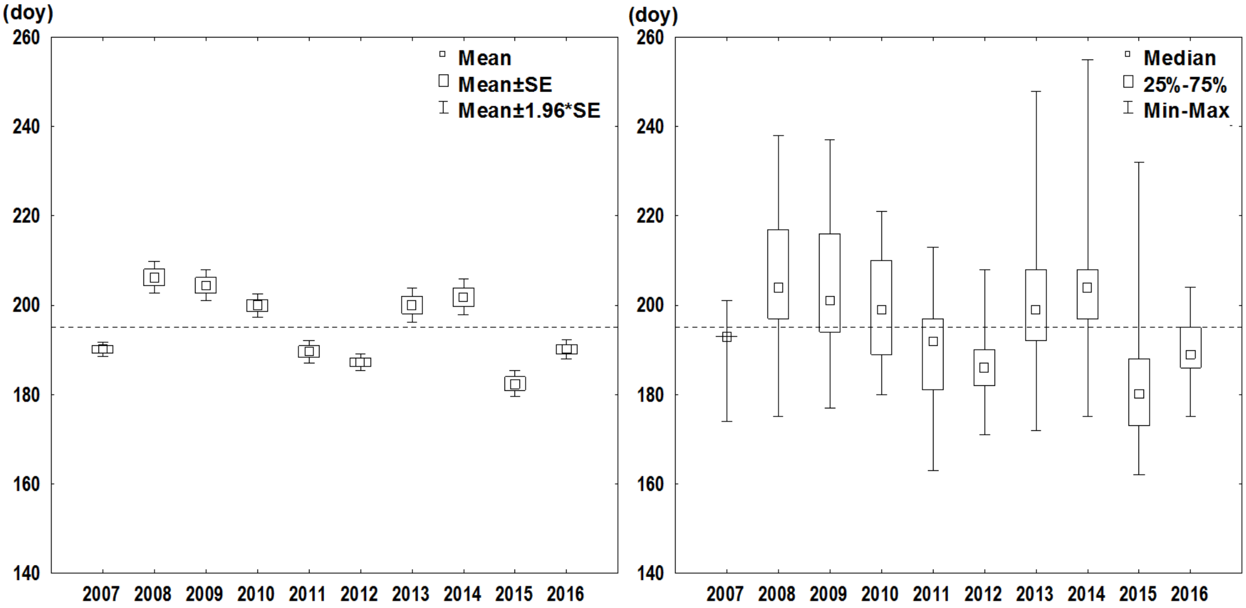


Figure III.5.B.e.11. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of flower bud (FB) for forbs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Analyzing each year, the beginning of FB occurred in mid-June (162 DOY, in 2015) and ranged up to late June (180 DOY, in 2010), while the FB completion ranged from mid-July (201 DOY, in 2007) to mid-September (255 DOY, in 2014) (Table III.5.B.e.6).

Considering the FB total duration, it lasted from 27 days (in 2007) to a maximum of 80 days (in 2014), while the FB peak duration ranged from 0 (in 2007) to 22 days (in 2009) (Fig. III.5.B.e.11)

Comparing the 75% anomalies, forbs showed the largest delay in 2008 (+14 days), while the earliest FB occurred in 2015 (-15 days) (Fig III.5.B.e.11), although we did not find statistically significant differences, as tested by t-test (p>0.05).
Over the whole study period (2007-2016), we did not identify any statistically significant trend of FB with time, as tested by linear regression.

Graminoids

As tested by one-way ANOVA, overall the study period (2007-2016) the FB of graminoids (Fig. III.5.B.e.12) exhibited statistically significant differences among years (F=11, p<0.01) (Fig. III.5.B.e.13).

Over the study period (2007-2016), mean and median values of FB were coincident, and occurred at mid-July (191 DOY), while the 75% occurred in late July (204 DOY) (Table III.5.B.e.7).

Table III.5.B.e.7. Non-parametric statistics of flower bud (FB) for graminoids computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	37	186	145	180	193	193	210	14.1
2008	31	206	182	197	211	217	238	12.2
2009	34	199	170	184	198	216	230	16.4
2010	37	194	172	180	193	206	221	14.4
2011	38	185	149	175	187	197	213	15.1
2012	38	182	154	174	182	190	208	13.0
2013	37	198	168	182	196	213	241	19.5
2014	35	196	164	175	204	215	239	21.8
2015	36	177	149	166	180	188	206	13.8
2016	31	187	153	175	195	201	209	15.6
2007-2016	354	191	145	177	191	204	241	17.7

The earliest onset of FB (145 DOY, mid-May) was recorded in 2007, while the latest in 2008 (182 DOY, end of June). The FB completion ranged from late July (208 DOY, in 2012) to late August (241 DOY, in 2013) (Table III.5.B.e.7).

For graminoids, the total duration of FB ranged from 54 days (in 2012) to 75 days (in 2014), while the peak duration of FB was concentrated to 13 days only (in 2007) or to 40 days (in 2014) (Fig. III.5.B.e.13).

Considering the anomalies of the 75% quartiles, in 2015 the FB displayed the largest advance (-16 days), while in 2008, it showed the largest delay (+13 days). However, tested by t-test we did not find statistically significant differences (p>0.05) (Fig. III.5.B.e.13).

Considering thus the whole study period, we did not find any statistically significant trend with time of FB, as tested by linear regression (p>0.05).

Figure III.5.B.e.12. Example of flower buds on *Carex curvula*.

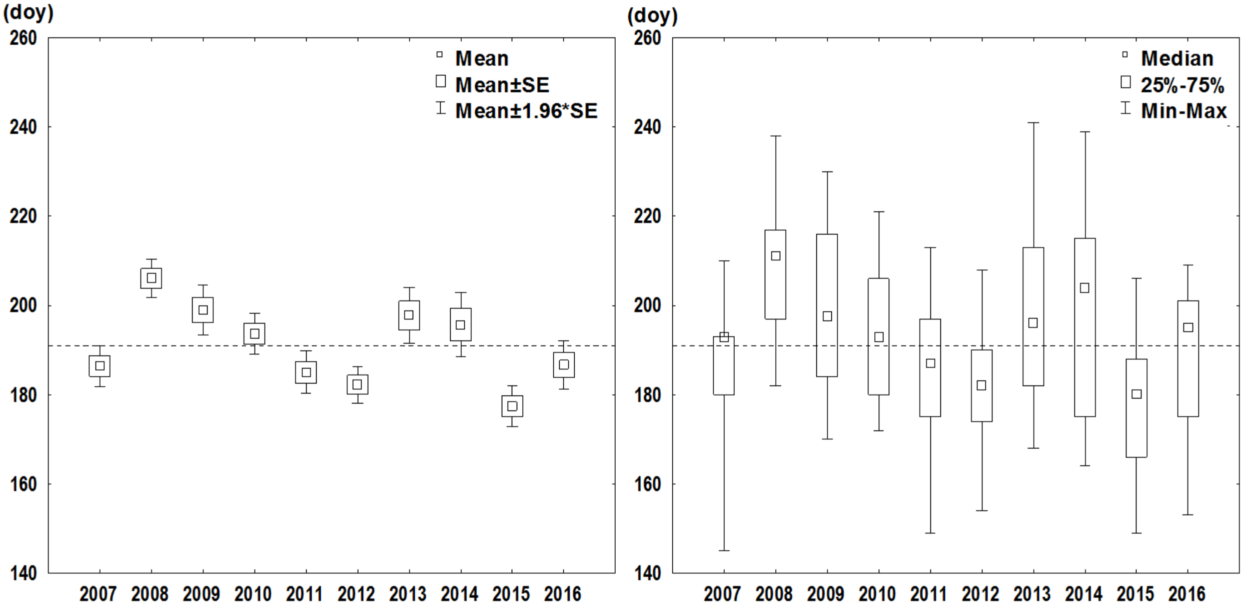


Figure III.5.B.e.13. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of flower bud (FB) for graminoids from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Comparison of trends among growth forms

Comparing the trends of FB among the selected growth forms, we found a large and statistically significant variability (Fig. III.5.B.e.14), as tested by one-way ANOVA (F=23, p<0.01).
According to the mean and median values, the evergreen dwarf shrubs were the first growth form starting FB (174 DOY, late June), with a statistically significant difference as tested by t-test (p<0.01), while for deciduous dwarf shrubs, forbs and graminoids occurred almost twenty days later (193, 193 and 191 DOY, mid-July).

The onset of FB occurred earlier for graminoids (145 DOY, late May) while deciduous dwarf shrubs were the latest (173 DOY, late June). However, the completion of FB occurred earlier for evergreen dwarf shrubs and evergreen shrubs, while forbs displayed the latest (Fig. III.5.B.e.14).

Herbaceous growth forms (i.e. graminoids and forbs) exhibited the longest total FB duration (respectively 96 and 93 days), while evergreen shrubs, evergreen dwarf shrubs and deciduous dwarf shrubs the shortest (respectively 49, 56 and 58 days). Deciduous shrubs and graminoids displayed the greatest FB peak duration (respectively 32 and 27 days), while the deciduous dwarf shrubs and evergreen dwarf shrubs the lowest (13 days).
The FB for evergreen dwarf shrubs was the only one identified as statistically significant different, as tested by t-test (p<0.01).

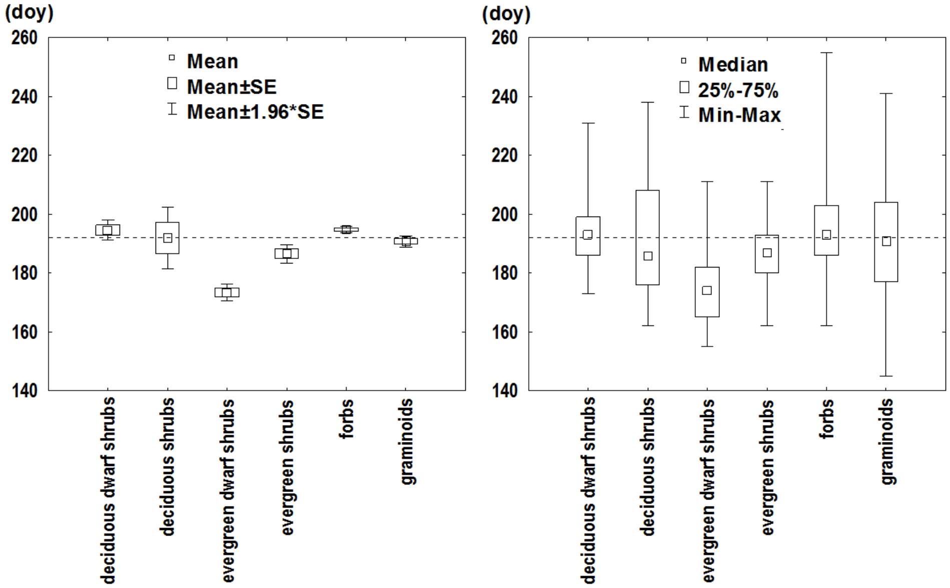


Figure III.5.B.e.14. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of flower bud (FB) between the selected growth forms over the period 2007-2016. The dotted black line represents the mean value for the whole dataset.

The trends with time of each single growth form identified a statistically significant advance of FB only for deciduous shrubs (Fig. III.5.B.e.6). Therefore this growth form could exhibit a larger adaptive ability to cope with the observed earlier SM and onset of growing season recorded in these last years.

III.5.B.f. *Flowering starts. Patterns of First Flowering day (FF)*

Analogously to the other phenophases, our analyses have been carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2007-2016), also the first flowering day (FF) showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=41.7, p<0.01) (Fig. III.5.B.f.1).

Table III.5.B.f.1. Non parametric statistics of first flowering day (FF) computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	116	193	170	193	193	193	210	5
2008	95	207	182	197	211	217	238	12
2009	109	208	177	201	205	216	244	15
2010	118	205	175	193	205	218	238	15
2011	120	198	149	187	199	208	222	15
2012	122	195	168	186	197	208	222	13
2013	112	213	182	199	210	224	270	20
2014	115	215	168	204	215	233	266	24
2015	120	190	155	182	188	199	247	14
2016	107	200	172	189	201	214	243	14
2007-2016	1134	202	149	191	201	213	270	17.3

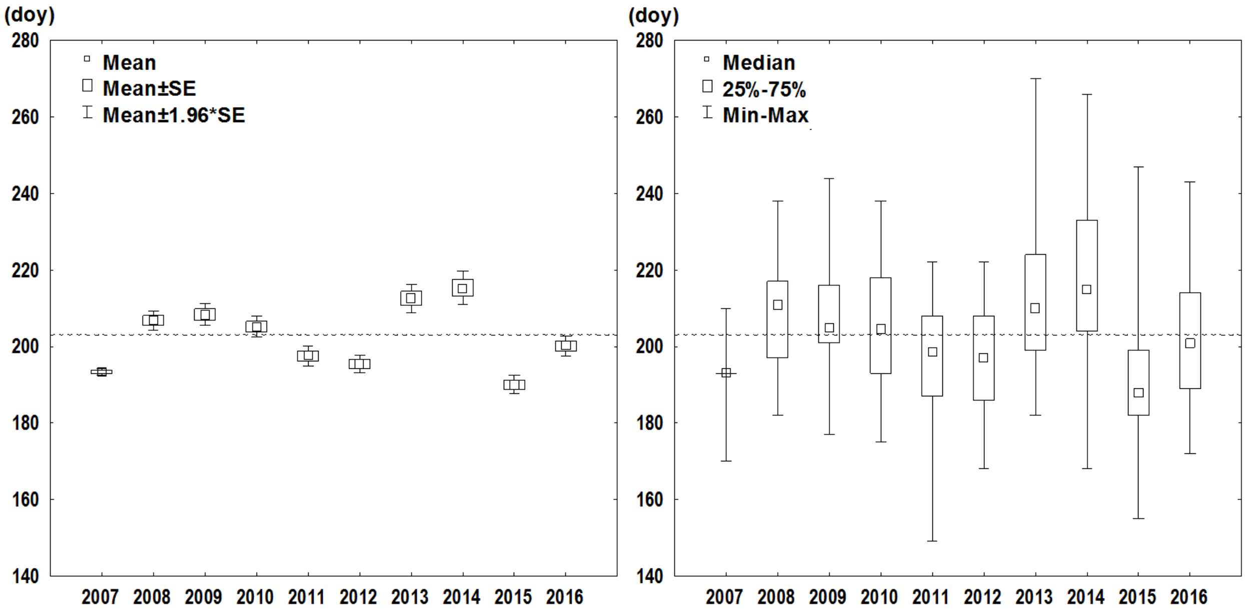


Figure III.5.B.f.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first flowering day (FF) from 2007 to 2016, at inter-specific level. The dotted black line represents the mean value for the whole period.

According to mean and median values, FF occurred in late July (respectively 202 and 201 DOY), while the 75% occurred at the beginning of August (213 DOY) (Table III.5.B.f.1).

The earliest onset of FF was recorded in 2011 in late May (149 DOY), while the latest in 2008 and 2013 at the beginning of July (182 DOY). The FF completion ranged from end of July (210 DOY, in 2007) until late September (270 DOY, in 2013) (Table III.5.B.f.1).

The total duration of FF showed a large variability, from only 40 days (in 2007) to 98 days (in 2014). The FF peak duration ranged from 15 days (in 2009) to 29 days (in 2014), and only in 2007 it was equal to 0 days (Fig. III.5.B.f.1).

Considering 75% quartiles anomalies over the whole dataset, FF showed the largest advance in 2007 (-20 days), and the largest delay in 2014 (+20 days), although both cases without statistically significant differences ($p>0.05$).

Analyzing thus the whole dataset, we did not find any statistically significant trend of FF with time, as tested by linear regression ($p>0.05$).

As tested by linear regression at the inter-annual level, there was a statistically significant relation between FF and FB ($\beta=0.9$, $R^2=0.74$, $p<0.01$) (Fig. III.5.B.f.2), which underlines that FF strongly depend from the patterns of FB.

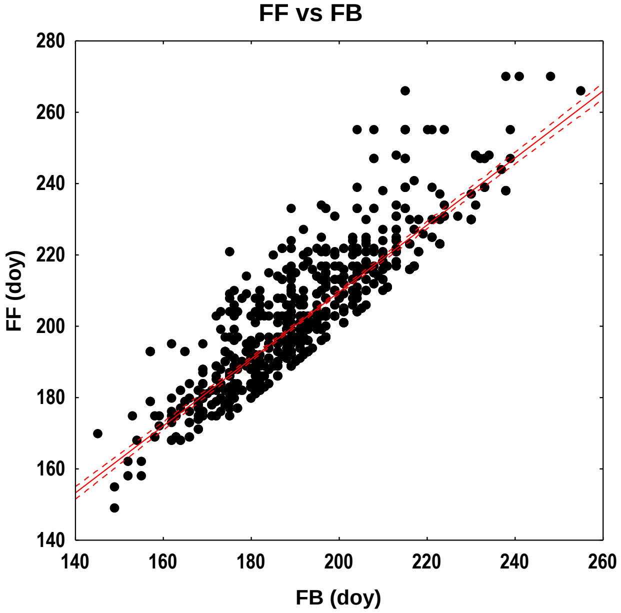


Figure III.5.B.f.2. Relation between first flowering day (FF) and flower buds (FB) as tested by linear regression at inter-annual and inter-specific level ($\beta=0.9$, $R^2=0.74$, $p<0.01$).

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FF of deciduous dwarf shrubs (i.e. *Salix herbacea*) (Fig. III.5.B.f.3) exhibited statistically significant differences among years (F=5, p<0.01) (Fig. III.5.B.f.4).

Over the study period (2007-2016), according to the mean and median values, the FF occurred at mid-July (respectively 199 and 198 DOY), while the 75% coincided to late July (204 DOY) (Table III.5.B.f.2).

Table III.5.B.f.2. Non-parametric statistics of first flowering day (FF) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev.**
2007	6	197	193	193	197	201	201	4.4
2008	5	201	189	197	204	204	211	8.3
2009	5	224	205	223	223	230	237	11.9
2010	6	199	183	189	198	206	221	13.7
2011	5	198	192	192	197	200	208	6.6
2012	6	194	186	186	194	197	208	8.5
2013	6	203	189	189	201	203	234	16.5
2014	5	203	197	204	204	204	208	4.0
2015	5	184	176	180	184	184	195	7.1
2016	7	194	181	186	195	201	201	8.0
2007-2016	56	199	176	191	198	204	237	12.9

Considering the intra-annual variability, the earliest onset of FF was recorded between late June (176 DOY, in 2015) and late July (205 DOY, in 2009). The FF completion spanned from mid-July (195 DOY, in 2015) to late August (237 DOY, in 2009) (Table III.5.B.f.2).
For deciduous dwarf shrubs, the total duration of FF ranged from 8 days (in 2007) to 45 days (in 2013), while the FF peak ranged from 0 (in 2014) to 17 days (in 2010) (Table III.5.B.f.2).

Analyzing the anomalies of the 75% quartiles, the FF showed a large variability, with the largest advance in 2015 (-20 days) and the greatest delay in 2009 (+26 days) (Fig. III.5.B.f.4). As tested by t-test, 2009 was the only year showing statistically significant differences (p<0.01), and thus identifiable as “extreme” concerning its FF, likewise already observed for FB.

Thus considering only the “normal” years of FF (excluding 2009) we did not find any statistically significant trend, as tested by linear regression.
Moreover, we found a high statistically significant linear relation between FF and FB, as tested by linear regression at the inter-annual level (β=0.9, R2=0.92, p<0.01).

Figure III.5.B.f.3. Flowers of a) male and b) female individuals of *Salix herbacea*.

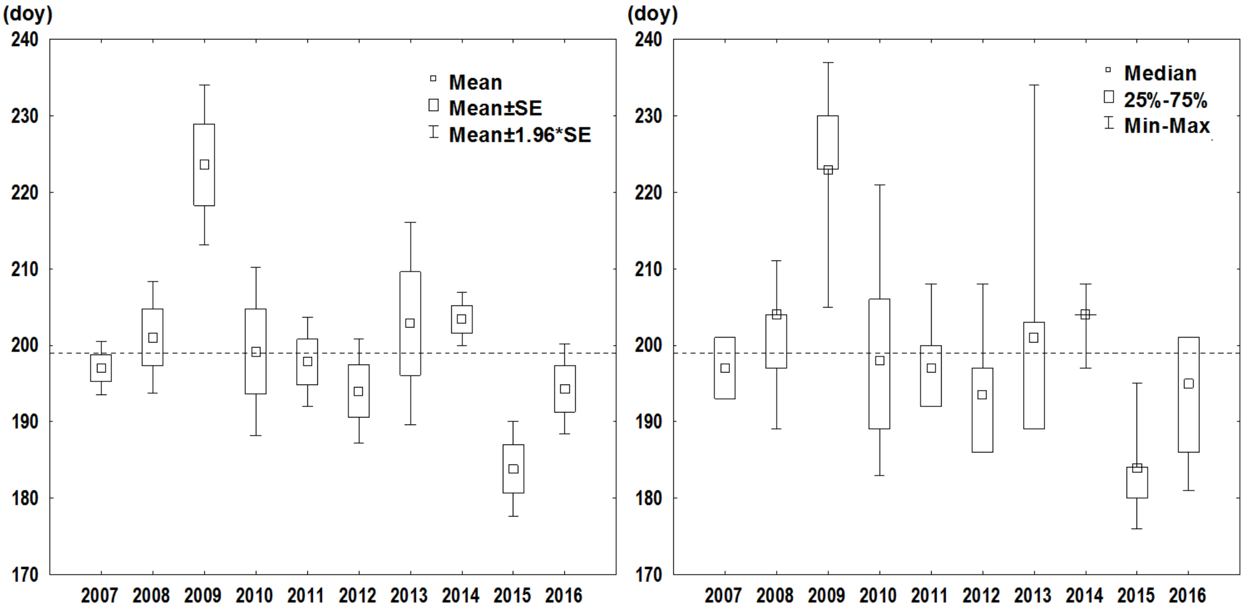


Figure III.5.B.f.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first flowering day (FF) for deciduous dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Deciduous shrubs

The FF for deciduous shrubs (i.e. *Vaccinium uliginosum*) was observed only in 7 years as in the years 2007, 2011 and 2013 there was no flowering. As tested by one-way ANOVA, over the years with available data, the FB exhibited statistically significant differences among years (F=32, p<0.01) (Fig III.5.B.f.5).

Table III.5.B.f.3. Non-parametric statistics of first flowering day (FF) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	0							
2008	2	228	217	217	228	238	238	14.8
2009	2	234	230	230	234	237	237	4.9
2010	2	201	199	199	201	203	203	2.8
2011	0							
2012	1	222	222	222	222	222	222	-
2013	0							
2014	4	204	204	204	204	204	204	-
2015	4	183	180	182	184	184	184	2.0
2016	3	197	195	195	195	201	201	3.5
2007-2016	18	205	180	195	204	217	238	17.8

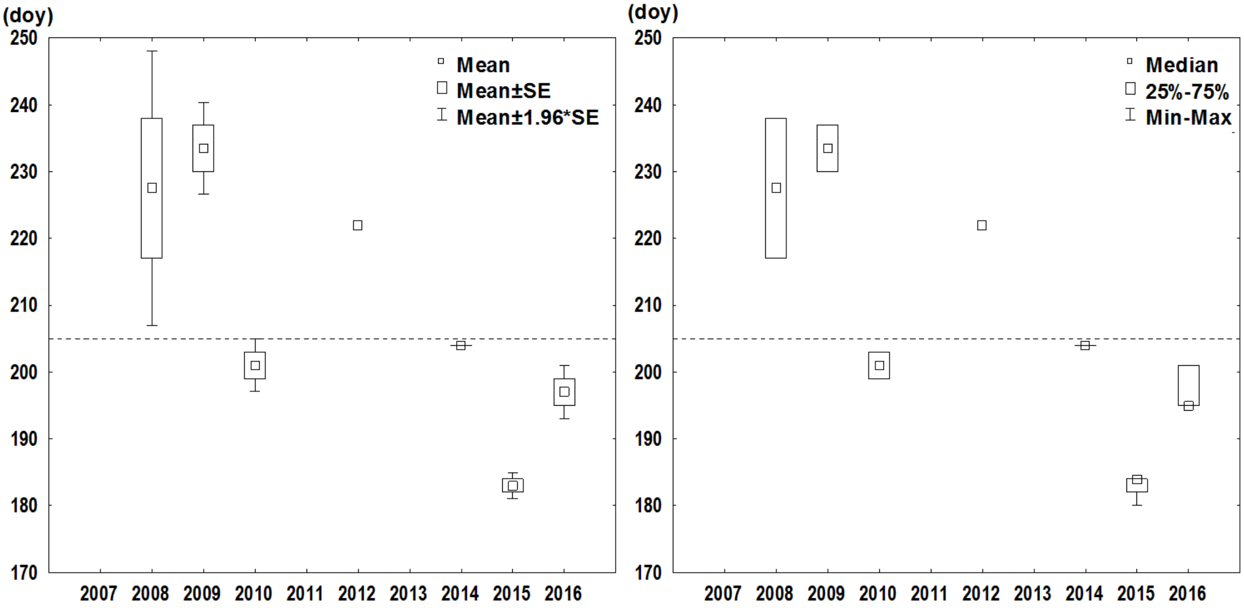


Figure III.5.B.f.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first flowering day (FF) for deciduous shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Over the study period (2007-2016), according to the mean and median values, the FF occurred at late July (respectively 205 and 204 DOY), while the 75% quartile occurred at the beginning of August (217 DOY) (Table III.5.B.f.3).

The FF followed a pattern similar to what observed for FB. Considering the intra-annual variability, the earliest onset of FF at the end of June (180 DOY, in 2015), while the latest at mid-August (230 DOY, in 2009). The FF completion was achieved between the beginning of July (184 DOY, in 2015) to late August (238 DOY, in 2008) (Table III.5.B.f.3).

The total duration of FF for deciduous shrubs ranged from 0 (in 2012 and 2014) to 21 days (respectively in 2008) (Table III.5.B.f.3).

Considering the anomalies of the 75% quartiles, the FF showed the largest delay in 2008 (+21 days), and the largest advance in 2015 (-33 days) (Fig. III.5.B.f.5). However, as tested by t-test, we did not identify statistically significant differences ($p>0.05$).

Analyzing thus the whole dataset, we found a statistically significant advance of FF over the study period ($\beta=-4.7$, $R^2=0.63$, $p=0.03$) (Fig. III.5.B.f.6).

Moreover, also deciduous dwarf shrubs displayed a high statistically significant linear relation between FF and FB ($\beta=0.7$, $R^2=0.85$, $p<0.01$).

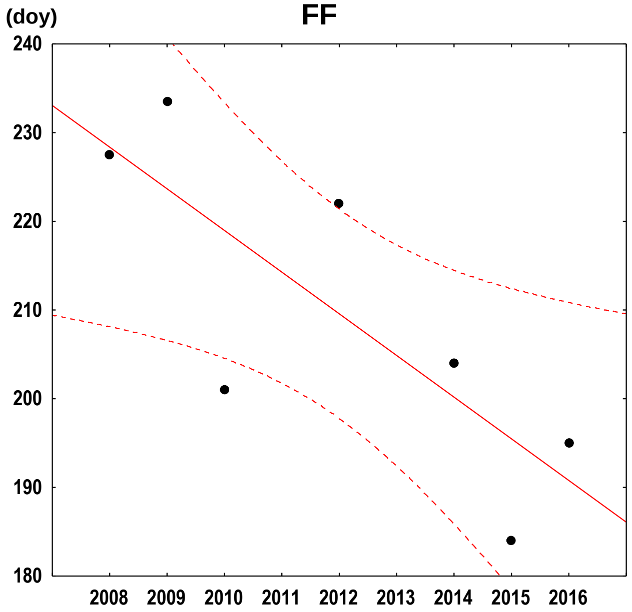


Figure III.5.B.f.6. Trend of FF with time ($\beta=-4.7$, $R^2=0.63$, $p=0.03$) for deciduous shrubs, as tested by linear regression.

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FF of evergreen dwarf shrubs (i.e. *Kalmia procumbens*) exhibited statistically significant differences among years ($F=4$, $p<0.01$) (Fig. III.5.B.f.7-8).

Over all the study period (2007-2016), according to the mean and median values, the FF for the evergreen dwarf shrubs occurred at beginning of July (respectively 183 and 182 DOY), or few days later (186 DOY) according to the 75% quartile (Table III.5.B.f.4).
The earliest onset of FF (162 DOY, mid-June) was recorded in 2015, while the latest in 2010 (183 DOY, beginning of July). The end of FF ranged from late June (178 DOY, in 2012) to end of July (211 DOY, in 2008) (Table III.5.B.f.4).

Table III.5.B.f.4. Non-parametric statistics of first flowering day (FF) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev..
2007	6	181	179	179	179	179	193	5.7
2008	3	194	182	182	189	211	211	15.1
2009	4	188	181	183	188	193	194	6.0
2010	6	186	183	183	186	186	193	3.7
2011	6	178	169	175	175	187	187	7.3
2012	6	175	171	174	174	178	178	2.7
2013	6	189	182	185	189	192	196	5.0
2014	6	184	177	177	182	182	204	10.1
2015	6	177	162	173	178	184	184	8.3
2016	6	182	179	179	181	186	186	3.2
2007-2016	55	183	162	178	182	186	211	8.2

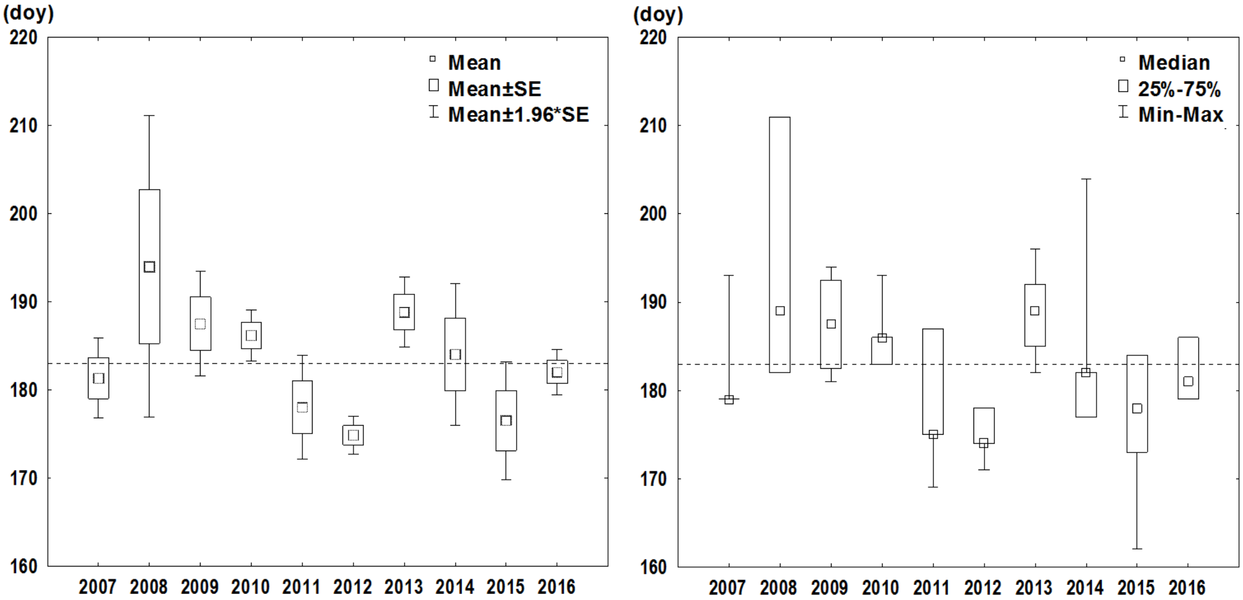


Figure III.5.B.f.7. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first flowering day (FF) for evergreen dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

The total duration of FF for evergreen dwarf shrubs ranged from only one week (in 2012 and 2016) to 29 days (in 2008), while the FF peak duration followed a similar variability, ranging from 0 days (in 2007) to 29 days (in 2008).

Figure III.5.B.f.8. Flowers of *Kalmia procumbens*.

Considering the anomalies of the 75% quartiles, the FF showed the largest delay in 2008 (+25 days). Likewise FB, 2008 was the only one year statistically significant different and thus identifiable as "extreme", as tested by t-test ($p<0.01$) (Fig. III.5.B.f.7).

Analyzing thus only "normal" years for the FF (removing 2008), we did not find statistically significant trend with time, tested by linear regression ($p>0.05$).

Also in this case FF exhibited a statistically significant relation with FB, as tested by linear regression at the inter-annual level ($\beta=0.5$, $R^2=0.53$, $p<0.01$).

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FF of evergreen shrubs (i.e. *Rhododendron ferrugineum*) exhibited statistically significant differences among years ($F=4$, $p<0.01$) (Fig. III.5.B.f.9).

Over all the study period (2007-2016), mean and median values of FF occurred at mid-July (194 and 193 DOY), while the 75% coincided at late July (199 DOY) (Table III.5.B.f.5).

Considering each single year, the earliest onset of FF was recorded in late June (178 DOY, in 2012), while the latest at mid-July (197 DOY, in 2014). The end of FF spanned from mid-July (193 DOY, in 2007) to early August (216 DOY, in 2009) (Table III.5.B.f.5).

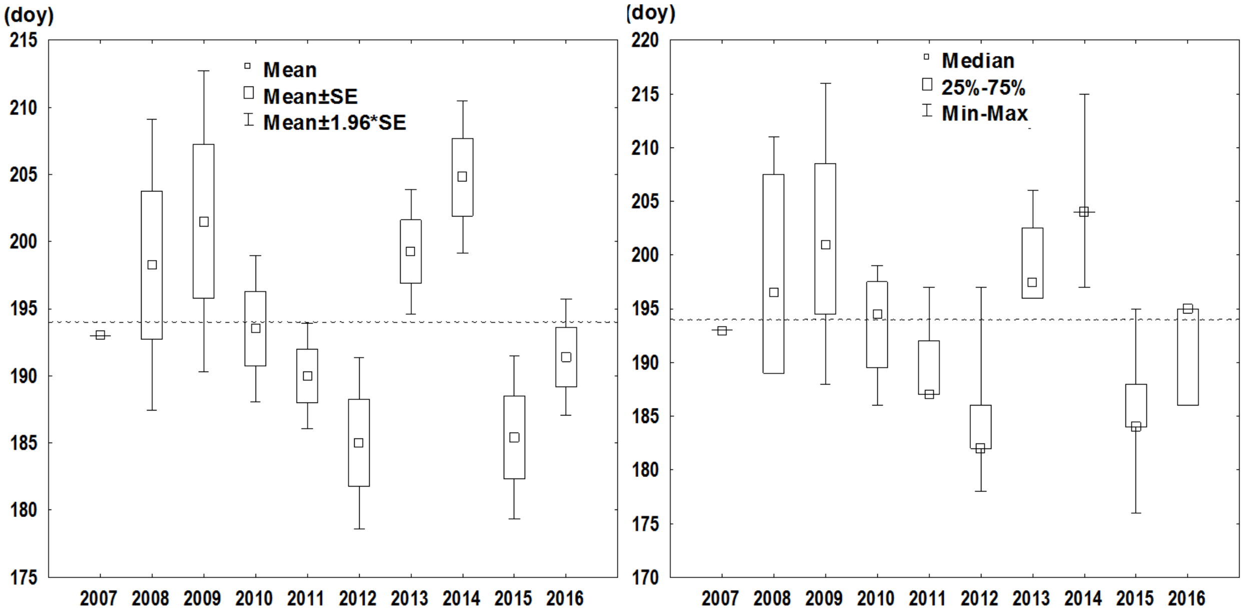


Figure III.5.B.f.9. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first flowering day (FF) for evergreen shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Table III.5.B.f.5. Non-parametric statistics of first flowering day (FF) for evergreen shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	4	193	193	193	193	193	193	-
2008	4	198	189	189	197	208	211	11.1
2009	4	202	188	195	201	209	216	11.4
2010	4	194	186	190	195	198	199	5.6
2011	5	190	187	187	187	192	197	4.5
2012	5	185	178	182	182	186	197	7.3
2013	4	199	196	196	198	203	206	4.7
2014	5	205	197	204	204	204	215	6.5
2015	5	185	176	184	184	188	195	6.9
2016	5	191	186	186	195	195	195	4.9
2007-2016	45	194	176	187	193	199	216	9.0

Thus considering only the period 2008-2016, the total duration of FF for the evergreen shrubs ranged from 9 days (in 2016) to 28 days (in 2009), while the FF peak duration ranged from 0 to 19 days maximum (respectively in 2014 and 2008) (Fig. III.5.B.f.9).

Considering the anomalies of the 75% quartiles, the FF showed the largest advance in 2012 (-13 days), and the largest delay in 2009 (+10 days), although we did not find statistically significant differences, as tested by t-test (p>0.05) (Fig. III.5.B.f.9).

Considering thus the whole period (2007-2016) we did not find statistically significant trend of the FF with time for evergreen shrubs, as tested by linear regression ($p>0.05$).

There was, again, a statistically significant relation between FF and FB, as tested by linear regression at the inter-annual level ($\beta=0.7$, $R^2=0.69$, $p<0.01$).

Forbs

Considering all the study period, FF of forbs (Fig. III.5.B.f.10) exhibited statistically significant differences among years, as tested by one-way ANOVA ($F=37$, $p<0.01$) (Fig. III.5.B.f.11).

The mean and median values for the FF over the whole period (2007-2016) were almost coincident (205 and 203 DOY, mid/late July), while the 75% quartile occurred at the beginning of August (213 DOY) (Table III.5.B.f.6).

Figure III.5.B.f.10. First flowering for *Cardamine resedifolia*.

The beginning of FF occurred, in mid-June (169 DOY, in 2011) and ranged up to mid-July (192 DOY, in 2013). The end of FF ranged from mid-July (201 DOY, in 2007) to late September (270 DOY, in 2013) (Table III.5.B.f.6).

The total duration of FF spanned from 22 days (in 2007) to a maximum of 78 days (in 2013), while the FF peak duration ranged from 11 (in 2011 and 2015) to 27 days (in 2014). Only in 2007 we recorded an anomalous peak duration of only 0 days (Table III.5.B.f.6.).

Comparing the 75% anomalies, FF showed the largest delay in 2014 (+20 days), while the earliest FF occurred in 2007 (-20 days). Tested by t-test we did not find statistically significant differences among years ($p>0.05$) (Fig. III.5.B.f.11).

Considering thus the whole study period (2007-2016) we did not identify statistically significant trend of FF with time, as tested by linear regression ($p>0.05$).

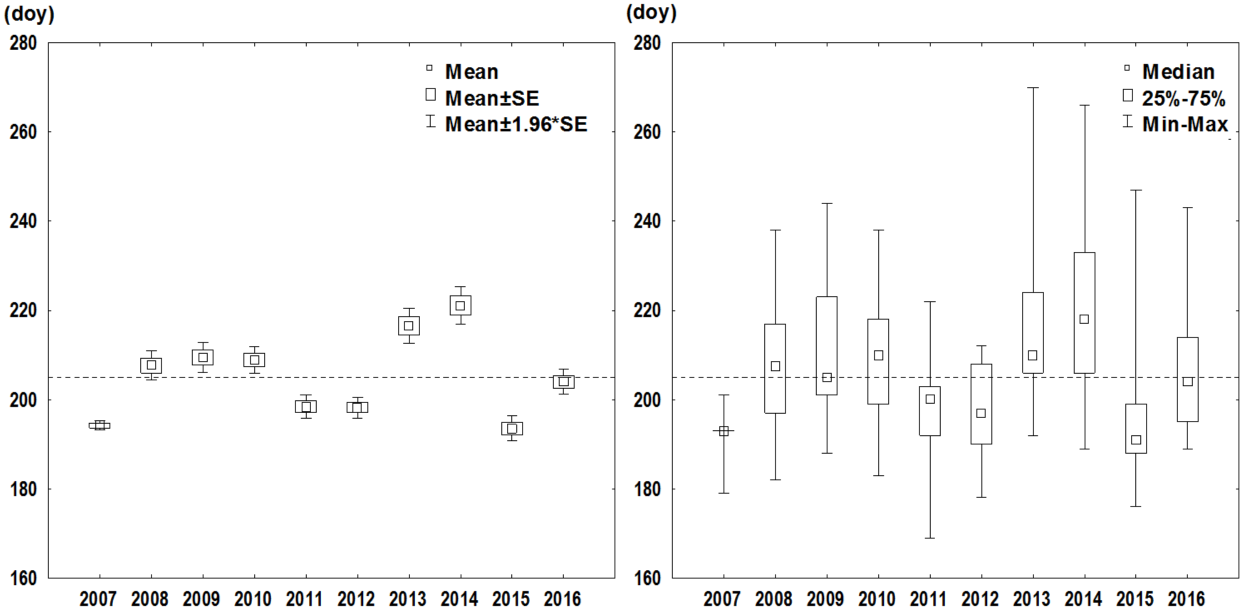


Figure III.5.B.f.11. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first flowering day (FF) for forbs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Table III.5.B.f.6. Non-parametric statistics of first flowering day (FF) for forbs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	194	179	193	193	193	201	4.3
2008	50	208	182	197	208	217	238	11.9
2009	59	210	188	201	205	223	244	13.1
2010	63	209	183	199	210	218	238	11.9
2011	66	198	169	192	200	203	222	10.9
2012	66	198	178	190	197	208	212	9.6
2013	60	217	192	206	210	224	270	15.6
2014	60	221	189	206	218	233	266	16.8
2015	64	194	176	188	191	199	247	11.4
2016	55	204	189	195	204	214	243	10.6
2007-2016	606	205	169	193	203	213	270	14.9

Likewise the other growth forms and the overall pattern, we found a statistically significant relation between FF and FB, as tested by linear regression ($\beta=0.8$, $R^2=0.70$, $p<0.01$).

Graminoids

As tested by one-way ANOVA, overall the study period (2007-2016) the FF of graminoids (Fig. III.5.B.f.12) exhibited statistically significant differences among years (F=7, p<0.01) (Fig. III.5.B.f.13).

Over the study period (2007-2016), mean and median values of FF were coincident, and occurred in late July (202 DOY), while the 75% quartile coincided with early August (216 DOY) (Table III.5.B.f.7).

Figure III.5.B.f.12. Flower of *Carex curvula*.

Considering the intra-annual variability, the earliest onset of FF was recorded between the end of May (149 DOY, in 2011) and the end of June (182 DOY, in 2008 and 2013). The FF completion ranged from late July (210 DOY, in 2007) to late September (270 DOY, in 2013) (Table III.5.B.f.7).

The total duration of FF ranged from 40 days (in 2007) to 98 days (in 2014), while the FF peak duration was concentrated to 13 days only (in 2008) or to 70 days (in 2014) (Fig. III.5.B.f.13).

Considering the anomalies of the 75% quartiles, in 2007 the FF displayed the largest advance (-23 days), while in 2014, it showed the largest delay (+31 days) (Fig. III.5.B.f.13). However, 2014 was the only one year identified as statistically significant different, as tested by t-test (p=0.01).

Considering thus only the “normal” years (removing 2014 as “extreme” FF) we did not observe any trend of FF with time, as tested by linear regression (p>0.05).

Likewise other growth forms, there was a statistically significant relation between FF and FB, as tested by linear regression (β=1.0, R^2=0.75, $p<0.01$).

Table III.5.B.f.7. Non-parametric statistics of first flowering day (FF) for graminoids computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	37	193	170	193	193	193	210	5.1
2008	31	207	182	204	211	217	238	11.8
2009	35	206	177	191	216	216	237	16.6
2010	37	204	175	183	210	221	230	18.9
2011	38	200	149	181	208	217	222	19.7
2012	38	195	168	178	197	208	215	16.3
2013	36	213	182	189	213	229	270	24.5
2014	35	215	168	177	221	247	266	34.1
2015	36	188	155	173	193	203	223	17.2
2016	31	200	172	179	204	214	222	17.8
2007-2016	354	202	149	186	202	216	270	21.0

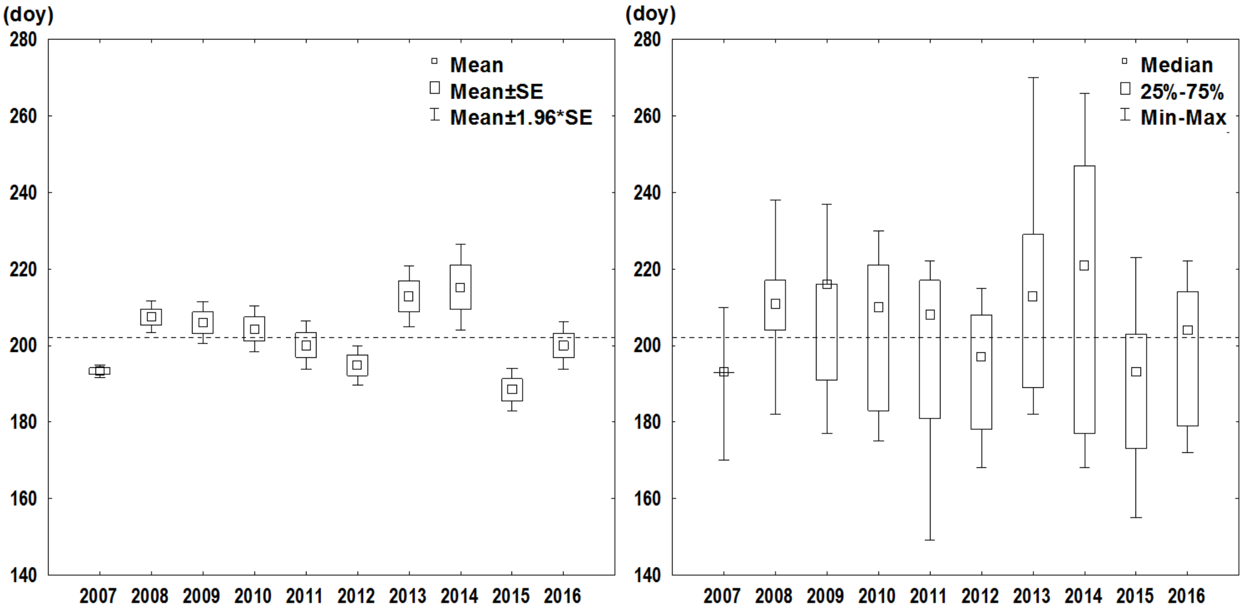


Figure III.5.B.f.13. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first flowering day (FF) for graminoids from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Comparison of trends among growth forms

Comparing the patterns of FF among the selected growth forms at the inter-annual level, we found large and statistically significant differences (Fig. III.5.B.f.14), as tested by one-way ANOVA (F=21, $p<0.01$).

Graminoids exhibited the greatest FF duration (121 days) and the greatest FF peak duration (30 days). On the opposite the evergreen shrubs exhibited the lowest FF duration (40 days) while evergreen dwarf shrubs the lowest FF peak duration (8 days).

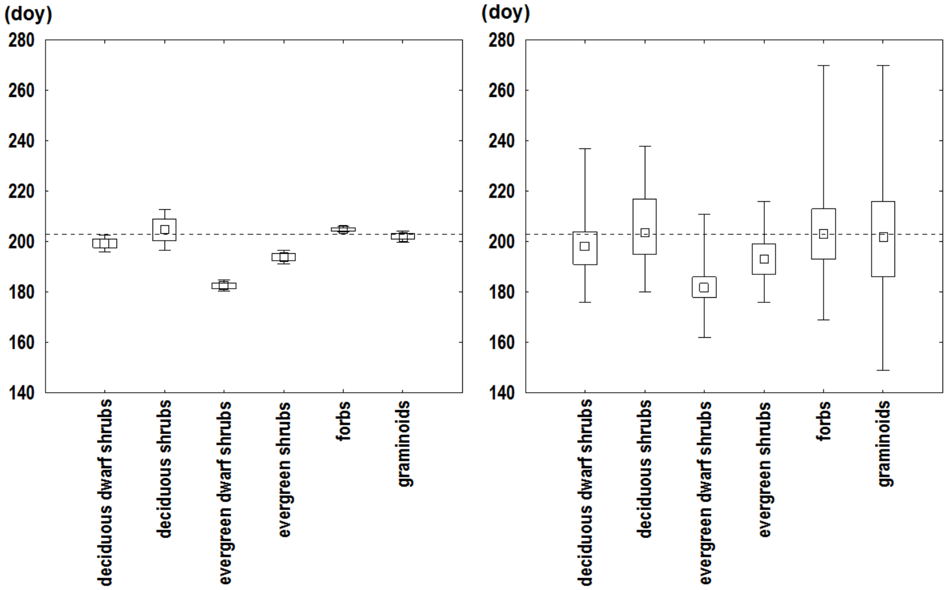


Figure III.5.B.f.14. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first flowering day (FF) between the selected growth forms over the period 2007-2016. The dotted black line represents the mean value for the whole period.

The first species starting FF were graminoids (149 DOY, end of May), likewise FB, while deciduous shrubs were the last species to start FF (180 DOY, end of June). The latest FF completion occurred simultaneously for graminoids and forbs at the end of September (270 DOY) (Fig. III.5.B.f.14). On the contrary, the evergreen dwarf shrubs were the first growth form to complete FF (211 DOY, end of July).

According to the 75% quartiles anomalies referred to all dataset, the evergreen dwarf shrubs and evergreen shrubs exhibited the earliest FF (respectively -27 and -14 days). As tested by t-test, the evergreen dwarf shrubs was the only one growth forms exhibiting a statistically significant advance of the FF (p<0.01)

Considering all species and all years (inter-annual and inter-specific), we did not observe any statistically significant trend with time concerning the FF.

However, likewise FB, the analysis of the single growth form highlighted that deciduous shrubs were the growth forms with the highest potential to exhibit an earlier FF. Indeed, only deciduous shrubs showed a statistically significant advance of FF with time, and then could provide a higher capability to cope their FB to an earlier start of the growing season compared to graminoids.

The patterns of FF thus resemble those of FB. Indeed, when tested by linear regression between FF and FB, we found statistically significant relation, both at inter-specific and inter-annual level but also at the intra-growth form and inter-annual level.

III.5.B.g. *In full bloom. Patterns of Main Flowering day (MF)*

Analogously to the other phenophases, our analyses have been carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2007-2016), also the main flowering day (MF) showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=30, $p<0.01$) (Fig. III.5.B.g.1).

Table III.5.B.g.1. Non parametric statistics of main flowering day (MF) computed for each single year, as well as for the entire monitoring period (2007-2016), at inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	116	201	179	201	201	201	219	5.8
2008	95	218	182	211	217	238	245	15.3
2009	117	211	181	201	216	223	244	14.7
2010	118	208	183	196	210	221	238	15.0
2011	120	202	169	192	202	213	232	14.2
2012	122	201	168	190	203	212	222	13.9
2013	112	214	182	199	210	226	270	20.1
2014	115	215	168	204	215	233	266	24.1
2015	120	194	162	188	191	203	247	12.7
2016	107	202	175	189	204	214	243	13.9
2007-2016	1142	206	162	194	204	216	270	17.2

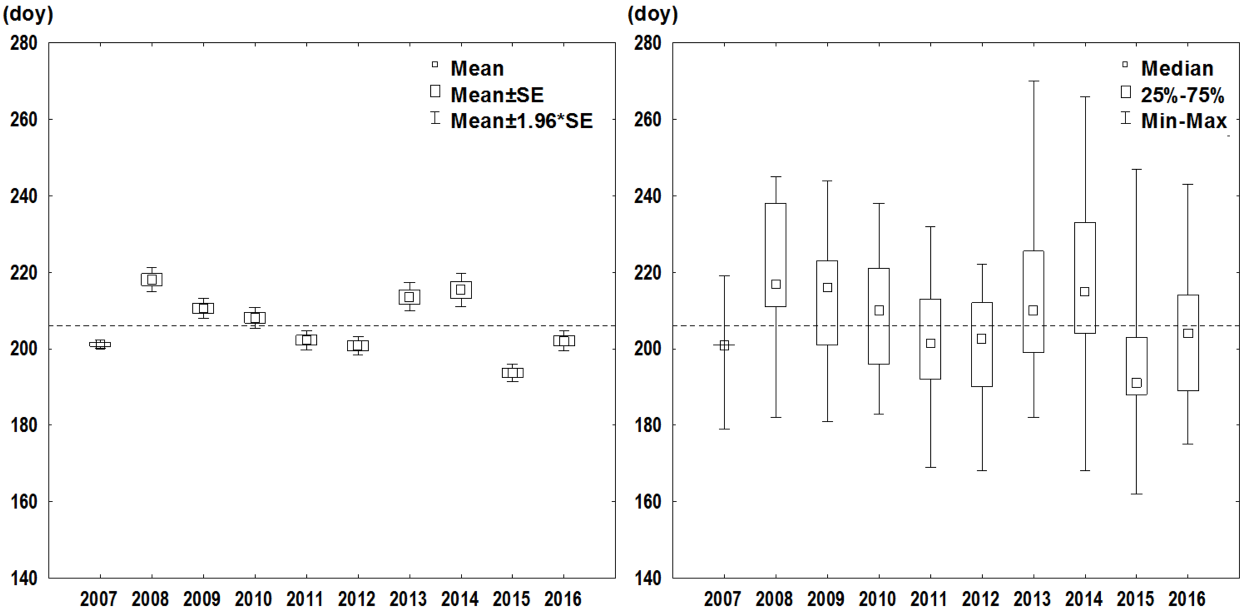


Figure III.5.B.g.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) from 2007 to 2016, at inter-specific level. The dotted black line represents the mean value for the whole period.

According to mean and median values, MF occurred in late July (respectively 206 and 204 DOY), while the 75% quartile occurred in early August (216 DOY) (Table III.5.B.g.1), only three days later than the 75% quartile of FF.

The earliest onset of MF was recorded in 2015 in mid-June (162 DOY), while the latest in 2010 at the beginning of July (183 DOY). The MF completion ranged from early August (219 DOY, in 2007) until late September (270 DOY, in 2013) (Table III.5.B.g.1).

The total duration of MF showed the same variability of FF, ranging from 40 days (in 2007) to 98 days (in 2014). Similarly, the MF peak duration ranged from 15 days (in 2015) to 29 days (in 2014), and only in 2007 it was equal to 0 days (Fig. III.5.B.g.1).

Considering 75% quartiles anomalies over the whole dataset, MF showed the largest advance in 2007 (-15 days), and the largest delay in 2014 (+22 days), although in both cases without statistically significant differences ($p>0.05$).
Analyzing thus the whole dataset (2007-2016), we did not find any statistically significant trend, as tested by linear regression ($p>0.05$).

Likewise FF, we found a high statistically significant relation between MF and FB, as tested by linear regression at the inter-annual and inter-specific level ($\beta=0.9$, $R^2=0.73$, $p<0.01$) (Fig. III.5.B.g.2a). As could be expected, we also observed a statistically significant relation between MF and FF at inter-annual and inter-specific level, as tested by linear regression ($\beta=1.0$, $R^2=0.92$, $p<0.01$) (Fig. III.5.B.g.2b).

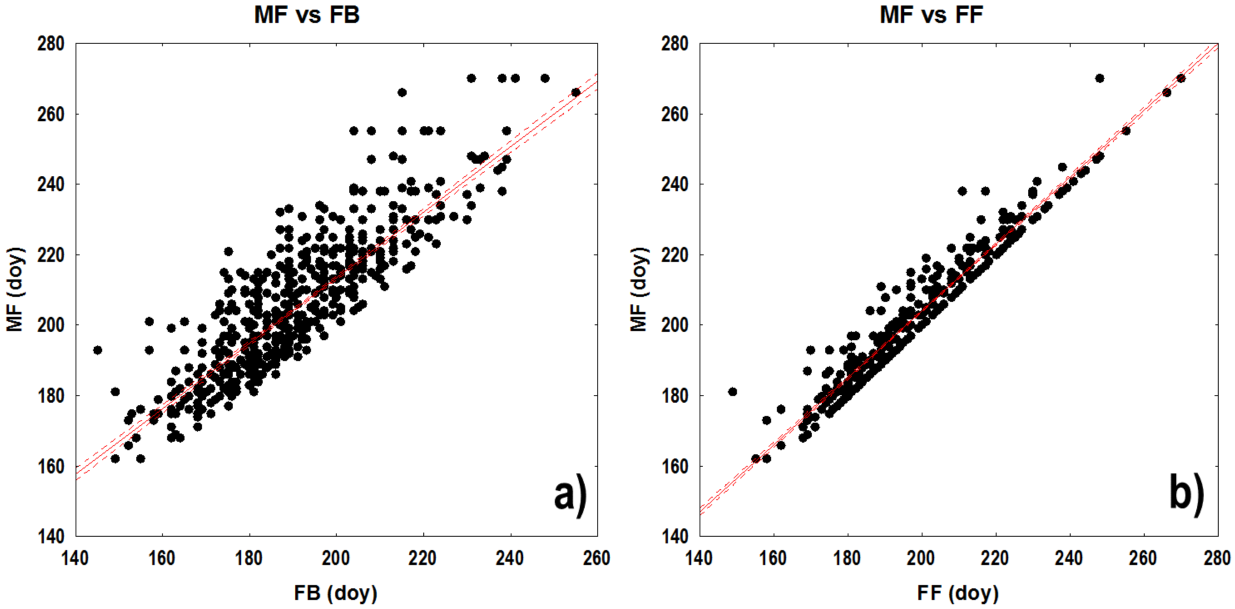


Figure III.5.B.g.2. Relation between a) main flowering day (MF) and flower buds (FB) as tested by linear regression at inter-annual and inter-specific level ($\beta=0.9$, $R^2=0.73$, $p<0.01$) and b) main flowering day (MF) and first flowering day (FF) as tested by linear regression an inter-annual and inter-specific level ($\beta=1.0$, $R^2=0.92$, $p<0.01$)

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the MF of deciduous dwarf shrubs (i.e. *Salix herbacea*) (Fig. III.5.B.g.3) exhibited statistically significant differences among years (F=7, p<0.01) (Fig. III.5.B.g.4).

Table III.5.B.g.2. Non-parametric statistics of main flowering day (MF) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	**Mean**	**Minimum**	**25%**	**Median**	**75%**	**Maximum**	**Std.Dev.**
2007	6	207	201	201	210	210	210	4.6
2008	5	217	204	211	217	217	238	12.7
2009	5	229	216	230	230	230	237	7.7
2010	6	203	189	193	201	206	225	13.0
2011	5	199	192	197	197	200	208	5.9
2012	6	200	190	190	197	212	212	10.1
2013	6	203	189	189	201	203	234	16.5
2014	5	203	197	204	204	204	208	4.0
2015	5	187	180	180	188	188	199	7.8
2016	7	196	186	186	195	204	204	7.7
2007-2016	56	204	180	195	203	210	238	13.9

Figure III.5.B.g.3. Example of main flowering of *Salix herbacea.*

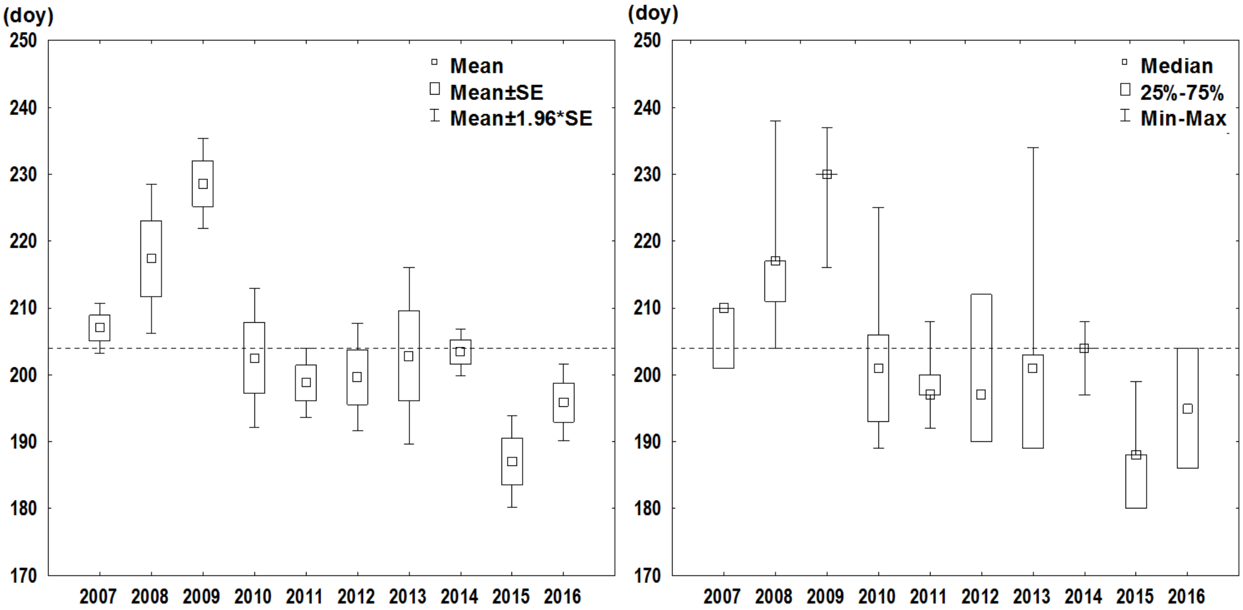


Figure III.5.B.g.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) for deciduous dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Over the study period (2007-2016), according to the mean and median values, the MF occurred in late July (respectively 204 and 203 DOY), while the 75% occurred one week later (210 DOY) (Table III.5.B.g.2).

Considering the intra-annual variability, the earliest onset of MF was recorded at the end of June (180 DOY, in 2015), while the latest in late July (204 DOY, in 2008). The end of MF spanned from mid-July (199 DOY, in 2015) to late August (238 DOY, in 2008) (Table III.5.B.g.2).

For deciduous dwarf shrubs, the total duration of MF ranged from 9 days (in 2007) to 36 days (in 2010), while the MF peak duration spanned from 0 days (in 2009 and 2014) to 22 days (in 2012) (Table III.5.B.g.2).

Analyzing the anomalies of the 75% quartiles, the MF showed the largest advance in 2015 (-22 days) and the greatest delay in 2009 (+20 days) (Fig. III.5.B.g.4). As tested by t-test, 2009 was the only one year that showed statistically significant differences ($p<0.01$), and was thus identifiable as “extreme” concerning its MF (likewise FB and FF).

Thus considering only the “normal” years of MF (excluding 2009) we observed a statistically significant advance of MF ($\beta=-2.1$, $R^2=0.59$, $p=0.02$) (Fig. III.5.B.g.5).

Moreover, there was a statistically significant relation between MF and FB ($\beta=0.9$, $R^2=0.79$, $p<0.01$) and between MF and FF ($\beta=1.0$, $R^2=0.82$, $p<0.01$), as tested by linear regression at the inter-annual level.

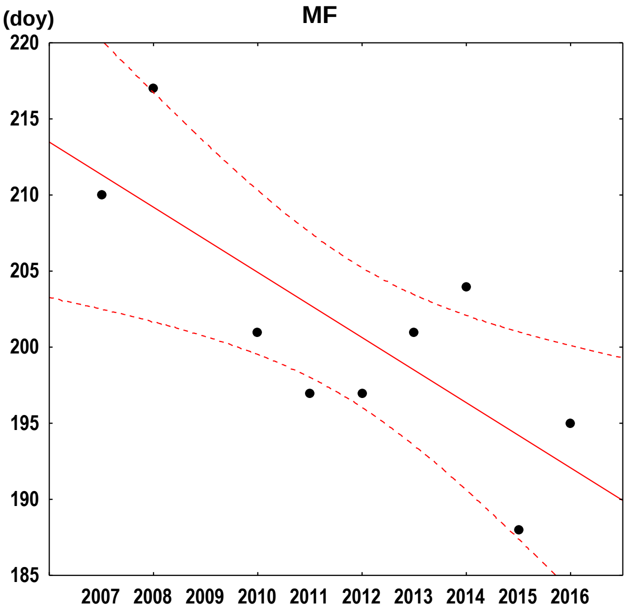


Figure III.5.B.g.5. Trends with time of MF (β=-2.1, R^2=0.59, p=0.02) for deciduous dwarf shrubs, as tested by linear regression.

Deciduous shrubs

The MF for deciduous shrubs (i.e. *Vaccinium uliginosum*) (Fig. III.5.B.g.6) was observed only in 7 years, as there was no flowering production in 2007, 2011 and 2013. As tested by one-way ANOVA, over the years with available data, the MF exhibited statistically significant differences among years (F=119, p<0.01) (Fig. III.5.B.g.7).

Photo III.5.B.g.6. Example of a) main flowering of *Vaccinium uliginosum*.

Over the study period (2007-2016), according to the mean and median values, the MF occurred at late July (respectively 207 and 204 DOY), while the 75% quartile occurred at early August (222 DOY) (Table III.5.B.g.3).

Table III.5.B.g.3. Non-parametric statistics of main flowering day (MF) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	0							
2008	2	242	238	238	242	245	245	4.9
2009	2	234	230	230	234	237	237	4.9
2010	2	201	199	199	201	203	203	2.8
2011	0							
2012	1	222	222	222	222	222	222	-
2013	0							
2014	4	204	204	204	204	204	204	-
2015	4	187	184	186	188	188	188	2.0
2016	3	197	195	195	195	201	201	3.5
2007-2016	18	207	184	195	204	222	245	19.0

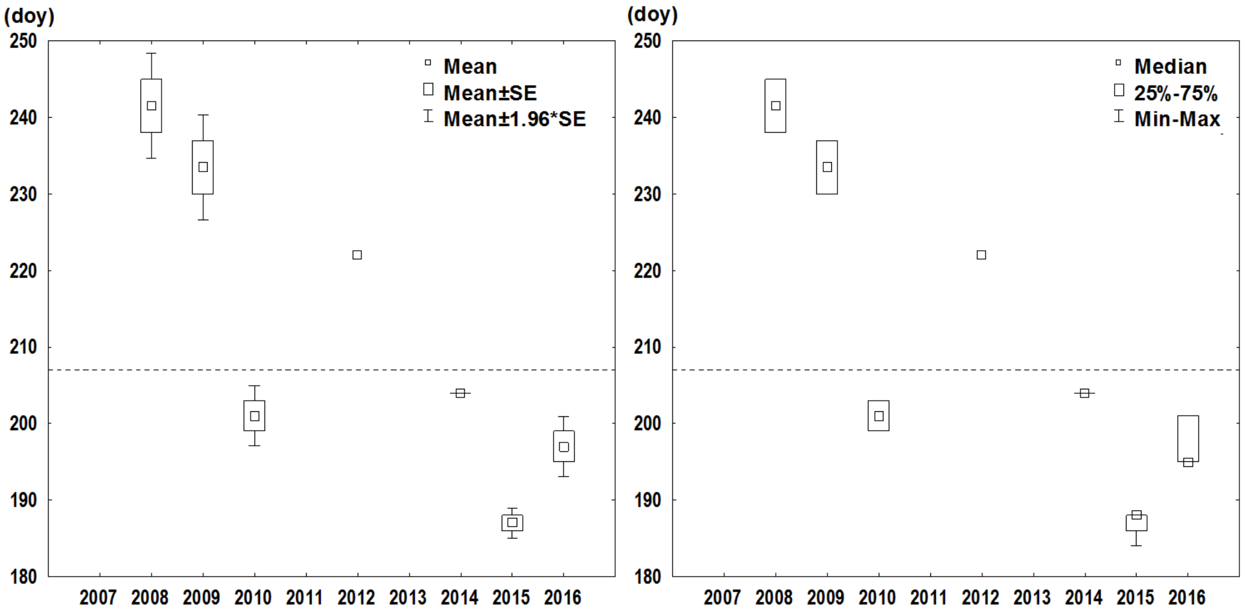


Figure III.5.B.g.7. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) for deciduous shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

The MF followed a pattern similar to what observed for FB and FF. The earliest onset of MF was recorded from early July (184 DOY, in 2015) to late August (238 DOY, in 2008), while the MF completion spanned from early July (188 DOY, in 2015) to early September (245 DOY, in 2008) (Table III.5.B.g.3).

The total duration of MF for deciduous shrubs ranged from 0 (in 2012 and 2014) to 7 days (in 2008 and 2009), and the MF peak duration was same as total duration (Table III.5.B.g.3).

Considering the anomalies of the 75% quartiles, the MF showed the largest delay in 2008 (+23 days), and the largest advance in 2015 (-34 days) (Fig. III.5.B.g.7), although as tested by t-test, we did not identify statistically significant differences ($p>0.05$).

Analyzing thus the whole dataset, we found a statistically significant advance of MF over the study period ($\beta=-5.5$, $R^2=0.70$, $p=0.02$) (Fig. III.5.B.g.8), thus resembling the advance of FB and FF.

Tested by linear regression at the inter-annual level, there was a statistically significant relation between MF and FB ($\beta=0.8$, $R^2=0.87$, $p<0.01$), and between MF and FF ($\beta=1.0$, $R^2=0.93$, $p<0.01$).

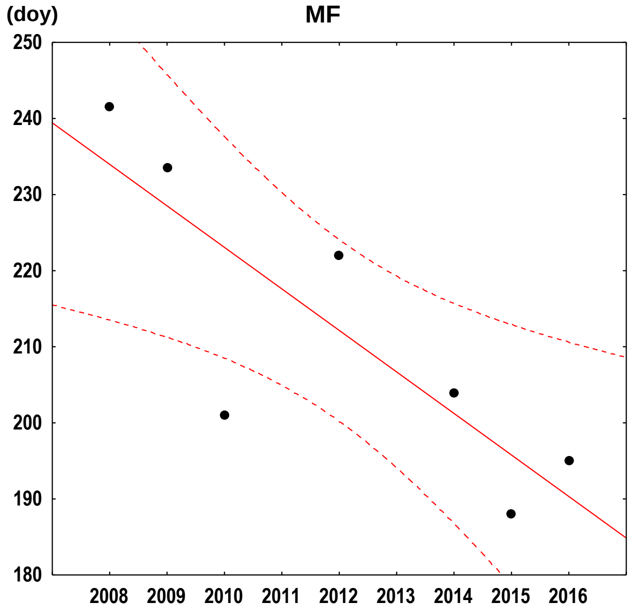


Figure III.5.B.g.8. Trend with time of MF ($\beta=-5.5$, $R^2=0.70$, $p=0.02$) for deciduous shrubs, as tested by linear regression.

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the MF of evergreen dwarf shrubs (i.e. *Kalmia procumbens*) (Fig. III.5.B.g.9) exhibited statistically significant differences among years ($F=4$, $p<0.01$) (Fig. III.5.B.g.10).

Over all the study period (2007-2016), according to the mean and median values, the MF for the evergreen dwarf shrubs occurred at early July (respectively 187 and 186 DOY), or at mid-July (192 DOY) according to the 75% quartile (Table III.5.B.g.4).

The earliest onset of MF was recorded in late June (174 DOY, in 2012) up to early July (189 DOY, in 2008). The end of MF ranged from early July (188 DOY, in 2015) to early August (217 DOY, in 2008) (Table III.5.B.g.4).

Table III.5.B.g.4. Non-parametric statistics of main flowering day (MF) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev..
2007	6	191	179	193	193	193	193	5.7
2008	3	203	189	189	204	217	217	14.0
2009	4	188	181	183	188	193	194	6.0
2010	6	188	183	186	189	189	193	3.4
2011	6	183	175	175	184	187	192	7.0
2012	6	181	174	182	182	182	186	3.9
2013	6	190	182	189	191	192	196	4.7
2014	6	184	177	177	182	182	204	10.1
2015	6	182	176	176	182	188	188	5.5
2016	6	185	181	181	186	189	189	3.6
2007-2016	55	187	174	182	186	192	217	7.9

Figure III.5.B.g.9. Example of main flowering of *Kalmia procumbens*.

The total duration of MF for evergreen dwarf shrubs ranged from 8 days (in 2016) to 28 days (in 2008). The MF peak duration followed a similar variability, ranging from 0 days (in 2007 and 2012) to 28 days (in 2008).

Considering the anomalies of the 75% quartiles, the MF showed the largest delay in 2008 (+25 days) and advanced in 2012 and 2014 (-10 days) (Fig. III.B.5.g.10). Likewise the patterns of FB and FF, 2008 was the only one year statistically significant different and thus identifiable as "extreme", as tested by t-test (p<0.01).

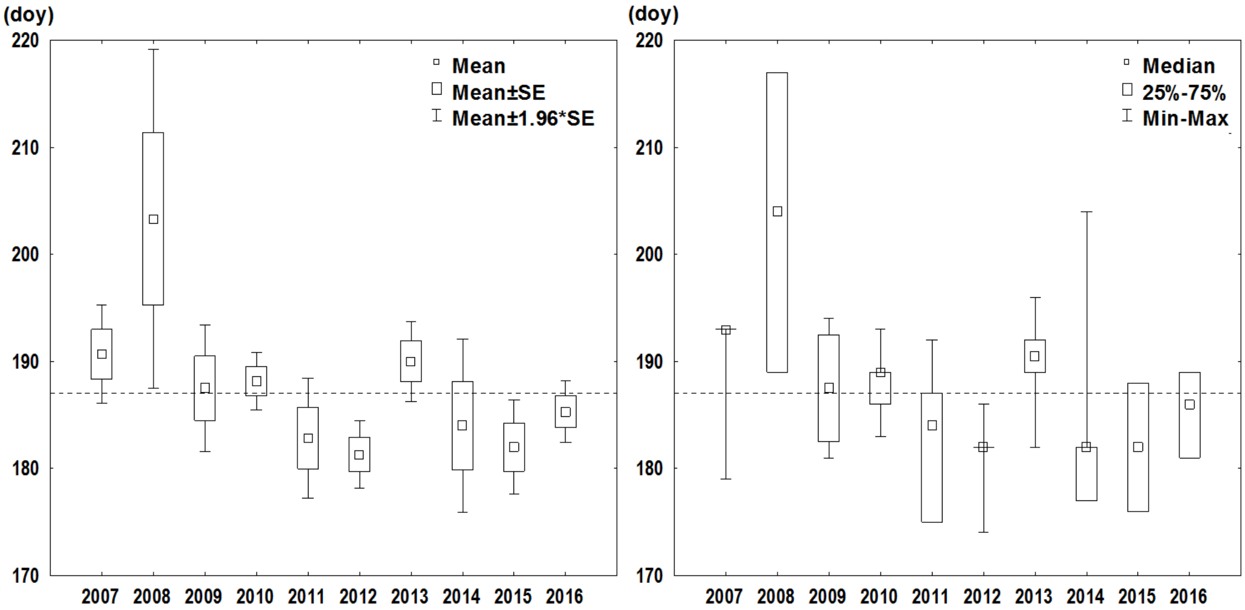


Figure III.5.B.g.10. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) for evergreen dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Considering thus only "normal" years for the MF (removing 2008), we did not find any statistically significant trend with time, tested by linear regression.

As already observed for the already analyzed growth forms, as tested by linear regression at inter-annual level, MF exhibited a statistically significant relation with FB, although in this case it explained only a small proportion of variance ($\beta=0.4$, $R^2=0.43$, $p<0.01$).
However we observed a statistically significant relation between MF and FF, as tested by linear regression at the inter-annual level ($\beta=0.8$, $R^2=0.69$, $p<0.01$).

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2007-2016) the FF of evergreen shrubs (i.e. *Rhododendron ferrugineum*) (Fig. III.5.B.g.11) exhibited statistically significant differences among years ($F=5$, $p<0.01$) (Fig. III.5.B.g.12).

Over all the study period (2007-2016), mean and median values of MF were coincident and occurred at mid-July (197 DOY), while the 75% occurred few days later (201 DOY) (Table III.5.B.g.5).

Considering each single year, the earliest onset of MF was recorded at the end of June (180 DOY,in 2015), up to mid-July (201 DOY, in 2007). The end of MF spanned from mid-July (195 DOY, in 2016) to early August (217 DOY, in 2008) (Table III.5.B.g.5).

Figure III.5.B.g.11. Example of main flowering of *Rhododendron ferrugineum*.

Table III.5.B.g.5. Non-parametric statistics of main flowering day (MF) for evergreen shrubs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	4	201	201	201	201	201	201	-
2008	4	207	197	201	208	214	217	8.7
2009	4	202	188	195	201	209	216	11.4
2010	4	196	189	193	198	199	199	4.7
2011	5	192	187	187	192	197	197	5.0
2012	5	188	182	186	186	190	197	5.7
2013	4	199	196	196	198	203	206	4.7
2014	5	205	197	204	204	204	215	6.5
2015	5	189	180	188	188	191	199	6.8
2016	5	193	189	189	195	195	195	3.3
2007-2016	45	197	180	189	197	201	217	8.5

The total duration of MF for the evergreen shrubs ranged from 0 days (in 2007) to 28 days (in 2009), while the MF peak duration ranged from 0 to 14 days maximum (respectively in 2014 and 2009) (Fig. III.5.B.g.12). However, as in 2007 our data did not show variance, to avoid underestimation, if we exclude 2007, the minimum total duration of MF is of 6 days (recorded in 2016).

Considering the anomalies of the 75% quartiles, the MF showed the largest advances in 2012 and 2015 (respectively -11 and -10 days), although not statistically significant, tested by t-test ($p>0.05$), and the largest delay in 2008 (+13 days), which was identified as statistically significant, as tested by t-test ($p=0.04$) (Fig. III.5.B.g.12).

Considering thus only the “normal” years (excluding 2008 as “extreme” year), we did not find statistically significant trend of the MF with time for evergreen shrubs, as tested by linear regression ($p>0.05$).

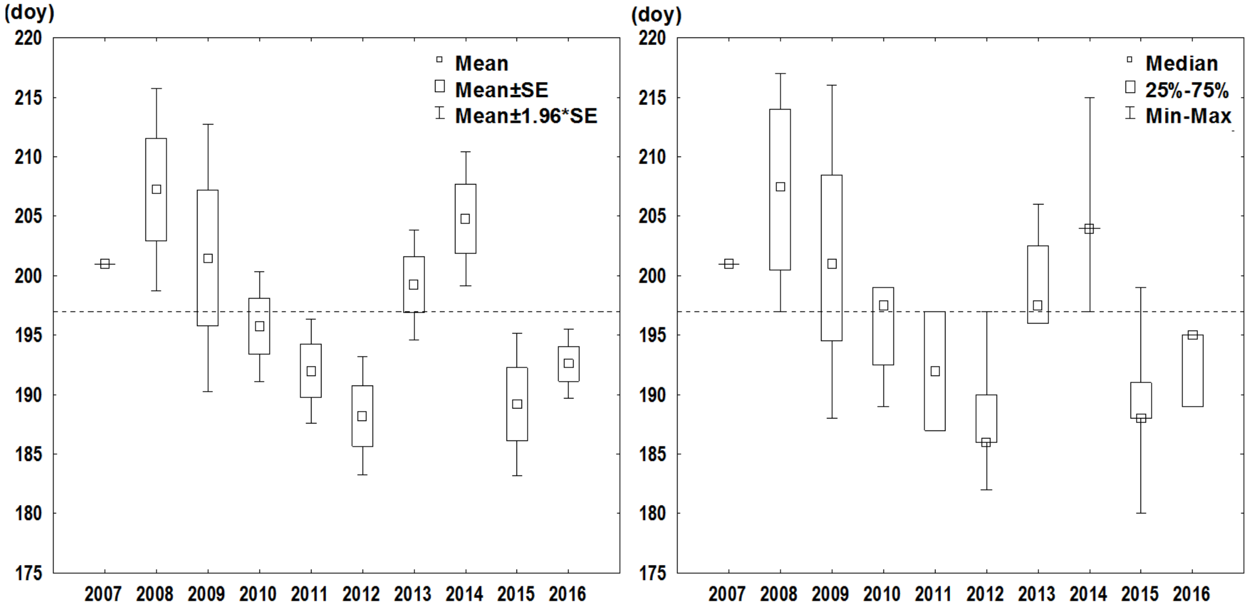


Figure III.5.B.g.12. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) for evergreen shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Also in this case there was a statistically significant relation between MF and FB ($\beta=0.6$, $R^2=0.57$, $p<0.01$), as well as between MF and FF ($\beta=0.8$, $R^2=0.79$, $p<0.01$), as tested by linear regression at the inter-annual level.

Forbs

Considering all the study period, MF of forbs (Fig. III.5.B.g.13) exhibited statistically significant differences among years, as tested by one-way ANOVA ($F=26$, $p<0.01$) (Fig. III.5.B.g.14).

The mean and median values of MF over the whole period (2007-2016) were almost coincident and corresponded to late July (209 and 208 DOY), while the 75% occurred at early August (216 DOY) (Table III.5.B.g.6).

The beginning of MF occurred in late July (175 DOY, in 2015) and ranged up to mid-July (193 DOY, in 2013). The end of MF ranged from early August (219 DOY, in 2007) to late September (270 DOY, in 2013) (Table III.5.B.g.6).
The total duration of MF spanned from 26 days (in 2007) to a maximum of 78 days (in 2013), while the MF peak duration ranged from 15 (in 2012 and 2015) to 27 days (in 2008 and 2014). Only in 2007 we recorded an anomalous peak duration of only 0 days (Table III.5.B.g.6.).

Table III.5.B.g.6. Non-parametric statistics of main flowering day (MF) for forbs computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	201	193	201	201	201	219	5.9
2008	50	218	182	211	217	238	245	15.2
2009	65	212	188	201	216	223	244	13.2
2010	63	211	186	203	213	221	238	11.4
2011	66	203	175	197	203	213	222	10.8
2012	66	203	182	197	208	212	222	10.7
2013	60	217	192	206	213	226	270	15.9
2014	60	221	189	206	218	233	266	16.8
2015	64	197	180	188	195	203	247	11.0
2016	55	206	189	195	209	214	243	11.4
2007-2016	612	209	175	199	208	216	270	14.6

Comparing the 75% anomalies, MF showed the largest delay in 2008 (+22 days), while the earliest MF occurred in 2007 (-15 days). Tested by t-test we did not find statistically significant differences among years ($p>0.05$) (Fig III.5.B.g.14).

Considering thus the period 2007-2016 we did not identify statistically significant trend of MF with time, as tested by linear regression.
Likewise the other growth forms and the overall pattern, we found a statistically significant relation between MF and FB ($\beta=0.9$, $R^2=0.72$, $p<0.01$), and between MF and FF ($\beta=0.9$, $R^2=0.90$, $p<0.01$), as tested by linear regression at the inter-annual level.

Figure III.5.B.g.13. Example of main flowering of *Leucanthemopsis alpina* in and *Doronicum clusii*.

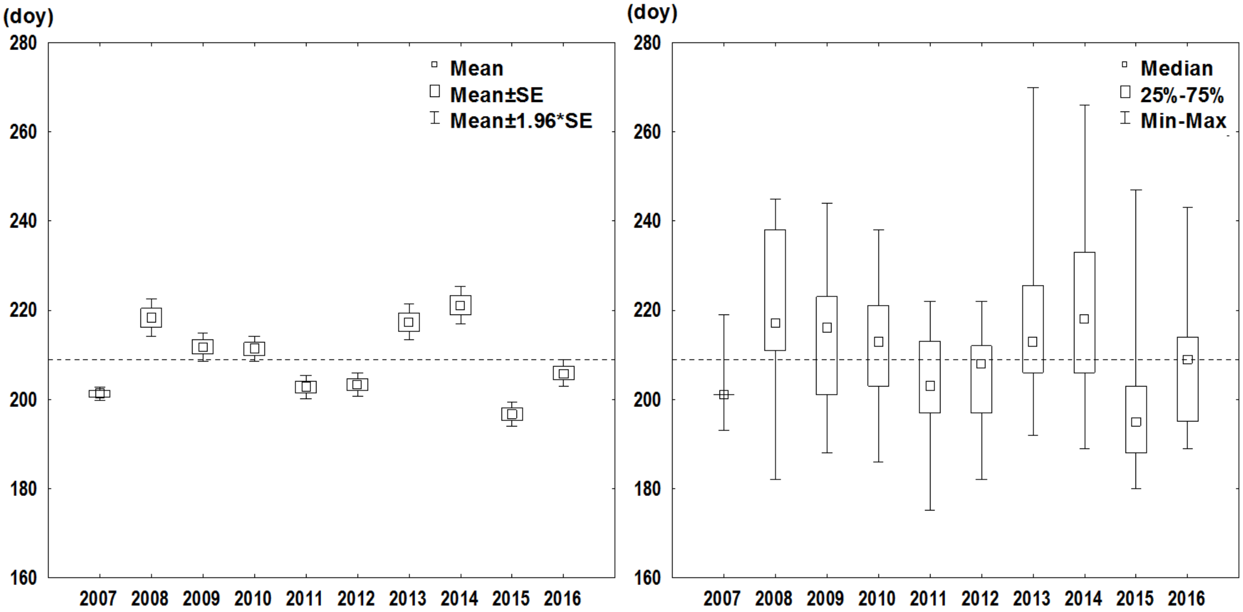


Figure III.5.B.g.14. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) of forbs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Graminoids

As tested by one-way ANOVA, overall the study period (2007-2016) the MF of graminoids (Fig. III.5.B.g.15) exhibited statistically significant differences among years (F=6, p<0.01) (Fig. III.5.B.g.16).

Figure III.5.B.g.15. Example of main flowering of *Anthoxanthum alpinum*.

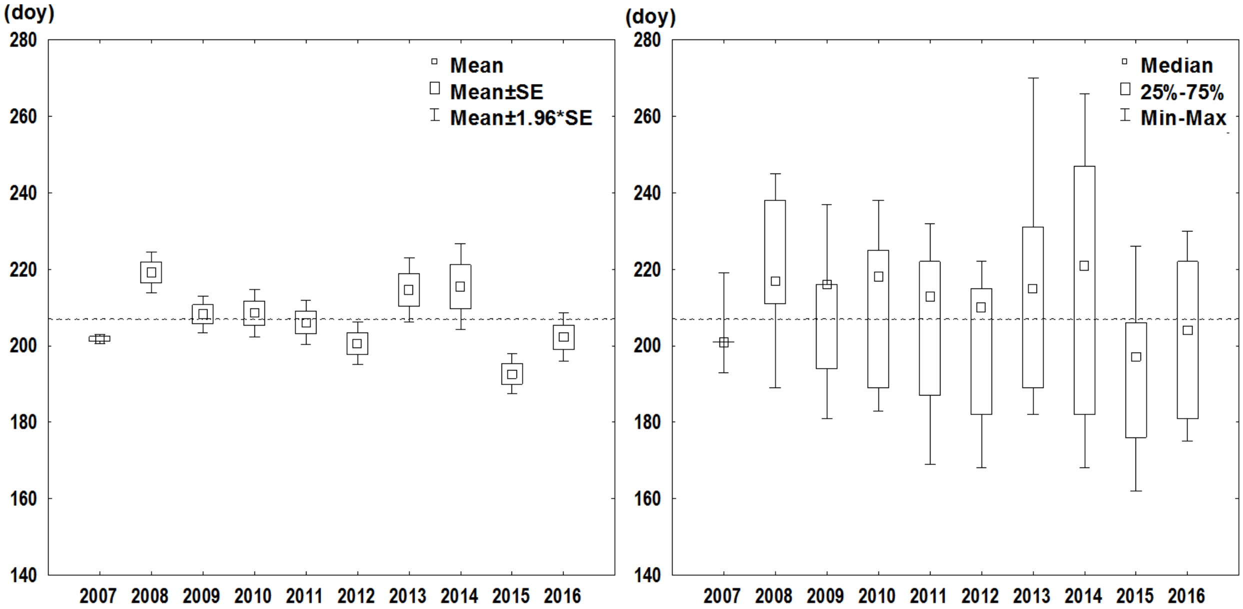


Figure III.5.B.g.16. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) for graminoids from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Table III.5.B.g.7. Non-parametric statistics of main flowering day (MF) for graminoids computed for each single year, as well as for the entire monitoring period (2007-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	37	202	193	201	201	201	219	3.8
2008	31	219	189	211	217	238	245	15.2
2009	37	208	181	194	216	216	237	14.8
2010	37	209	183	189	218	225	238	19.1
2011	38	206	169	187	213	222	232	18.4
2012	38	201	168	182	210	215	222	17.5
2013	36	215	182	189	215	231	270	25.4
2014	35	215	168	182	221	247	266	34.0
2015	36	193	162	176	197	206	226	16.0
2016	31	202	175	181	204	222	230	18.0
2007-2016	356	207	162	189	208	221	270	20.8

Over the study period (2007-2016), mean and median values of MF were almost coincident, and occurred in late July (207 and 208 DOY), while the 75% quartile coincided with early August (221 DOY) (Table III.5.B.g.7).

Considering the intra-annual variability, the earliest onset of MF was recorded between mid-June (162 DOY, in 2015) and mid-July (193 DOY, in 2007).

The MF completion ranged from early August (219 DOY, in 2007) to late September (270 DOY, in 2013) (Table III.5.B.g.7).

The total duration of MF ranged from 26 days (in 2007) to 98 days (in 2014), while the MF peak duration ranged over 22 days (in 2009) or to 65 days (in 2014) (Fig. III.5.B.g.16). Likewise forbs, also for graminoids our data documented low variability in 2007.

Considering the anomalies of the 75% quartiles, in 2007 the MF displayed the largest advance (-20 days), while in 2014, it showed the largest delay (+26 days), although we did not find any statistically significant differences, as tested by t-test ($p>0.05$) (Fig. III.5.B.g.16).

Analyzing the whole dataset, we did not observe any trend of MF with time, as tested by linear regression ($p>0.05$). However, considering all the population data of MF, we observed over the same period a statistically significant advance of the earliest MF (provided by the minimum) ($\beta=-2.5$, $R^2=0.57$, $p<0.01$) (Fig. III.5.B.g.17).

Also in this case, we observed a statistically significant relation between MF and FB ($\beta=1.0$, $R^2=0.74$, $p<0.01$), and between MF and FF ($\beta=1.0$, $R^2=0.93$, $p<0.01$) as tested by linear regression at the inter-annual level.

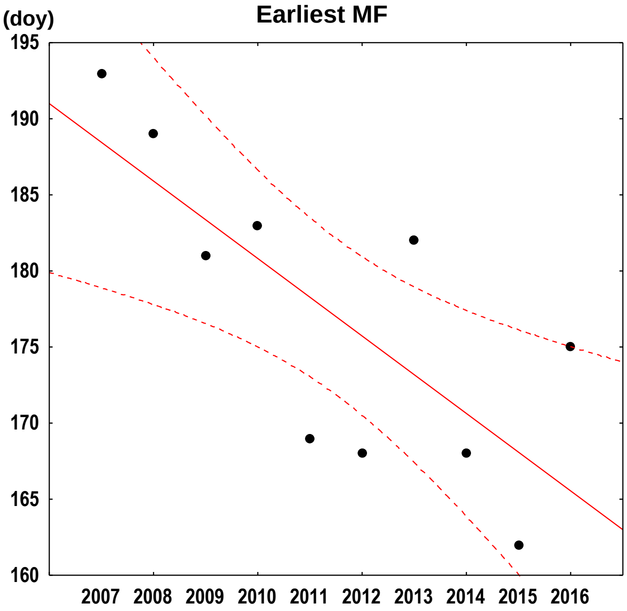


Figure III.5.B.g.17. Trend with time of the earliest MF ($\beta=-2.5$, $R^2=0.57$, $p<0.01$) for the graminoids, as tested by linear regression on the whole study period (2007-2016).

Comparison of trends among the growth forms

Comparing the patterns of MF among the selected growth forms at the inter-annual level, we found large and statistically significant differences (Fig. III.5.B.g.18), as tested by one-way ANOVA ($F=22$, $p<0.01$).

Graminoids exhibited the greatest MF duration (108 days) and the greatest MF peak duration (32 days). On the opposite the evergreen shrubs exhibited the shortest MF duration (37 days), while evergreen dwarf shrubs the shortest MF peak duration (10 days).

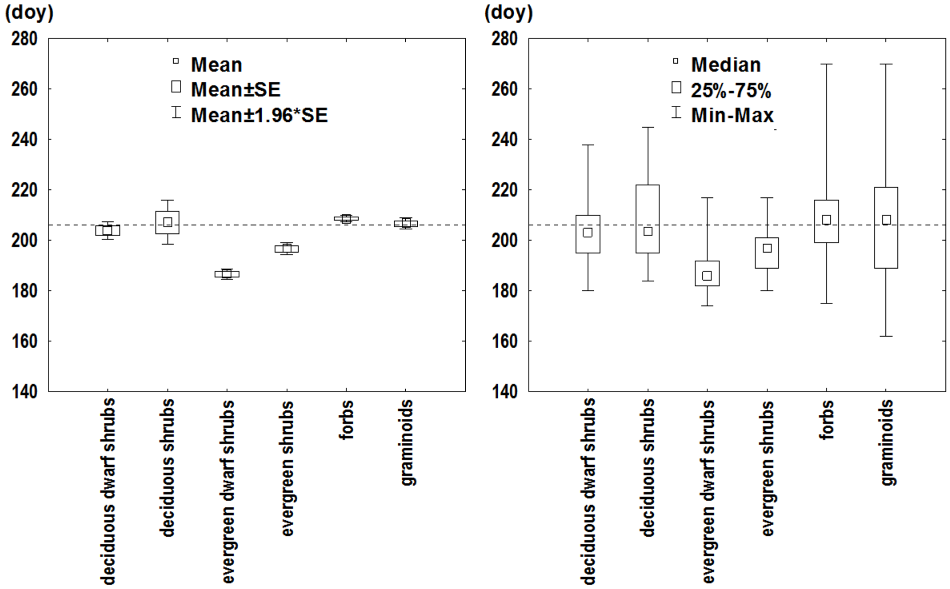


Figure III.5.B.g.18. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) between the selected growth forms over the period 2007-2016. The dotted black line represents the mean value for the whole period.

Likewise FB and FF, the first growth form starting MF were graminoids (162 DOY, mid-June), while deciduous shrubs were the last (184 DOY, end of June). The latest MF completion occurred simultaneously for graminoids and forbs at the end of September (270 DOY). On the opposite the evergreen dwarf shrubs and evergreen shrubs were the first two growth forms completing MF (217 DOY, beginning of August) (Fig. III.5.B.g.18).

According to the 75% quartiles anomalies referred to all dataset, the evergreen dwarf shrubs and evergreen shrubs exhibited the earliest MF (respectively -24 and -15 days). As tested by t-test, the evergreen dwarf shrubs was the only one growth forms exhibiting a statistically significant advance of the MF ($p<0.01$), similarly to what observed for FB and FF.

Also in this case, the analysis of each single growth form highlighted different responses. In particular, concerning MF, deciduous dwarf shrubs, deciduous shrubs and graminoids were the most sensitive species.

Moreover, considering all the flowering phenological stages, MF displayed the largest responses over the study period, exhibiting an advance for 50% of the selected growth forms, while on the opposite, FB was the less sensitive (only deciduous shrubs advanced).
Deciduous dwarf shrubs and deciduous shrubs showed a statistically significant advance of MF with time, and was thus the most sensitive growth forms being able to benefit of an earlier onset of the growing season, compared to graminoids, which only advanced the start of the MF onset.

The highest slope coefficient was displayed by deciduous shrubs, which were already been identified as the most responsive species in relation to FB and FF. For this growth form, the flowering phenology shifted simultaneously among the subsequent phenophases (i.e. shifts of FB, FF and MF). This growth form could thus be identified potentially as the most adaptable since all the flowering parameters shifted simultaneously.

Graminoids only showed the same responses for FF and MF, but not for FB, indicating that their flowering phenophase could change at different rates, with important consequences on the community level phenological pattern.

Deciduous dwarf shrubs did not advance their FB and FF, but only displayed a strong advance of MF. Similarly, to graminoids, the shift in flowering phenology for deciduous dwarf shrubs did not occur simultaneously, but only for some stages (i.e. MF), indicating potential risk for the community level phenological pattern.

Thus, graminoids and deciduous dwarf shrubs documented lower adaptation capability compared to deciduous shrubs.

The lack of relation with SM of the flowering stages, allow to hypothesize that other factors are implied in shaping flowering responses. Moreover, since we observed different responses when comparing the flowering stages among each other, we could also hypothesize that each of the selected flowering stages are regulated by different factors.

A detailed investigation on biotic and abiotic factors influencing the observed phenological pattern is reported in chapter III.5.B.k.

III.5.B.h. *Patterns of seed development (SD)*

Likewise the other phenophases, our analyses have been carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2007-2015), also the seed development (SD) showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=56, p<0.01) (Fig. III.5.B.h.1).

According to mean and median values, SD occurred in early August (respectively 216 and 215 DOY), while the 75% quartile occurred in mid-August (227 DOY) (Table III.5.B.h.1), that correspond to almost one week later the 75% quartile of MF.

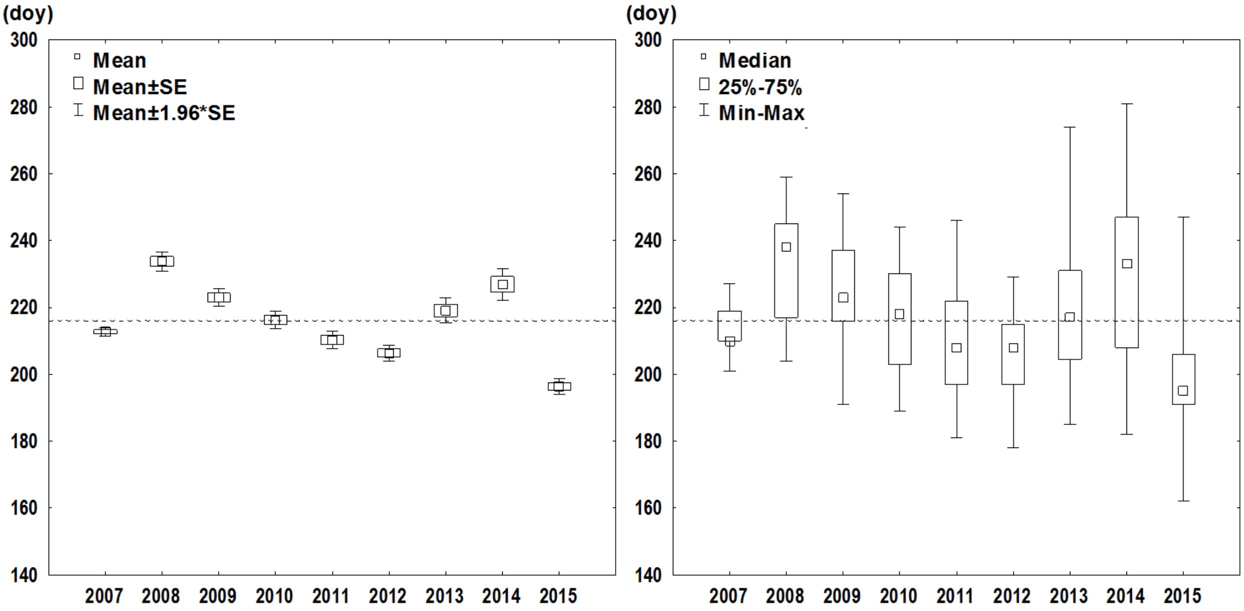


Figure III.5.B.h.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed development (SD) from 2007 to 2016, at inter-specific level. The dotted black line represents the mean value for the whole period.

The earliest onset of SD was recorded in mid-June (162 DOY, in 2015), while the latest in late July (204 DOY, in 2008). The SD completion ranged from mid-August (227 DOY, in 2007) until early October (281 DOY, in 2013) (Table III.5.B.h.1).

The total duration of SD spanned from 26 days (in 2007) to 99 days (in 2014), while the SD peak duration ranged from 9 days (in 2007) to 39 days (in 2014) (Fig. III.5.B.h.1).

Considering the 75% quartiles anomalies over the whole dataset, SD showed the largest advance in 2015 (-21 days), and the largest delay in 2014 and 2008 (respectively +22 and +18 days), although all without statistically significant differences, as tested by t-test ($p>0.05$).

Table III.5.B.h.1. Non-parametric statistics of seed development (SD) computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	116	213	201	210	210	219	227	6.5
2008	92	234	204	217	238	245	259	14.0
2009	116	223	191	216	223	237	254	14.6
2010	116	216	189	203	218	230	244	14.8
2011	120	210	181	197	208	222	246	14.2
2012	121	206	178	197	208	215	229	13.1
2013	112	219	185	205	217	231	274	20.0
2014	107	227	182	208	233	247	281	24.5
2015	113	196	162	191	195	206	247	12.4
2007-2015	1013	216	162	203	215	227	281	18.6

Analyzing thus he whole study period (2007-2015), we did not find any statistically significant trend of SD with time, as tested by linear regression ($p>0.05$). However, since we observed an advance of the onset of SM (see chap. III.5.B.a), we tested also trends with time of the onset of SD. It displayed a statistically significant advance over time, in response to the earlier onset of the growing season, as tested by linear regression ($\beta=-4.1$, $R^2=0.79$, $p<0.01$) (Fig. III.5.B.h.2).

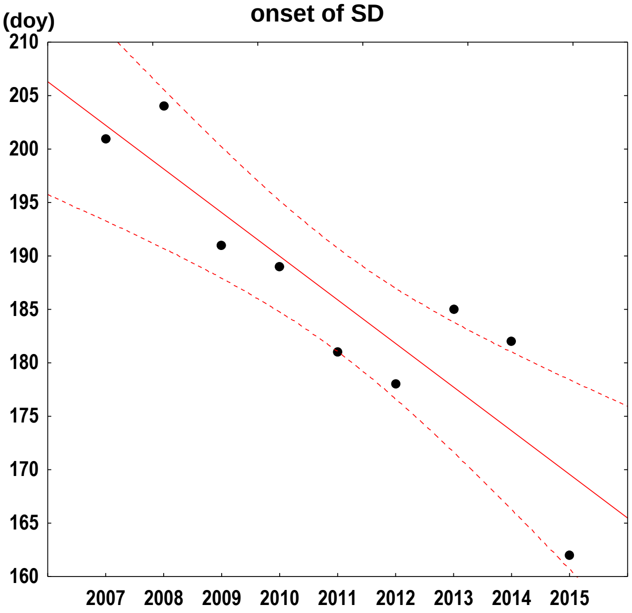


Figure III.5.B.h.2. Trend with time of the onset of SD ($\beta=-2.1$, $R^2=0.79$, $p<0.01$) observed at inter-specific level, as tested by linear regression.

As could be expected, we found statistically significant relations between SD and the flowering stages, as tested by linear regression at inter-annual and inter-specific level: SD vs FB (β=1.0, $R^2=0.70$, $p<0.01$), SD vs FF (β=0.9, $R^2=0.80$, $p<0.01$) and SD vs MF (β=1.0, $R^2=0.88$, $p<0.01$) (Fig. III.5.B.h.3).

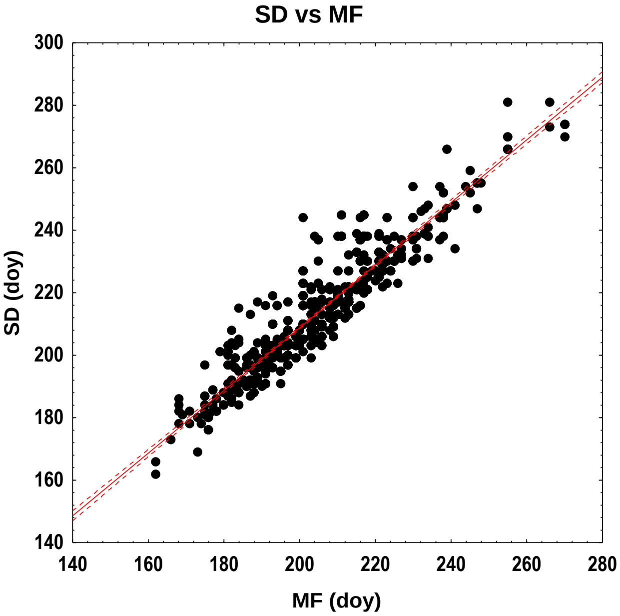


Figure III.5.B.h.3. Relation between seed development (SD) and main flowering day (MF) as tested by linear regression at inter-annual and inter-specific level (β=1.0, $R^2=0.88$, $p<0.01$).

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2015) the SD of deciduous dwarf shrubs (i.e. *Salix herbacea*) (Fig. III.5.B.h.4) exhibited statistically significant differences among years (F=10, $p<0.01$) (Fig. III.5.B.h.5).

Over the study period (2007-2015), according to the mean and median values, the SD occurred in early August (respectively 213 and 210 DOY), while the 75% quartile coincided with mid-August (220 DOY) (Table III.5.B.h.2).

Considering the intra-annual variability, the earliest onset of SD was recorded at the beginning of July (184 DOY, in 2015), while the latest at mid-August (223 DOY, in 2009). The end of SD spanned from mid-July (199 DOY, in 2015) to mid-September (252 DOY, in 2008) (Table III.5.B.h.2).

Table III.5.B.h.2. Non-parametric statistics of seed development (SD) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	6	216	210	210	219	219	219	4.6
2008	4	240	217	231	245	249	252	15.5
2009	5	233	223	230	230	237	244	8.0
2010	6	212	196	199	212	221	230	13.4
2011	5	207	200	203	203	208	222	8.8
2012	6	205	190	197	208	212	215	9.5
2013	6	210	199	199	207	210	238	14.7
2014	5	211	204	208	215	215	215	5.1
2015	5	189	184	184	188	188	199	6.1
2007-2015	48	213	184	202	210	220	252	16.4

For deciduous dwarf shrubs, the total duration of SD ranged from 9 days (in 2007) to 39 days (in 2013), while the SD peak duration spanned from 4 days (in 2015) to 22 days (in 2010) (Table III.5.B.h.2).

Figure III.5.B.h.4. Example of SD of *Salix herbacea*.

Analyzing the anomalies of the 75% quartiles, the SD showed the largest advance in 2015 (-32 days) and the greatest delay in 2008 (+29 days). As tested by t-test, 2008 was the only one year that showed statistically significant differences (p=0.04), and was thus identifiable as “extreme” (Fig. III.5.B.h.5).

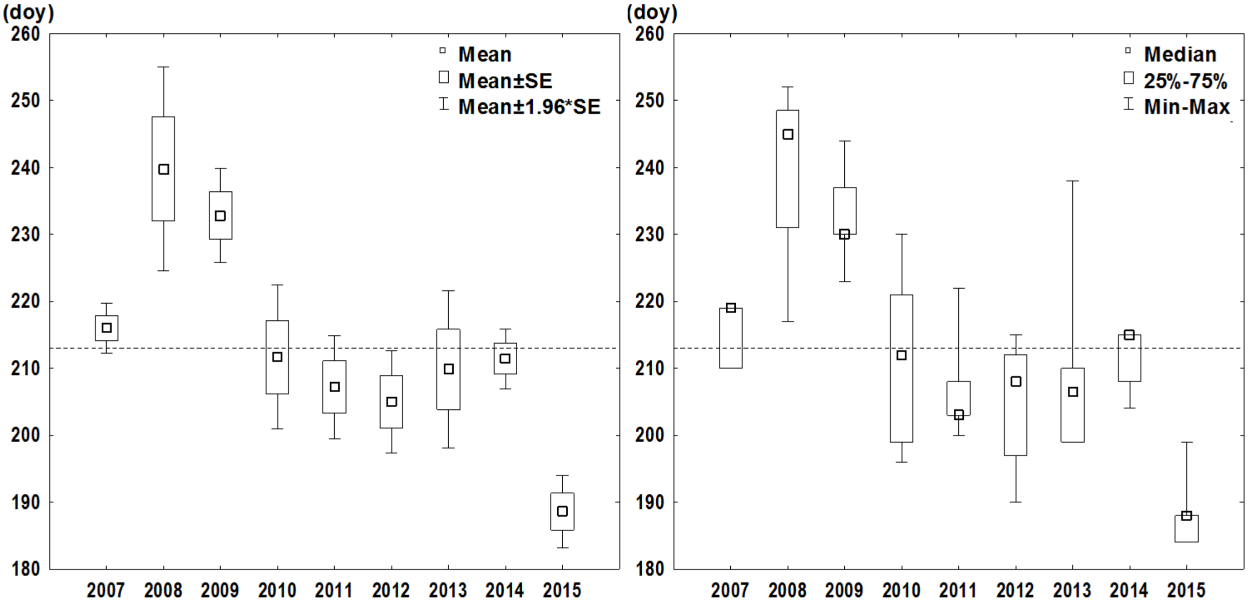


Figure III.5.B.h.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed development (SD) for deciduous dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

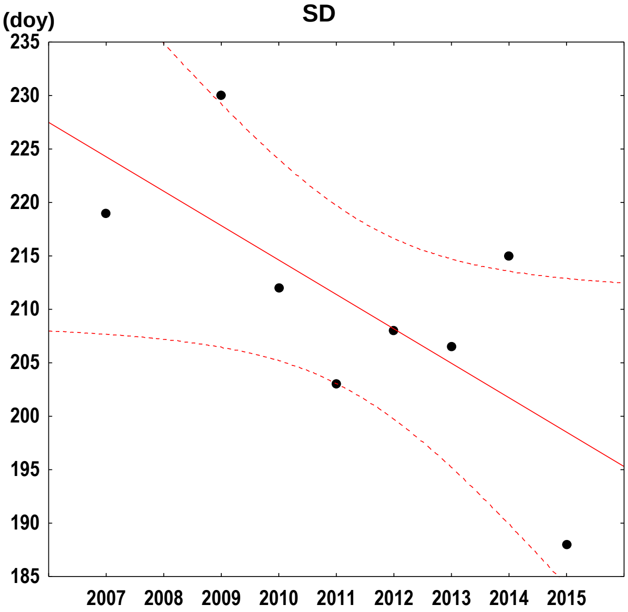


Figure III.5.B.h.6. Trend with time of SD (β=-3.2, R^2=0.49, p=0.05) for deciduous dwarf shrubs, as tested by linear regression.

Thus considering only the "normal" years of SD (excluding 2008 as "extreme" year of SD) we observed a statistically significant advance of SD (β=-3.2, R^2=0.49, p=0.05) (Fig. III.5.B.h.6).

Moreover, we found a statistically significant relation between SD and FB ($\beta=0.9$, $R^2=0.56$, $p<0.01$), SD and FF ($\beta=0.9$, $R^2=0.58$, $p<0.01$) and between SD and MF ($\beta=0.1$, $R^2=0.84$, $p<0.01$), as tested by linear regression at the inter-annual level.

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2015) the SD of evergreen dwarf shrubs (i.e. *Kalmia procumbens*) (Fig. III.5.B.h.7) exhibited statistically significant differences among years (F=11, $p<0.01$) (Fig. III.5.B.h.8).

Over all the study period (2007-2015), mean and median values were coincident and occurred at mid-July (196 DOY), and the 75% quartile occurred only 4 days later (201 DOY) (Table III.5.B.h.4).

Table III.5.B.h.4. Non-parametric statistics of seed development (SD) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev..
2007	6	201	201	201	201	201	201	-
2008	3	220	204	204	217	238	238	17.2
2009	5	206	201	201	201	205	223	9.5
2010	6	196	189	196	196	199	199	3.7
2011	6	191	187	187	190	197	197	4.9
2012	6	187	178	186	190	190	190	4.8
2013	6	196	185	196	198	199	199	5.4
2014	6	193	189	189	189	197	204	6.3
2015	6	185	176	180	186	191	191	6.1
2007-2015	50	196	176	189	196	201	238	10.6

Figure III.5.B.h.7. Example of SD of *Kalmia procumbens.*

The earliest onset of SD was recorded in late June (176 DOY, in 2015), while the latest in late July (204 DOY, in 2008). The end of SD ranged from early July (190 DOY, in 2012) to early August (238 DOY, in 2008) (Table III.5.B.h.4).

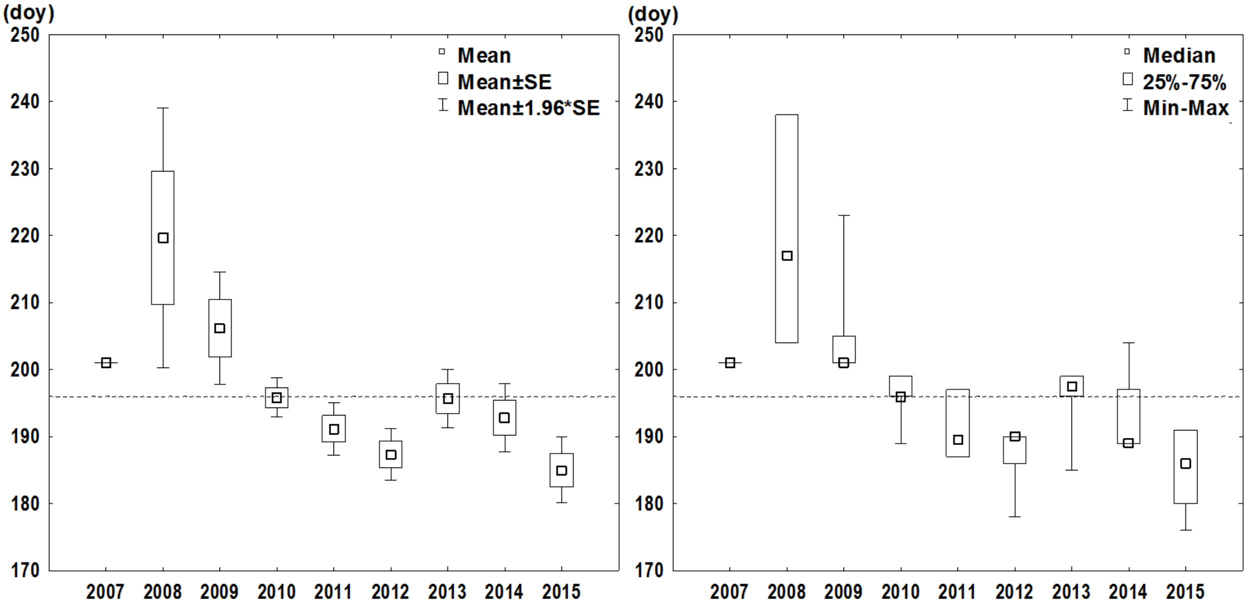


Figure III.5.B.h.8. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed development (SD) for evergreen dwarf shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

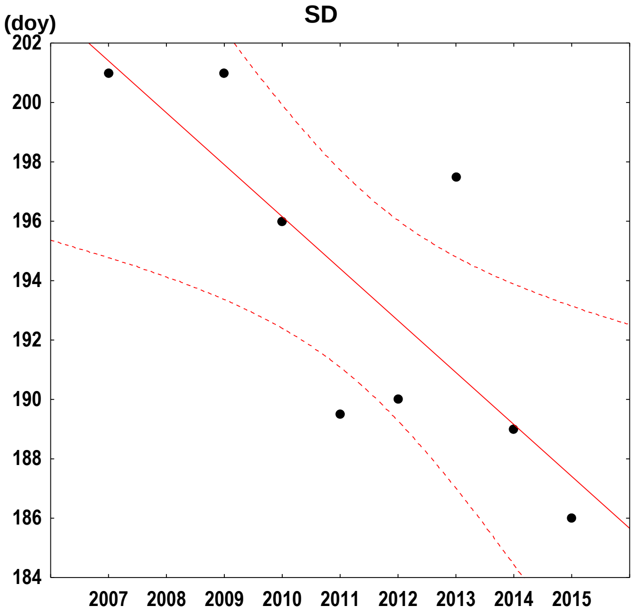


Figure III.5.B.h.9. Trend with time of SD (β=-1.8, R^2=0.64, p=0.02) for evergreen dwarf shrubs, as tested by linear regression.

The total duration of SD for evergreen dwarf shrubs ranged from 10 days (in 2010 and 2011) to 34 days (in 2008). In 2007 we documented a very low variance of SD, as already observed also for MF. Without considering 2007 (to avoid underestimation), the SD peak duration ranged from 3 days (in 2010 and 2013) to 34 days (in 2008) (Table III.5.B.h.4).

Considering the anomalies of the 75% quartiles, the SD showed the largest delay in 2008 (+37 days). Likewise for the flowering patterns, 2008 was the only one year statistically significant different and thus identifiable as "extreme", as tested by t-test ($p<0.01$). Indeed, the SM was much delayed in that year and this could partially explain the delay of SD (observed also for MF) (Fig. III.5.B.h.8).

Considering thus only the "normal" years of SD (removing 2008), we found a statistically significant advance of SD with time, as tested by linear regression ($\beta=-1.8$, $R^2=0.64$, $p=0.02$) (Fig. III.5.B.h.9).

Interestingly, as tested by linear regression at inter-annual level, FB explained only a small proportion of SD variance ($\beta=0.5$, $R^2=0.35$, $p<0.01$) as well as FF ($\beta=0.9$, $R^2=0.56$, $p<0.01$). On the contrary, MF showed a statistically significant relation with SD ($\beta=1.0$, $R^2=0.71$, $p<0.01$).

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2007-2015) the SD of evergreen shrubs (i.e. *Rhododendron ferrugineum*) (Fig. III.5.B.h.10) exhibited statistically significant differences among years ($F=6$, $p<0.01$) (Fig. III.5.B.h.11).

Figure III.5.B.h.10. Example of SD of *Rhododendron ferrugineum.*

Table III.5.B.h.5. Non-parametric statistics of seed development (SD) for evergreen shrubs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	4	210	210	210	210	210	210	-
2008	4	225	211	211	225	238	238	15.6
2009	4	215	201	203	211	227	237	16.1
2010	4	201	199	199	201	203	203	2.3
2011	5	199	197	197	197	203	203	3.3
2012	5	196	186	190	197	197	208	8.4
2013	4	205	199	201	205	208	210	4.7
2014	5	214	204	208	208	215	233	11.5
2015	5	191	184	191	191	191	199	5.3
2007-2015	40	205	184	197	203	210	238	12.9

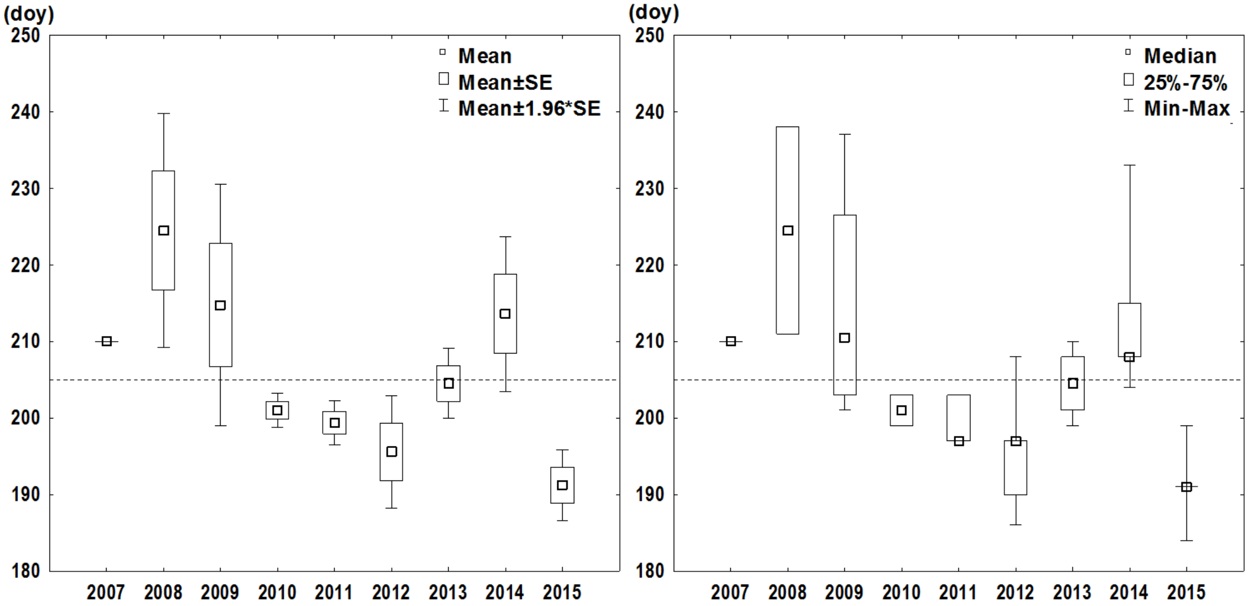


Figure III.5.B.h.11. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed development (SD) for evergreen shrubs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Over all the study period (2007-2015), mean and median values of SD occurred in late July (respectively 205 and 203 DOY), while the 75% quartile occurred one week later (210 DOY) (Table III.5.B.h.5).

Considering each single year, the earliest onset of SD was recorded between early July (184 DOY, in 2015) and late July (211 DOY, in 2008). The end of SD spanned from mid-July (199 DOY, in 2015) to late August (238 DOY, in 2008) (Table III.5.B.h.5).

In 2007 all the statistics occurred the same day (210 DOY). Therefore, in this year our data did not show variance. For this reason, we excluded this year from further analyses on SD peak and duration to avoid underestimation.

Thus considering the whole period 2007-2015, the total duration of SD for the evergreen shrubs ranged from 4 days (in 2010) to 36 days (in 2009), while the SD peak duration ranged from 4 to 27 days (in 2008) (Fig. III.5.B.h.11).

Considering the anomalies of the 75% quartiles, the SD showed the largest advances in 2015 (-19 days) while the largest delay in 2008 (+28 days), which was the only one year identified as statistically significant different, as tested by t-test (p=0.03) (Fig. III.5.B.h.11).

Considering thus only the "normal" years (excluding 2008 as "extreme" year of SD), we did not find statistically significant trend of the SD with time for evergreen shrubs, as tested by linear regression (p>0.05).

Like for evergreen dwarf shrubs, as tested by linear regression at inter-annual level, also in this case FB explained only a small proportion of SD variance (β=0.8, R^2=0.43, p<0.01) and the same for FF (β=1.0, R^2=0.57, p<0.01). Only MF showed a high statistically significant relation with SD (β=1.4, R^2=0.85, p<0.01).

Forbs

Considering all the study period, SD of forbs exhibited statistically significant differences among years, as tested by one-way ANOVA (F=44, p<0.01) (Fig. III.5.B.h.12-13).

The mean and median value of SD over the whole period (2007-2015) were almost coincident and corresponded to early August (218 and 216 DOY), while the 75% occurred at mid-August (227 DOY) (Table III.5.B.h.6).

Table III.5.B.h.6. Non-parametric statistics of seed development (SD) of forbs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	214	201	210	210	219	227	6.9
2008	50	233	204	217	238	245	259	14.5
2009	65	225	194	216	223	237	254	13.7
2010	63	219	193	206	221	225	244	12.5
2011	66	210	181	200	208	222	232	12.0
2012	66	209	186	197	212	215	229	9.9
2013	60	223	196	213	217	229	274	16.3
2014	59	231	197	215	233	239	273	17.4
2015	62	199	184	191	199	206	247	10.8
2007-2015	554	218	181	206	216	227	274	16.5

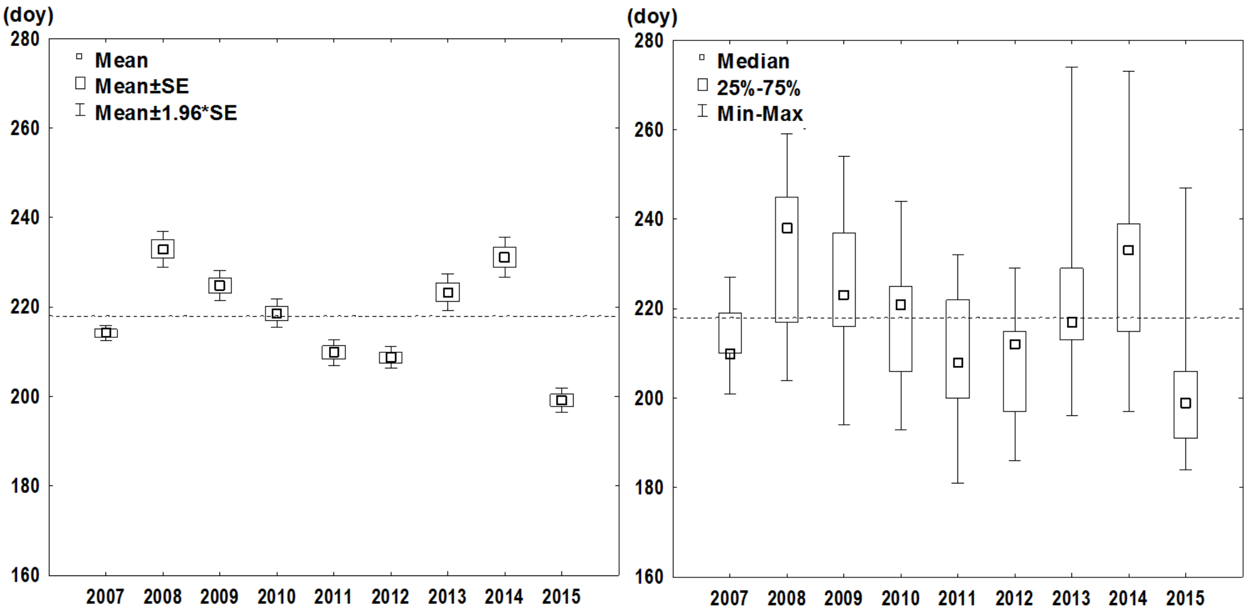


Figure III.5.B.h.12. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed development (SD) of forbs from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Figure III.5.B.h.13. Example of SD of *Geum reptans.*

The beginning of SD occurred at the end of June (181 DOY, in 2011) and ranged up to late July (204 DOY, in 2008). The end of SD ranged from mid-August (227 DOY, in 2007) to the end of September (273 DOY, in 2014) (Table III.5.B.h.6).

The total duration of SD spanned from 26 days (in 2007) to a maximum of 78 days (in 2013), while the SD peak duration ranged from 9 (in 2007) to 24 days (in 2014) (Table III.5.B.h.6.).

Comparing the 75% anomalies, SD showed the largest delay in 2008 (+18 days), while the earliest SD occurred in 2015 (-21 days). Tested by t-test we did not find statistically significant differences among years ($p>0.05$) (Fig. III.5.B.h.12).

Considering thus the whole study period we did not identify statistically significant trend of SD with time, as tested by linear regression ($p>0.05$).

Differently than shrubs, there was a statistically significant relation between SD and FB ($\beta=1.0$, $R^2=0.71$, $p<0.01$), SD and FF ($\beta=0.9$, $R^2=0.77$, $p<0.01$), and SD and MF ($\beta=1.0$, $R^2=0.84$, $p<0.01$) as tested by linear regression at the inter-annual level.

Graminoids

As tested by one-way ANOVA, overall the study period (2007-2015) the SD of graminoids (Fig. III.5.B.h.14) exhibited statistically significant differences among years ($F=14$, $p<0.01$) (Fig. III.5.B.h.15).

Figure III.5.B.h.14. Example of SD of *Carex curvula* (the black small ball is its parasitic fungi *Anthracoidea curvulae*).

Table III.5.B.h.7. Non-parametric statistics of seed development (SD) of graminoids computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	37	212	210	210	210	210	227	4.2
2008	31	237	217	238	238	245	252	11.6
2009	37	221	191	205	223	237	244	15.6
2010	37	218	196	199	221	230	244	17.0
2011	38	216	181	197	222	232	246	16.6
2012	38	207	178	190	215	222	229	16.6
2013	36	219	192	192	220	234	274	24.9
2014	32	230	182	201	233	261	281	33.6
2015	35	195	162	180	203	206	223	15.4
2007-2015	321	217	162	201	216	232	281	21.6

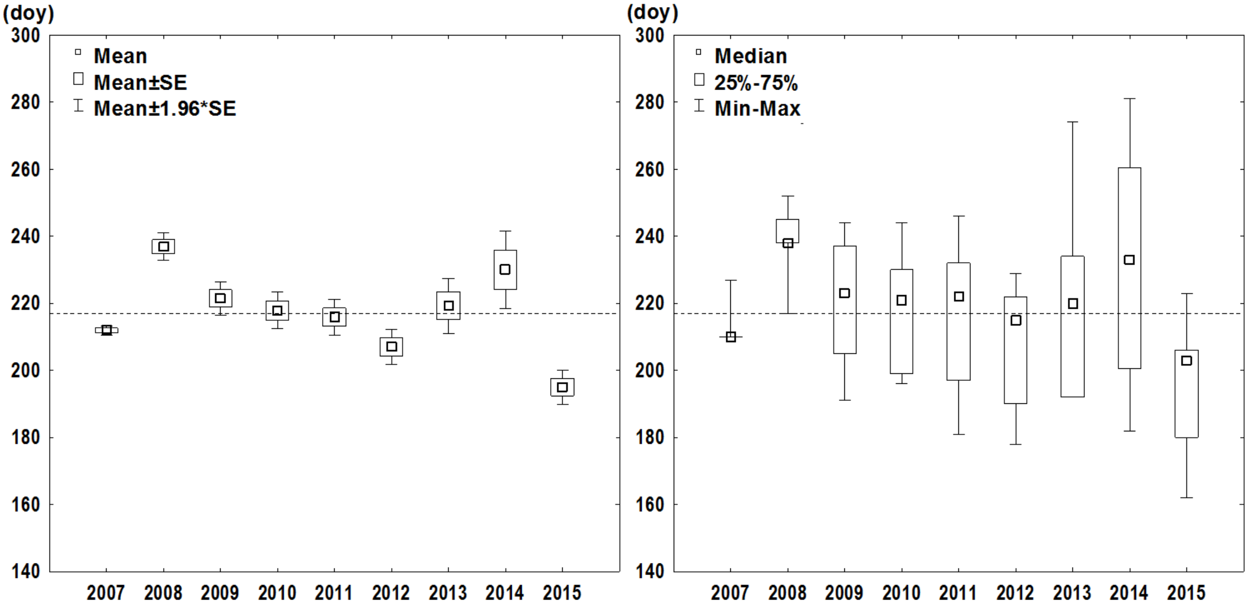


Figure III.5.B.h.15. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed development (SD) of graminoids from 2007 to 2016. The dotted black line represents the mean value for the whole period.

Over the study period (2007-2015), mean and median values of SD were almost coincident, and occurred in early August (217 and 216 DOY), while the 75% quartile coincided with mid-August (232 DOY) (Table III.5.B.h.7).

Considering the intra-annual variability, the earliest onset of SD (162 DOY, mid-June) was recorded in 2015, while the latest in 2008 (217 DOY, early August). The SD completion ranged from mid-August (223 DOY, in 2015) to early October (281 DOY, in 2014) (Table III.5.B.h.7).

Graminoids documented low variability in 2007, with a consequent SD peak duration of 0 days. For this reason, we excluded this year from analysis of SD duration and peak to avoid underestimation. The total duration of SD ranged from 17 days (in 2007) to 99 days (in 2014), while the SD peak duration ranged over 7 days (in 2008) or to 60 days (in 2014) (Fig. III.5.B.h.15).

Considering the anomalies of the 75% quartiles, in 2015 the SD displayed the largest advance (-26 days), while in 2014, it showed the largest delay (+29 days), although we did not find any statistically significant differences, as tested by t-test ($p>0.05$).

Over the whole dataset, we did not observe any trend of SD with time, as tested by linear regression ($p>0.05$). However, considering all the population data of SD, we observed over the same period a statistically significant advance of the onset of SD ($\beta=-5.2$, $R^2=0.73$, $p<0.01$) (Fig. III.5.B.h.16).

Also in this case, we observed a high statistically significant relation between SD and FB ($\beta=1.0$, $R^2=0.71$, $p<0.01$), SD and FF ($\beta=0.9$, $R^2=0.85$, $p<0.01$), and SD and MF ($\beta=1.0$, $R^2=0.90$, $p<0.01$), as tested by linear regression at the inter-annual level.

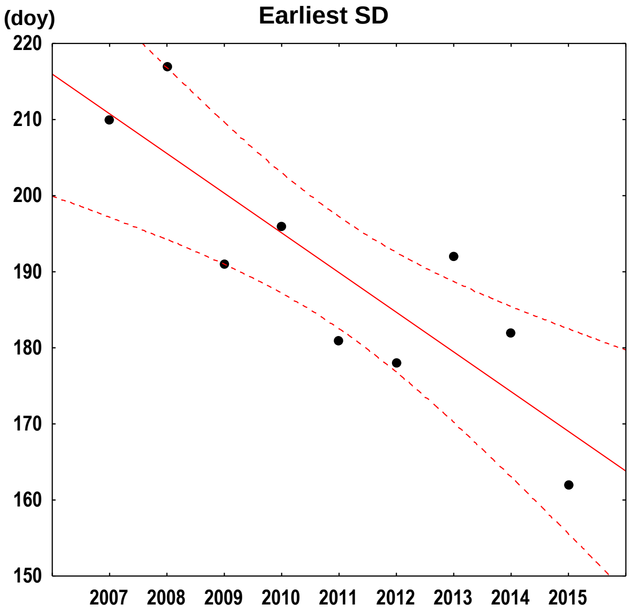


Figure III.5.B.h.16. Trend with time of the onset of SD ($\beta=-5.2$, $R^2=0.73$, $p<0.01$) for graminoids, as tested by linear regression on the whole study period (2007-2015).

Comparison of trends among growth forms

Comparing the patterns of SD among the selected growth forms at the inter-annual level, we found statistically significant differences (Fig. III.5.B.h.17), as tested by one-way ANOVA ($F=21$, $p<0.01$).

The trends of SD among the selected growth forms were similar to those of flowering. Graminoids exhibited the longest SD duration (119 days) and SD peak duration (31 days). On the opposite, the evergreen shrubs exhibited the shortest SD duration (54 days), while evergreen dwarf shrubs and evergreen shrubs the shortest SD peak duration (respectively 12 and 13 days).

Likewise flowering, the first growth form starting SD were graminoids (162 DOY, mid-June), while deciduous dwarf shrubs and evergreen dwarf shrubs were the last to start SD (both 184 DOY, end of June). The latest SD completion was documented for graminoids in early October (281 DOY). On the opposite, the evergreen dwarf shrubs and evergreen shrubs were the first two growth forms completing SD (238 DOY, late August) (Fig. III.5.B.h.17).

According to the 75% quartiles anomalies referred to all the dataset, the evergreen dwarf shrubs exhibited the earliest SD (-26 days), although without statistically significant differences, as tested by t-test (p<0.01).

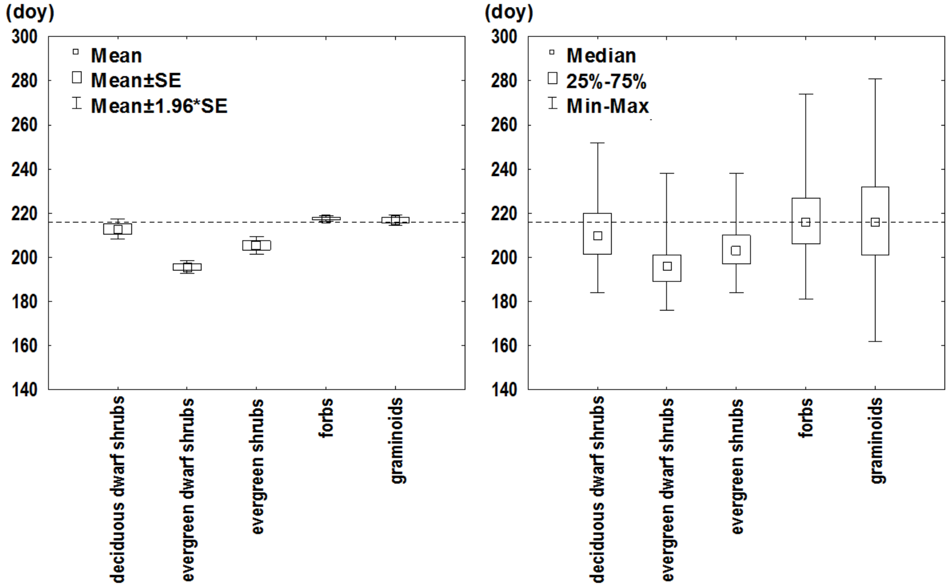


Figure III.5.B.h.17. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed development (SD) between the selected growth forms over the period 2007-2015. The dotted black line represents the mean value for the whole period.

Flowering stages occurred earlier and were more concentrated for evergreen shrubs, while herbaceous species (i.e. graminoids and forbs) started later their flowering phenology and ranged over a larger period (see chap. III.5.B.g. and Fig. III.5.B.g.18).
Also in this case, we documented different responses in relation to the growth form types. Deciduous dwarf shrubs and evergreen dwarf shrubs showed a statistically significant advance of SD with time, and was thus identifiable as being able to profit of the earliest onset of the growing season. In the same way, graminoids exhibited too the ability to profit from earlier SM, showing an advance of the onset of the SD, coupled with a larger flexibility of SD duration up to the beginning of autumn which could allow this growth form to profit of a potential autumn warming.

Moreover, according to the high statistically significant relation observed between SD and the flowering phenological stages (in particular MF), both at inter-specific and intra-growth form level, we could hypothesize that shifts in the start of flowering season could induce changes in the timing of seed development.

III.5.B.i. *Patterns of seed ripening (SR)*

Likewise the other phenophases, our analyses will be carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2007-2015), also the seed ripening (SR) showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=70, p<0.01) (Fig. III.5.B.i.1).

According to mean and median values, SR occurred at the end of August (respectively 241 and 244 DOY), while the 75% quartile occurred in early September (250 DOY) (Table III.5.B.i.1), that correspond to more than two weeks later the 75% quartile of SD.

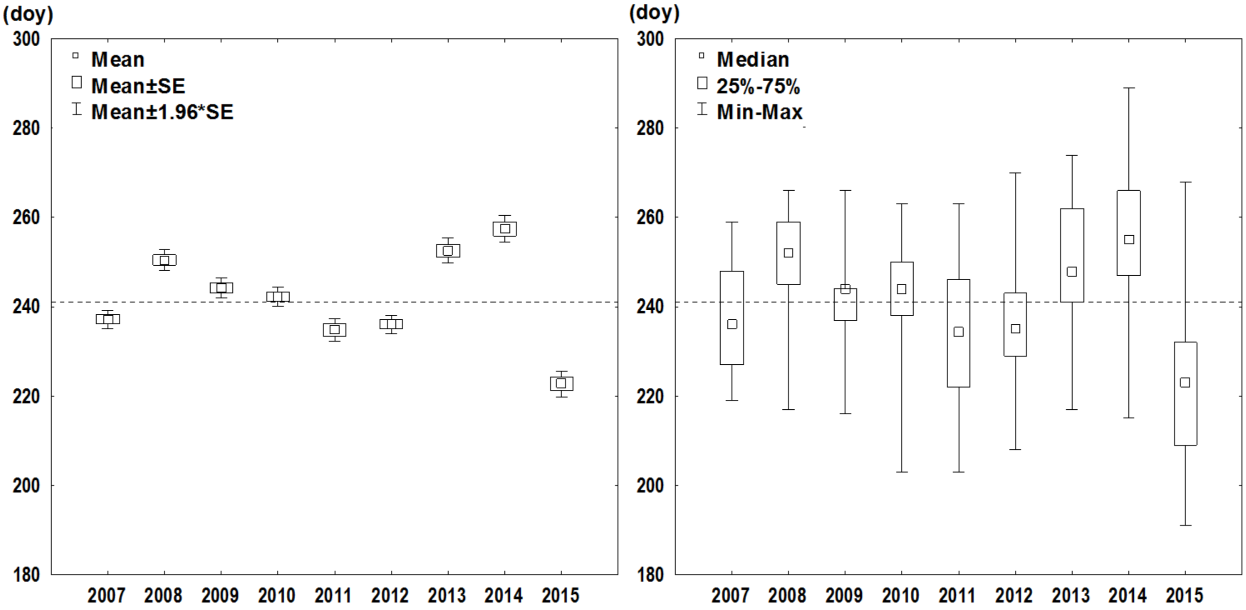


Figure III.5.B.i.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed ripening (SR) from 2007 to 2015, at the inter-specific level. The dotted black line represents the mean value for the whole period.

The earliest onset of SR was recorded in mid-July (191 DOY, in 2015), while the latest in early August (219 DOY, in 2007). The SR completion ranged from mid-September (263 DOY, in 2010 and 2011) until mid-October (289 DOY, in 2014) (Table III.5.B.i.1).
The total duration of SR spanned from 40 days (in 2007) to 77 days (in 2015), while the SR peak duration ranged from 7 days (in 2009) to 24 days (in 2011) (Fig. III.5.B.i.1).

Considering 75% quartiles anomalies over the whole dataset, SR showed the largest advance in 2015 (-18 days), and the largest delay in 2014 (respectively +16 days) (Fig. III.5.B.i.1). However, as tested by t-test we did not identify statistically significant differences (p>0.05).

Table III.5.B.i.1. Non-parametric statistics of seed ripening (SR) at the inter-specific level, computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	116	237	219	227	236	248	259	11.3
2008	91	250	217	245	252	259	266	10.9
2009	115	244	216	237	244	244	266	11.9
2010	116	242	203	238	244	250	263	11.8
2011	120	235	203	222	235	246	263	14.6
2012	120	236	208	229	235	243	270	11.5
2013	99	253	217	241	248	262	274	14.3
2014	97	257	215	247	255	266	289	15.2
2015	111	223	191	209	223	232	268	15.4
2007-2015	985	241	191	230	244	250	289	16.3

Analyzing thus he whole study period (2007-2015), we did not find any statistically significant trend of SR with time, as tested by linear regression ($p>0.05$). However we observed a delay of the latest SR (provided by its maximum) over the study period, as tested by linear regression ($\beta=2.1$, $R^2=0.44$, $p=0.05$) (Fig. III.5.B.i.2), indicating the high potentially capability of alpine plants of exploiting a longer growing season, in a Fall warming scenario.

Figure III.5.B.i.2. Trend with time of the latest SR ($\beta=2.1$, $R^2=0.44$, $p=0.05$) observed at inter-specific level, as tested by linear regression over the whole period 2007-2015.

As tested by linear regression at the inter-specific and inter-annual level, we observed statistically significant relations with the previous reproductive phenology stages. However, proportion of SR variance explained was always low: SR vs SD ($\beta=0.6$, $R^2=0.40$, $p<0.01$); SR vs FB ($\beta=0.6$, $R^2=0.29$, $p<0.01$), SR vs FF ($\beta=0.6$, $R^2=0.38$, $p<0.01$) and SR vs MF ($\beta=0.6$, $R^2=0.37$, $p<0.01$).

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2015) the SR of deciduous dwarf shrubs (i.e. *Salix herbacea*) (Fig. III.5.B.i.3) exhibited statistically significant differences among years (F=7, $p<0.01$) (Fig. III.5.B.i.4).

Table III.5.B.i.2. Non-parametric statistics of seed ripening (SR) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	6	244	236	236	248	248	248	6.2
2008	4	257	238	249	263	266	266	13.3
2009	5	255	244	244	254	266	266	11.0
2010	6	244	230	238	247	250	250	8.2
2011	5	237	222	232	237	237	257	12.7
2012	6	241	229	235	239	243	258	10.1
2013	5	248	241	248	248	248	255	4.9
2014	5	255	239	247	255	266	266	11.8
2015	5	220	206	216	226	226	226	8.9
2007-2015	47	244	206	236	244	254	266	13.8

Figure III.5.B.i.3. Example of SR of *Salix herbacea*.

Over the study period (2007-2015), the mean and median values of SR were coincident, and occurred at the beginning of September (244 DOY), while the 75% quartile occurred 10 days later in mid-September (254 DOY) (Table III.5.B.i.2).

Considering the intra-annual variability, the earliest onset of SR was recorded in late July (206 DOY, in 2015), while the latest at the beginning of September (244 DOY, in 2009). The SR completion spanned from mid-August (226 DOY, in 2015) to late September (266 DOY, in 2008, 2009 and 2014) (Table III.5.B.i.2).

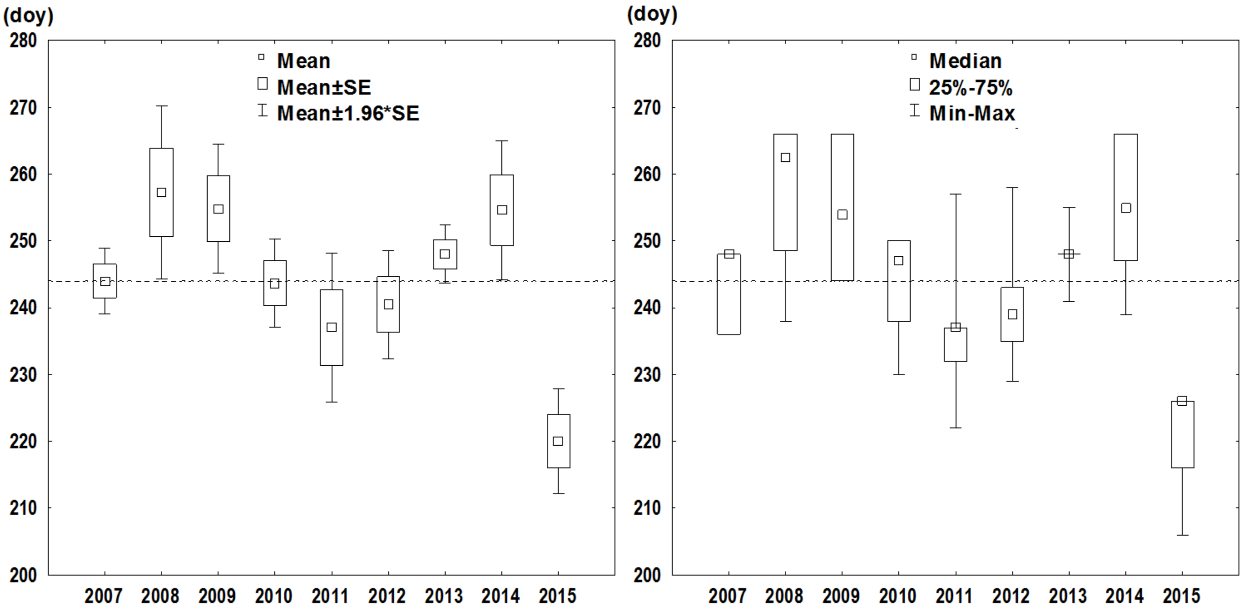


Figure III.5.B.i.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed ripening (SR) for deciduous dwarf shrubs from 2007 to 2015. The dotted black line represents the mean value for the whole period.

The total duration of SR ranged from 12 days (in 2007) to 35 days (in 2011), while the SR peak duration spanned from 0 days (in 2013) to 22 days (in 2009) (Fig. III.5.B.i.4).

Analyzing the anomalies of the 75% quartiles, the SR showed the largest advance in 2015 (-28 days) and the greatest delays in 2008, 2009 and 2014 (+12 days) (Fig. III.5.B.i.4). However, as tested by t-test, we did not observe statistically significant differences ($p>0.05$).

Thus considering all the study period we did not observe any statistically significant SR trends with time, as tested by linear regression ($p>0.05$).

Moreover, even if we found statistically significant relation with the previous reproductive phenology stages, they only explained a small proportion of SR variance, as tested by linear regression at the inter-annual level: SR vs SD ($\beta=0.6$, $R^2=0.51$, $p<0.01$), SR vs FB ($\beta=0.6$, $R^2=0.33$, $p<0.01$), SR vs FF ($\beta=0.7$, $R^2=0.38$, $p<0.01$), SR vs MF ($\beta=0.7$, $R^2=0.45$, $p<0.01$).

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2015) the SR of evergreen dwarf shrubs (i.e. *Kalmia procumbens*) exhibited statistically significant differences among years (F=5, p<0.01) (Fig. III.5.B.i.5-6).

Table III.5.B.i.4. Non-parametric statistics of seed ripening (SR) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev..
2007	6	248	248	248	248	248	248	-
2008	3	245	238	238	245	252	252	7.0
2009	5	243	230	244	244	244	254	8.6
2010	6	246	244	244	244	250	250	3.1
2011	6	237	222	222	239	246	252	13.1
2012	6	244	229	243	243	250	258	9.6
2013	5	259	248	255	255	262	274	9.8
2014	6	254	247	247	255	255	266	7.0
2015	6	236	226	232	239	239	239	5.5
2007-2015	49	246	222	243	246	250	274	10.2

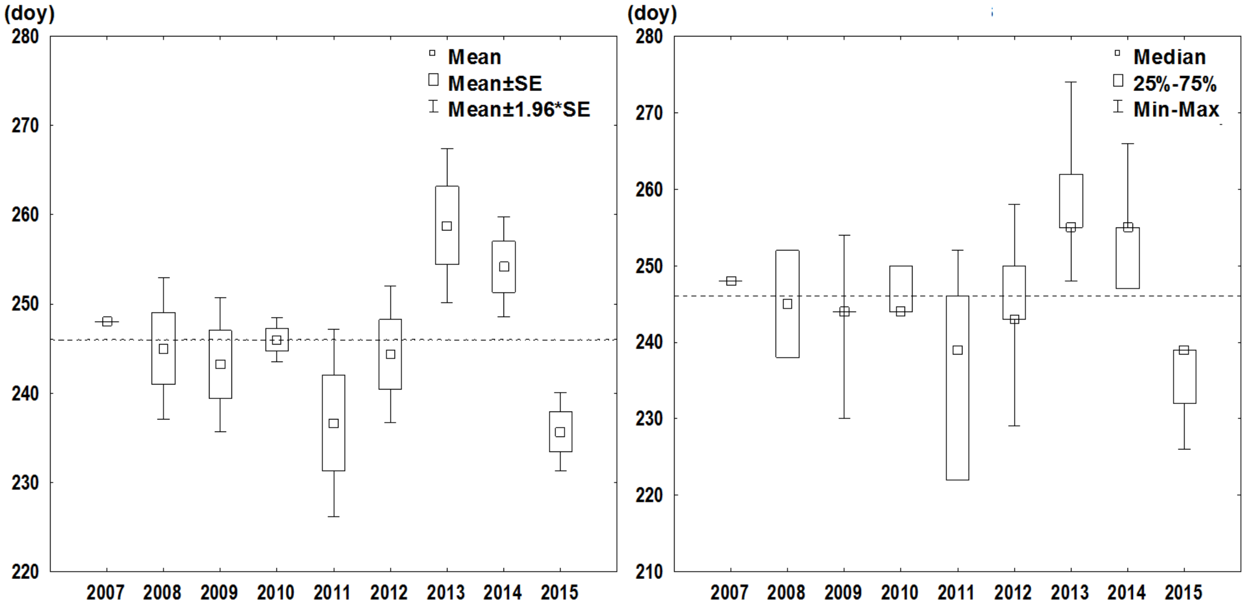


Figure III.5.B.i.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed ripening (SR) for evergreen dwarf shrubs from 2007 to 2015. The dotted black line represents the mean value for the whole period.

Over all the study period (2007-2015), mean and median values were coincident and occurred at early September (246 DOY), and the 75% quartile occurred only 4 days later (250 DOY) (Table III.5.B.i.4).

The earliest onset of SR was recorded at mid-August (222 DOY, in 2011), while the latest in early September (248 DOY, in 2007 and 2013). The end of SR ranged from late August (239 DOY, in 2015) to the beginning of October (274 DOY, in 2013) (Table III.5.B.i.4).

The total duration of SR for evergreen dwarf shrubs ranged from 0 days (in 2007) to 30 days (in 2011), while the SR peak duration ranged from 0 days (in 2007 and 2009) to 24 days (in 2011) (Fig. III.5.B.i.5).

Considering the anomalies of the 75% quartiles, the SR showed the largest delay in 2013 (+12 days) and the greatest advance in 2015 (-11 days). As tested by t-test, the year 2013 was the only one identified as statistically significant different ($p=0.03$), and thus as “extreme” year of SR.

Considering thus only the “normal” years of SR (removing 2013), we did not find any statistically significant advance of SR with time, as tested by linear regression ($p>0.05$).

As tested by linear regression at the inter-annual and inter-specific level, the evergreen shrubs, did not display statistically significant relation between SR and SD ($p>0.05$). Moreover, even if we found statistically significant relation with the flowering phenology stages, they only explained a small proportion of SR variance. Indeed, as tested by linear regression at the inter-annual level: SR vs FB ($\beta=0.3$, $R^2=0.10$, $p=0.02$), SR vs FF ($\beta=0.6$, $R^2=0.22$, $p<0.01$), SR vs MF ($\beta=0.5$, $R^2=0.16$, $p<0.01$).

Figure III.5.B.i.6. Example of SR of *Kalmia procumbens.*

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2007-2015) the SR of evergreen shrubs (i.e. *Rhododendron ferrugineum*) (Fig. III.5.B.i.7) exhibited statistically significant differences among years (F=3, p<0.01) (Fig III.5.B.i.8).

Figure III.5.B.i.7. Example of SR of *Rhododendron ferrugineum.*

Table III.5.B.i.5. Non-parametric statistics of seed ripening (SR) for evergreen shrubs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	4	248	248	248	248	248	248	-
2008	4	247	238	238	245	256	259	10.5
2009	4	248	237	241	244	255	266	12.6
2010	4	254	238	244	257	263	263	12.0
2011	5	251	222	257	257	257	263	16.5
2012	4	262	250	254	264	270	270	9.8
2013	3	273	270	270	274	274	274	2.3
2014	5	265	255	266	266	266	273	6.5
2015	5	259	251	257	257	264	264	5.5
2007-2015	38	256	222	248	257	266	274	12.0

Over all the study period (2007-2015), mean and median values of SR occurred in mid-September (respectively 256 and 257 DOY), while the 75% occurred in late September (266 DOY) (Table III.5.B.i.5).

Considering each single year, the earliest onset of SR was recorded between mid-August (222 DOY, in 2011) and late September (270 DOY, in 2013). The end of SR spanned from early September (248 DOY, in 2007) to the beginning of October (274 DOY, in 2013) (Table III.5.B.i.5).

The total duration of SR for the evergreen shrubs ranged from 0 days (in 2007) to 41 days (in 2011), while the SR peak duration ranged from 0 (in 2007 and 2011) to 19 days (in 2010) (Fig. III.5.B.i.8).

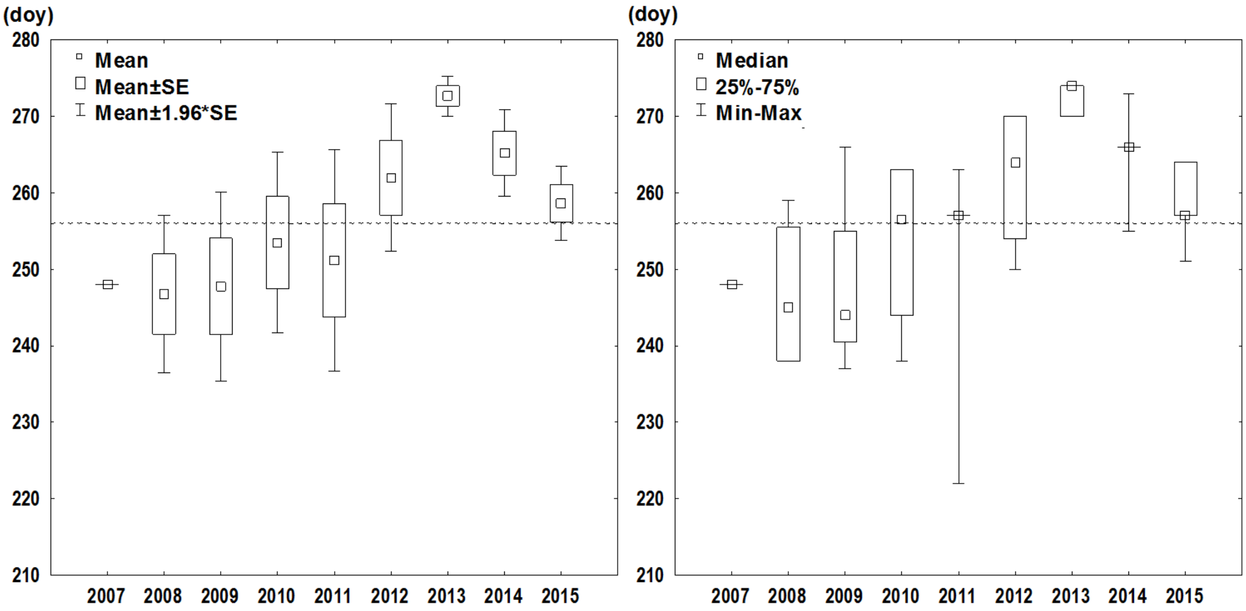


Figure III.5.B.i.8. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed ripening (SR) for evergreen shrubs from 2007 to 2015. The dotted black line represents the mean value for the whole period.

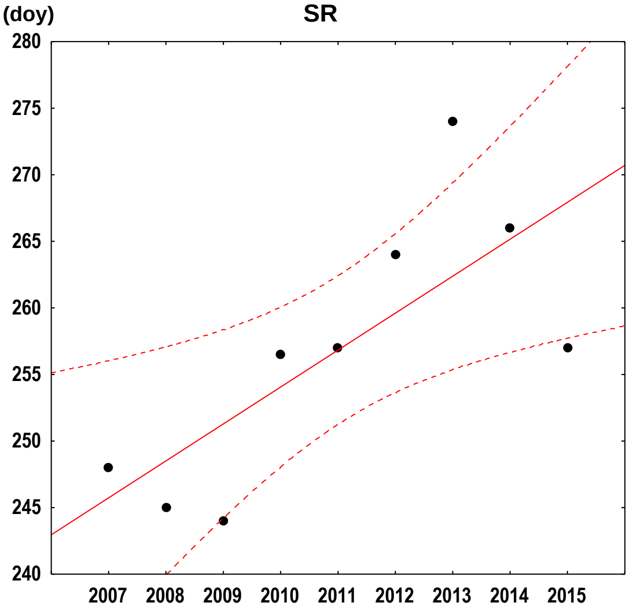


Figure III.5.B.i.9. Trend with time of the SR (β=2.8, R^2=0.57, p=0.02) observed for evergreen shrubs, as tested by linear regression over the whole period 2007-2015.

Analyzing the anomalies of the 75% quartiles, the SR showed the largest advance in 2007 (-18 days) while the largest delay in 2008 (only +8 days), although all not statistically significant, as tested by t-test ($p>0.05$) (Fig. III.5.B.i.8).

Thus, over the whole dataset of the evergreen shrubs, we found a statistically significant delay of SR with time, as tested by linear regression ($\beta=2.8$, $R^2=0.57$, $p=0.02$) (Fig. III.5.B.i.9).

For this growth form, we did not find any statistically significant relations between the timing of SR and any of the previous reproductive phenology stages (FB, FF, MF and SD), as tested by linear regression at the inter-annual level ($p>0.05$).

Forbs

Considering all the study period, SR of forbs (Fig. III.5.B.i.10) exhibited statistically significant differences among years, as tested by one-way ANOVA ($F=44$, $p<0.01$) (Fig. III.5.B.i.11).

The mean and median value of SR over the whole period (2007-2015) were almost coincident and corresponded to late August (239 and 238 DOY), while the 75% occurred at early September (248 DOY) (Table III.5.B.i.6).

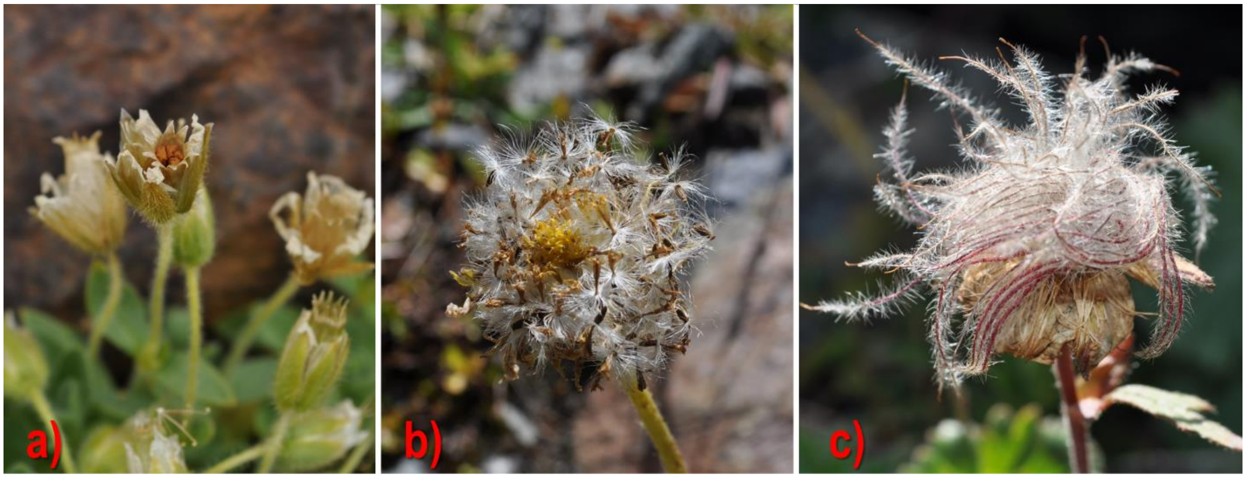


Figure III.5.B.i.10. Example of SR of some forbs species: a) *Cerastium uniflorum*, b) *Doronicum clusii* and c) *Geum reptans*.

The beginning of SR occurred at mid-July (191 DOY, in 2015) and ranged up to late August (233 DOY, in 2014). The end of SR ranged from mid-September (257 DOY, in 2011) to mid-October (289 DOY, in 2014) (Table III.5.B.i.6).

The total duration of SR spanned from 40 days (in 2007) to a maximum of 77 days (in 2015), while the SR peak duration ranged from 6 (in 2012) to 28 days (in 2013) (Fig. III.5.B.i.11).

Comparing the 75% anomalies, SR showed the largest delay in 2014 (+18 days), while the largest advance occurred in 2015 (-25 days). The year 2015 was identified as statistically significant different, as tested by t-test (p=0.04), and was thus identifiable as “extreme” years of SR (Fig III.5.B.i.11).

Table III.5.B.i.6. Non-parametric statistics of seed ripening (SR) of forbs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	237	219	227	236	248	259	12.8
2008	49	249	217	238	245	259	266	12.1
2009	64	244	216	237	244	244	266	11.3
2010	63	243	221	238	244	250	263	9.2
2011	66	232	203	222	232	246	257	13.2
2012	66	232	208	229	229	235	258	10.0
2013	54	248	224	234	248	262	274	14.6
2014	52	255	233	247	255	266	289	12.2
2015	60	217	191	209	216	223	268	13.1
2007-2015	537	239	191	229	238	248	289	16.1

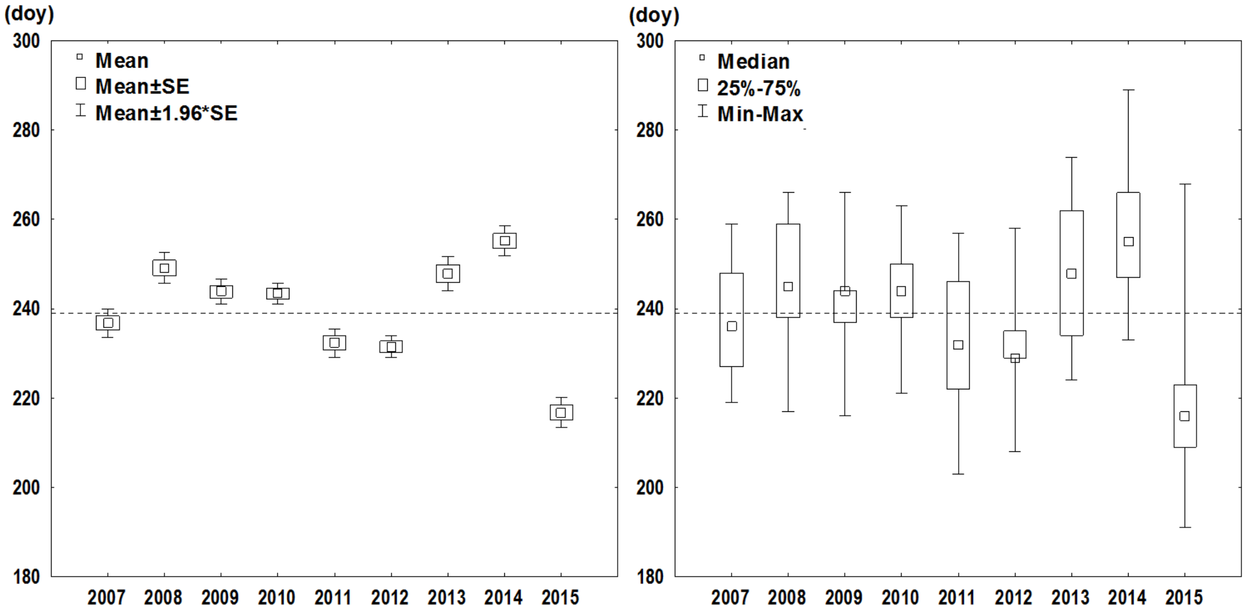


Figure III.5.B.i.11. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed ripening (SR) of forbs from 2007 to 2015. The dotted black line represents the mean value for the whole period.

Considering thus only the “normal” years (2007-2014) we did not identify any statistically significant trend of SR with time, as tested by linear regression (p>0.05).

As tested by linear regression at the inter-annual level, and differently from shrubs, there was a statistically significant relation between SR and SD (β=0.9, R^2=0.66, $p<0.01$). Moreover, as tested by linear regression, we detected statistically significant relation between SD and the flowering phenology stages: SR vs FB (β=1.0, R^2=0.71, $p<0.01$), SR vs FF (β=0.9, R^2=0.77, $p<0.01$), and SR vs MF (β=1.0, R^2=0.84, $p<0.01$).

Graminoids

As tested by one-way ANOVA, overall the study period (2007-2015) the SR of graminoids (Fig. III.5.B.i.12) showed statistically significant differences among years (F=14, $p<0.01$) (Fig. III.5.B.i.13).

Figure III.5.B.i.12. Example of SR of *Carex curvula.*

Over the study period (2007-2015), mean and median values of SR were almost coincident, and occurred at the beginning of September (242 and 244 DOY), while the 75% quartile coincided with mid-September (252 DOY) (Table III.5.B.i.7).

Considering the intra-annual variability, the earliest onset of SR (203 DOY, mid-July) was recorded in 2010 and 2011, while the latest in 2008 (238 DOY, late August). The SR completion ranged from the beginning of September (248 DOY, in 2007) to mid-October (289 DOY, in 2014) (Table III.5.B.i.7).

Table III.5.B.i.7. Non-parametric statistics of seed ripening (SR) of graminoids computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	37	234	219	227	236	236	248	8.3
2008	31	253	238	245	252	259	266	8.5
2009	37	243	216	237	244	244	266	13.1
2010	37	238	203	225	244	250	263	15.6
2011	38	236	203	222	246	246	257	16.0
2012	38	239	222	235	243	243	258	9.0
2013	32	258	217	248	262	270	274	12.2
2014	29	261	215	247	255	281	289	21.0
2015	35	226	206	219	226	232	254	12.6
2007-2015	314	242	203	232	244	252	289	17.0

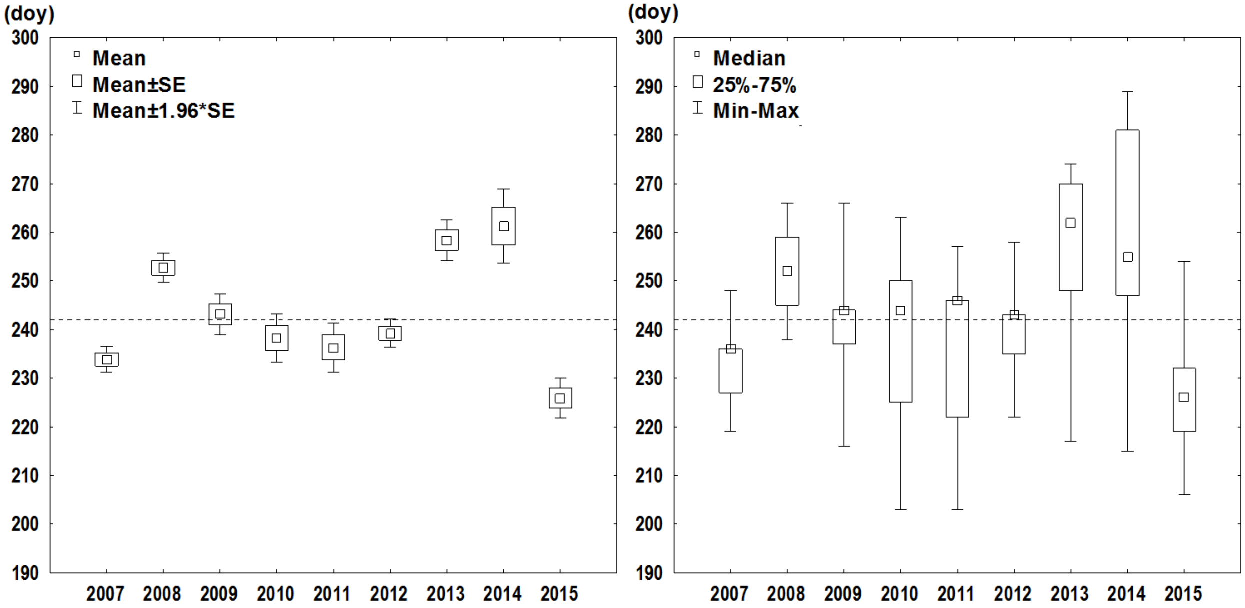


Figure III.5.B.i.13. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed ripening (SR) of graminoids from 2007 to 2015. The dotted black line represents the mean value for the whole period.

The total duration of SR ranged from 29 days (in 2007) to74 days (in 2014), while the SR peak duration ranged over 7 days (in 2009) or to 34 days (in 2014) (Fig. III.5.B.i.13).

Considering the anomalies of the 75% quartiles, in 2015 the SR displayed the largest advance (-20 days), while in 2014, it showed the largest delay (+29 days), which was the only one year identifiable as “extreme”, as tested by t-test (p=0.04) (Fig. III.5.B.i.13).

Analyzing thus only the “normal” years, we did not observe any trend of SR with time, as tested by linear regression (p>0.05).

As tested by linear regression at the inter-annual level, we found statistically significant relation with the previous reproductive phenology stages. However, they only explained a small proportion of SR variance: SR vs SD ($\beta=0.6$, $R^2=0.46$, $p<0.01$), SR vs FB ($\beta=0.6$, $R^2=0.38$, $p<0.01$), SR vs FF ($\beta=0.6$, $R^2=0.51$, $p<0.01$), SR vs MF ($\beta=0.6$, $R^2=0.46$, $p<0.01$).

Comparison of trends among growth forms

Comparing the trends of SR among the selected growth forms at the inter-annual level, we found statistically significant differences (Fig. III.5.B.i.14), as tested by one-way ANOVA ($F=12$, $p<0.01$).

In terms of SR total duration, the patterns among the selected growth forms were similar to those of the flowering stages. Graminoids and forbs exhibited the longest SR duration (respectively 98 and 86 days) while for shrubs was shorter of almost one month (Fig. III.5.B.i.14).

The length of SR peak duration was comparable for deciduous dwarf shrubs, evergreen shrubs, forbs and graminoids (ranging from 18 to 20 days), but was shorter for evergreen dwarf shrubs (only 7 days).

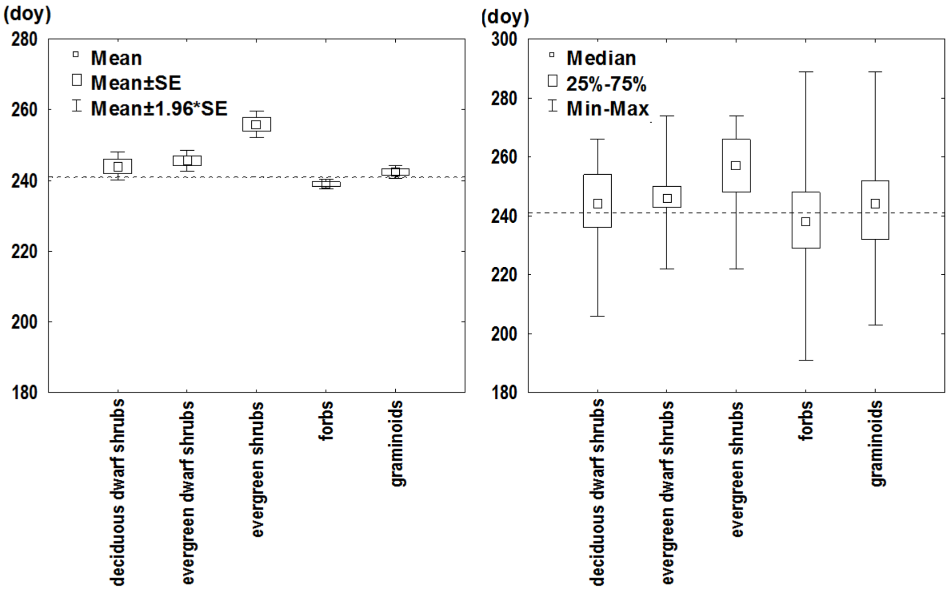


Figure III.5.B.i.14. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of seed ripening (SR) between the selected growth forms over the period 2007-2015. The dotted black line represents the mean value for the whole period.

Forbs were the first growth form starting SR (191 DOY, mid-July), while evergreen dwarf shrubs and evergreen shrubs were the latest (respectively 243 and 248 DOY, beginning of September). The latest SR completion was documented for graminoids and forbs simultaneously, in mid-October (289 DOY). On the opposite the deciduous dwarf shrubs was the first growth form completing SR (266 DOY, late September) (Fig. III.5.B.i.14).

According to 75% quartiles anomalies referred to all dataset, the evergreen shrubs exhibited the latest and statistically significant SR (+16 days), as tested by t-test (p=0.01).

Flowering and seed development stages occurred later for graminoids and forbs, and ranged over a larger period, while evergreen shrubs started earlier and ranged over shorter period (see chap. III.5.B.g and III.5.B.h).

The total duration remained similar (i.e. longer for herbaceous growth form), but the evergreen dwarf shrubs and evergreen shrubs (p=0.01) started later in the season, indicating that they need more time to gain the SR.

Moreover, evergreen shrubs did not show statistically significant relation with the previous reproductive phenology stages, highlighting that SR responses to changes in growing season length could be different.

Comparing the 75% quartiles of SD and 75% quartiles of SR (i.e. time request for seed ripening; SD-SR) over the study period, we found a statistically significant lengthening of the time requested for ripening only for deciduous dwarf shrubs and evergreen shrubs.

As tested by linear regression on the “normal years” of SD and SR of deciduous dwarf shrubs (excluding 2008, identified as “extreme” SD for deciduous dwarf shrubs), they showed a lengthening of SD-SR at the rate of +2.1 days/year (R^2=0.53, p=0.04). As deciduous dwarf shrubs displayed a statistically significant advance of SD (see chap III.5.B.h), the lengthening of SD-SR mainly depended on the earlier start of SD.
Similarly, as tested by linear regression on “normal years” of evergreen shrubs (excluding 2008, identified as “extreme” SD for evergreen shrubs), they showed a statistically significant expansion of SD-SR at the rate of +4.3 days/year (R^2=0.51, p=0.05).
Contrary to deciduous dwarf shrubs, the evergreen shrubs did not show any trend of SD (see chap III.5.B.h). Therefore, the delay of SR observed for evergreen shrubs, lead in more time request for seed ripening, stressing the capability of this growth form to exploit longer growing season caused by Fall warming.

III.5.B.j. *Patterns of leaf senescence (LS)*

Likewise the other phenophases, our analyses have been carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2007-2015), also the leaf senescence (LS) showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=138, p<0.01) (Fig. III.5.B.j.1).

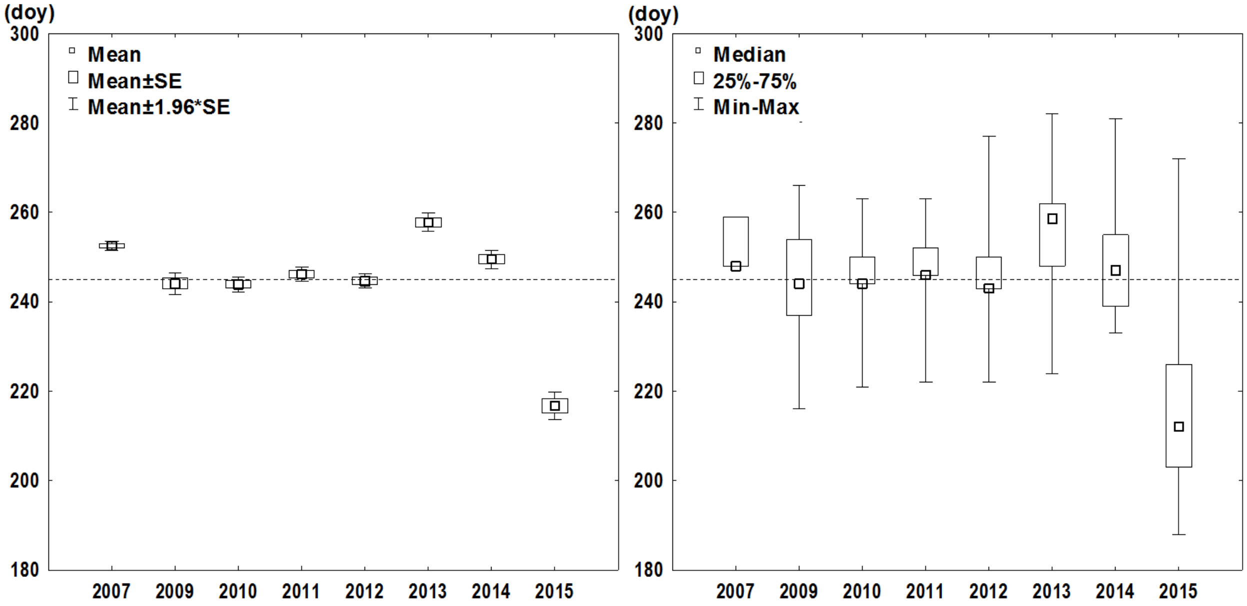


Figure III.5.B.j.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf senescence (LS) from 2007 to 2015, at the inter-specific level. The dotted black line represents the mean value for the whole period.

Table III.5.B.j.1. Non parametric statistics of leaf senescence (LS) at the inter-specific level, computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	109	253	248	248	248	259	259	5.4
2008	-	-	-	-	-	-	-	-
2009	110	244	216	237	244	254	266	13.0
2010	115	244	221	244	244	250	263	9.2
2011	109	246	222	246	246	252	263	8.3
2012	113	245	222	243	243	250	277	8.6
2013	112	258	224	248	259	262	282	11.2
2014	111	250	233	239	247	255	281	11.2
2015	111	217	188	203	212	226	272	16.6
2007-2015	890	244	188	239	246	255	282	15.8

According to the mean and median values, LS occurred in early September (respectively 244 and 246 DOY), while the 75% quartile occurred almost ten day later, in mid-September (255 DOY) (Table III.5.B.j.1).

The earliest onset of LS was recorded in early July (188 DOY, in 2015), while the latest in early September (248 DOY, in 2007). The LS completion ranged from mid-September (259 DOY, in 2007) until early October (282 DOY, in 2013) (Table III.5.B.j.1).

The total duration of SR spanned from 11 days (in 2007) to 84 days (in 2015), while the LS peak duration ranged from 6 days (in 2010 and 2011) to 23 days (in 2015) (Fig. III.5.B.j.1).

Considering 75% quartiles anomalies over the whole dataset, LS showed the largest advance in 2015 (-29 days), and the largest delay in 2013 (+7 days). As tested by t-test we identified 2015 as statistically significant different and thus as an "extreme" year of LS ($p<0.01$).

As tested by linear regression over only the normal years (2007-2014), we did not observe any LS trend with time. However, analyzing all the data population, we observed a statistically significant delay of the latest LS ($\beta=4.0$, $R^2=0.82$, $p<0.01$) (Fig. III.5.B.j.2), thus underlying a lengthening of the end of the growing season.

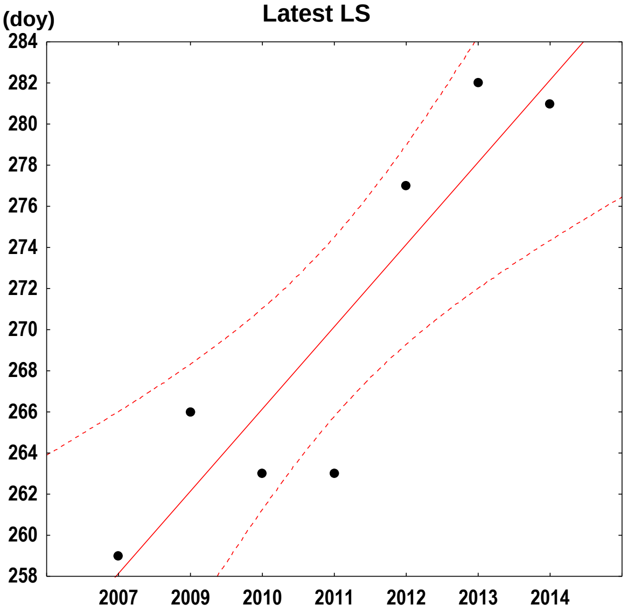


Figure III.5.B.j.2. Trend with time of the latest LS ($\beta=4.0$, $R^2=0.82$, $p<0.01$) observed at the inter-specific level, as tested by linear regression over the "normal" years (2007-2014).

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2007-2015) the LS of deciduous dwarf shrubs (i.e. *Salix herbacea*) exhibited statistically significant differences among years (F=11, p<0.01) (Fig. III.5.B.j.3-4).

Over the study period (2007-2015), the mean and median values of LS occurred in early September (251 and 248 DOY), while the 75% quartile occurred in mid-September (259 DOY) (Table III.5.B.j.2).

Table III.5.B.j.2. Non-parametric statistics of leaf senescence (LS) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	6	255	248	248	259	259	259	5.7
2008	-	-	-	-	-	-	-	-
2009	6	255	244	244	255	266	266	12.0
2010	7	249	244	244	250	250	263	6.8
2011	6	251	246	246	246	257	263	7.5
2012	7	250	243	250	250	250	258	4.3
2013	7	269	262	262	270	270	282	6.7
2014	7	243	233	239	247	247	247	5.7
2015	7	240	226	232	239	247	247	8.2
2007-2015	53	251	226	244	248	259	282	11.1

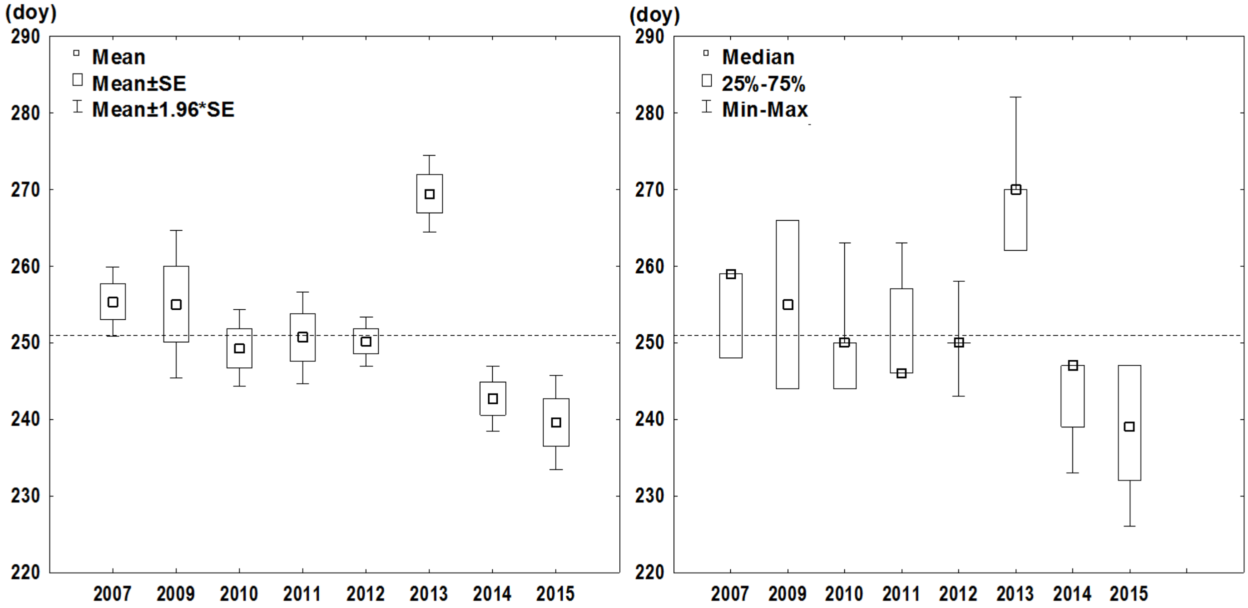


Figure III.5.B.j.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf senescence (LS) for deciduous dwarf shrubs from 2007 to 2015. The dotted black line represents the mean value for the whole period.

Figure III.5.B.j.4. Example of LS of *Salix herbacea*.

Considering the intra-annual variability, the earliest onset of LS was recorded in mid-August (226 DOY, in 2015), while the latest in early September (248 DOY, in 2007). The end of LS spanned from early September (247 DOY, in 2014 and 2015) to late September (266 DOY, 2009) (Table III.5.B.j.2).

The total duration of LS ranged from 11 days (in 2007) to 22 days (in 2009), while the LS peak duration spanned from 0 days (in 2012) to 22 days (in 2009) (Fig. III.5.B.j.3).

Analyzing the anomalies of the 75% quartiles, the LS showed the largest advance in 2014 and 2015 (-12 days) and the greatest delays in 2013 (+11 days). However, as tested by t-test, we did not observe statistically significant differences ($p>0.05$) (Fig. III.5.B.j.3).

Thus considering all the study period, we did not observe any statistically significant LS trends with time, as tested by linear regression ($p>0.05$).

Deciduous shrubs

As tested by one-way ANOVA, overall the study period (2007-2015) the LS of deciduous shrubs (i.e. *Vaccinium uliginosum*) exhibited statistically significant differences among years ($F=4$, $p<0.01$) (Fig. III.5.B.j.5-6).

Over the study period (2007-2015), the mean and median values of LS occurred in early September (251 and 252 DOY), while the 75% quartile occurred within only one week (257 DOY) (Table III.5.B.j.2).

Table III.5.B.j.2. Non-parametric statistics of leaf senescence (LS) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	3	255	248	248	259	259	259	6.4
2008	-	-	-	-	-	-	-	-
2009	3	248	237	237	254	254	254	9.8
2010	4	242	230	237	244	247	250	8.5
2011	4	255	246	249	255	260	263	7.2
2012	3	248	235	235	250	258	258	11.7
2013	4	270	255	263	272	278	282	11.3
2014	4	251	247	247	251	255	255	4.6
2015	4	241	223	231	243	251	254	13.3
2007-2015	29	251	223	246	252	257	282	12.4

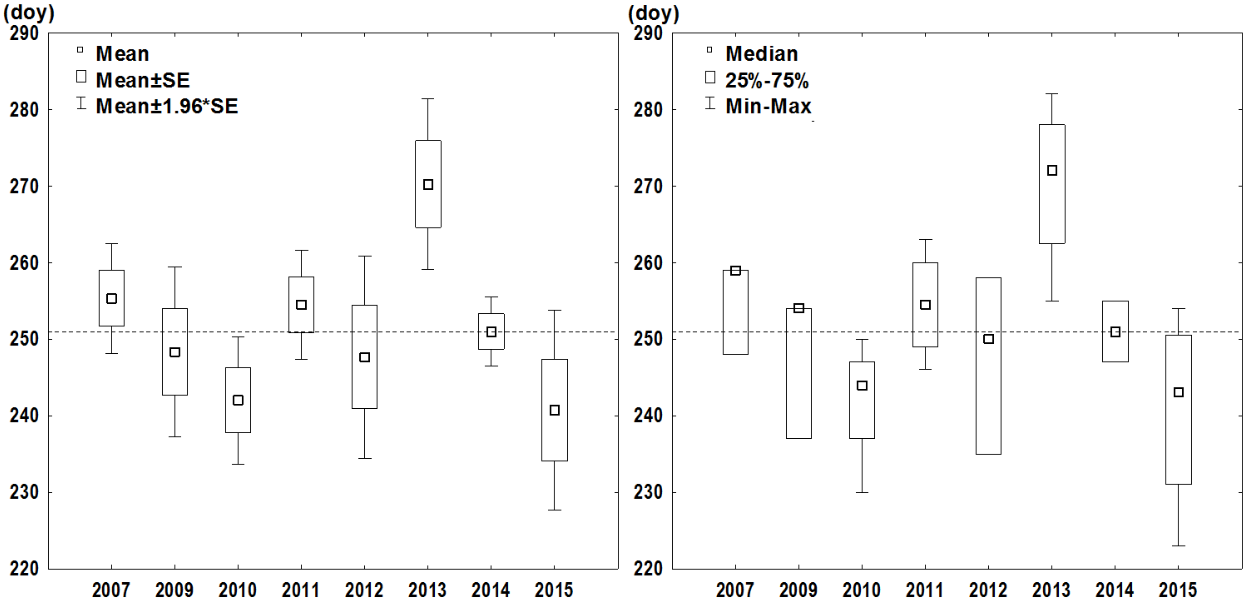


Figure III.5.B.j.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf senescence (LS) for deciduous shrubs from 2007 to 2015. The dotted black line represents the mean value for the whole period.

Considering the intra-annual variability, the earliest onset of LS was recorded at mid-August (223 DOY, in 2015), while the latest at the beginning of September (248 DOY, in 2007). The end of LS spanned from early September (250 DOY, in 2010) to early October (282 DOY, in 2013) (Table III.5.B.j.2).

The total duration of LS ranged from 8 days (in 2014) to 31 days (in 2015), while the LS peak duration spanned from 8 days (in 2014) to 23 days (in 2012) (Fig. III.5.B.j.5).

Analyzing the anomalies of the 75% quartiles, the LS showed the largest advance in 2010 (-10 days) and the greatest delays in 2013 (+21 days). As tested by t-test, in 2013 we observed statistically significant differences ($p<0.01$), and was thus identified as "extreme" year of LS (Fig. III.5.B.j.5).

Thus considering only the "normal" years, we did not observe any statistically significant LS trends with time, as tested by linear regression ($p>0.05$).

Figure III.5.B.j.6. Example of LS of *Vaccinium uliginosum*.

Forbs

Considering all the study period, LS of forbs exhibited statistically significant differences among years, as tested by one-way ANOVA ($F=81$, $p<0.01$) (Fig III.5.B.j.7-8).

The mean and median value of LS over the whole period (2007-2015) were almost coincident and corresponded to early September (245 and 247 DOY), while the 75% occurred at mid-September, less than 10 days later (255 DOY) (Table III.5.B.j.6).

The beginning of LS occurred at mid-July (199 DOY, in 2015) and ranged up to early September (248 DOY, in 2007). The completion of LS ranged from mid-September (259 DOY, in 2007) to early October (282 DOY, in 2013) (Table III.5.B.j.6).

The total duration of LS spanned from 11 days (in 2007) to a maximum of 73 days (in 2015), while the LS peak duration ranged from 6 (in 2010) to 14 days (in 2013 and 2015) (Fig. III.5.B.j.7).

Comparing the 75% anomalies, LS showed the earliest and statistically significant advance in 2015 (-29 days), as tested by t-test ($p<0.01$), which was thus identified as "extreme" year of LS (Fig III.5.B.j.7).

Table III.5.B.j.6. Non-parametric statistics of leaf senescence (LS) of forbs computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	63	253	248	248	248	259	259	5.5
2008	-	-	-	-	-	-	-	-
2009	64	247	223	244	244	254	266	11.7
2010	67	247	230	244	244	250	263	7.1
2011	61	245	232	237	246	246	263	8.1
2012	65	245	222	243	243	250	270	8.6
2013	63	258	224	248	262	262	282	11.7
2014	63	251	233	247	255	255	281	11.2
2015	63	219	199	212	216	226	272	15.5
2007-2015	509	245	199	241	247	255	282	15.0

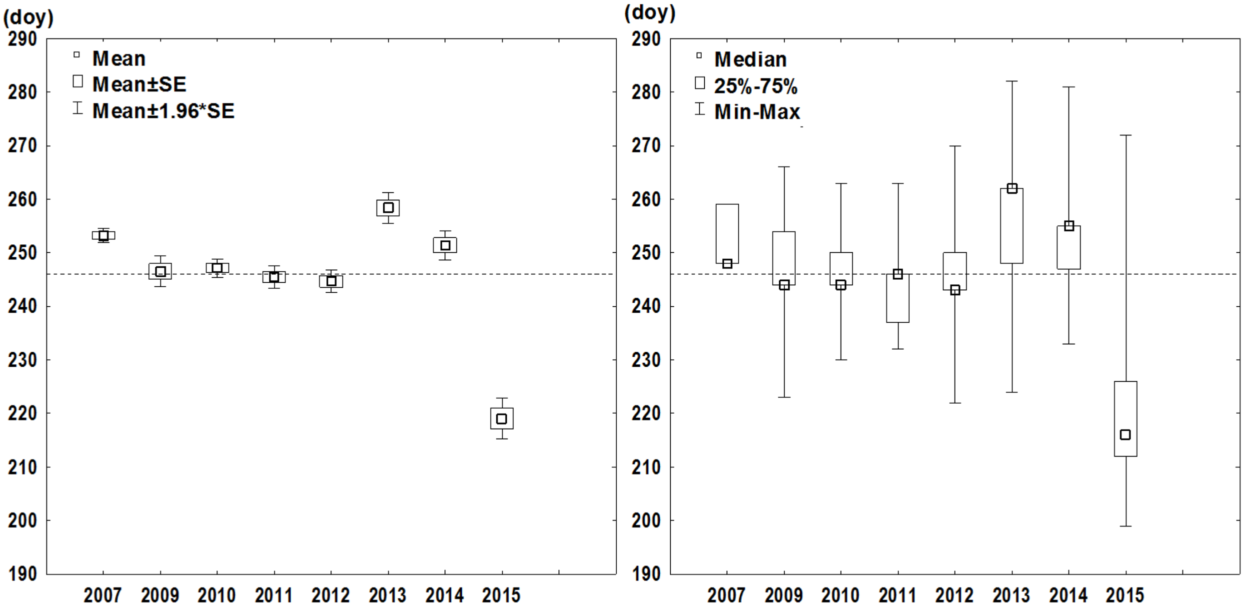


Figure III.5.B.j.7. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf senescence (LS) of forbs from 2007 to 2015. The dotted black line represents the mean value for the whole period.

Considering thus only the "normal" years (2007-2014) there wasn't any statistically significant trend of LS with time ($p>0.05$). However, we identified a statistically significant delay of the latest LS, as tested by linear regression ($\beta=3.3$, $R^2=0.79$, $p<0.01$) (Fig. III.5.B.j.9).

Figure III.5.B.j.8. Example of LS of *Geum reptans*.

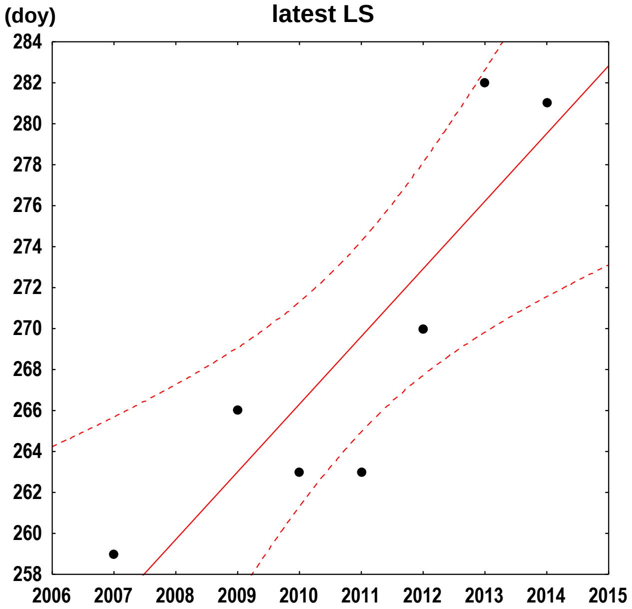


Figure III.5.B.j.9. Trend with time of the latest LS (β=4.0, $R^2=0.82$, $p<0.01$) of forbs, as tested by linear regression over the "normal" years (2007-2014).

Graminoids

As tested by one-way ANOVA, overall the study period (2007-2015) the LS of graminoids showed statistically significant differences among years (F=88, $p<0.01$) (Fig. III.5.B.j.10-11).

Table III.5.B.j.7. Non-parametric statistics of leaf senescence (LS) of graminoids computed for each single year, as well as for the entire monitoring period (2007-2015).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2007	37	251	248	248	248	248	259	4.8
2008	-	-	-	-	-	-	-	-
2009	37	238	216	223	244	244	266	13.0
2010	37	237	221	225	244	244	250	9.7
2011	38	246	222	246	246	252	257	8.6
2012	38	244	229	243	243	250	277	8.9
2013	38	253	234	248	255	262	270	8.3
2014	37	247	233	239	247	255	273	11.9
2015	37	206	188	199	203	212	247	10.3
2007-2015	299	240	188	232	244	250	277	16.9

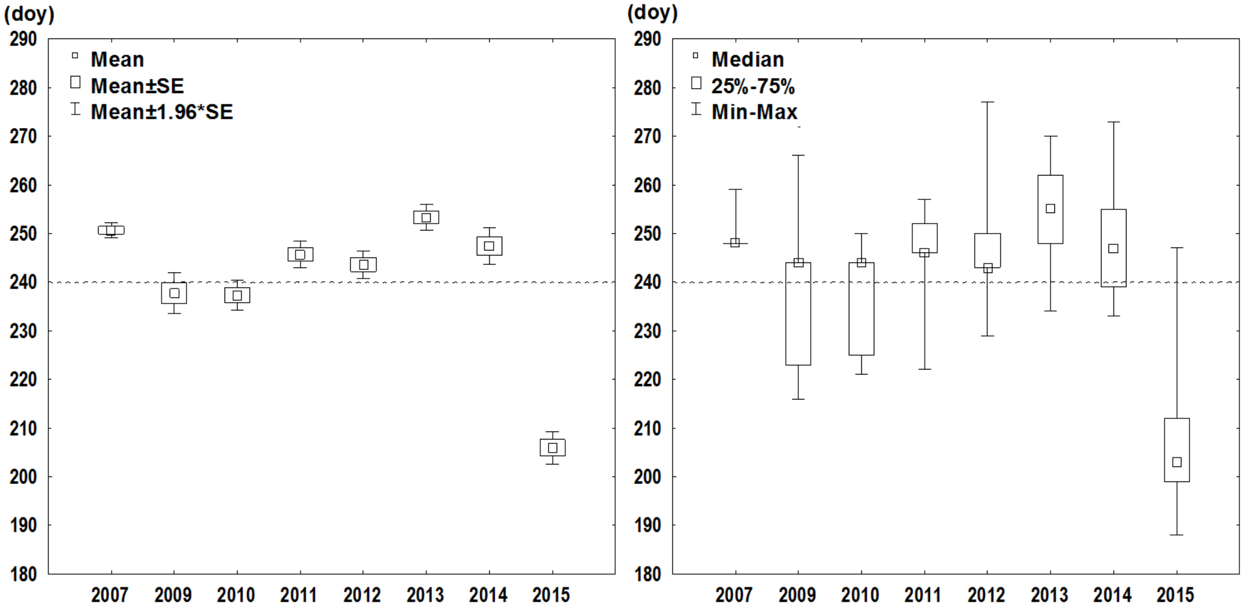


Figure III.5.B.j.10. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf senescence (LS) of graminoids from 2007 to 2015. The dotted black line represents the mean value for the whole period.

Over the study period (2007-2015), mean and median values of LS occurred at the end of August/beginning of September (respectively 240 and 244 DOY), while the 75% quartile occurred c.10 days later (250 DOY) (Table III.5.B.j.7).

The earliest onset of LS ranged from early July (188 DOY, in 2015) to early September (248 DOY, in 2007). The LS completion ranged from the beginning of September (247 DOY, in 2015) to early October (277 DOY, in 2012) (Table III.5.B.j.7). The total duration of LS ranged from 11 days (in 2007) to 59 days (in 2015), while the LS peak duration ranged from 0 days (in 2007) or to 21 days (in 2009) (Fig. III.5.B.j.10).

Considering the anomalies of the 75% quartiles, in 2015 the LS displayed the largest advance (-38 days), while in 2013, it showed the largest delay (+12 days) (Fig. III.5.B.j.10). The year 2015 was the only one whit statistically significant differences, and thus identifiable as “extreme” (p<0.01).

Analyzing thus only the “normal” years (2007-2014), we did not observe any trend of SR with time, as tested by linear regression ($p>0.05$). However, analyzing the pattern of all the data population, we observed a statistically significant delay of the 75% quartile of LS, as tested by linear regression ($\beta=2.3$, $R^2=0.58$, $p=0.05$) (Fig. III.5.B.j.12).

Figure III.5.B.j.11. Example of LS of a) *Agrostis alpina* and b) *Carex curvula*.

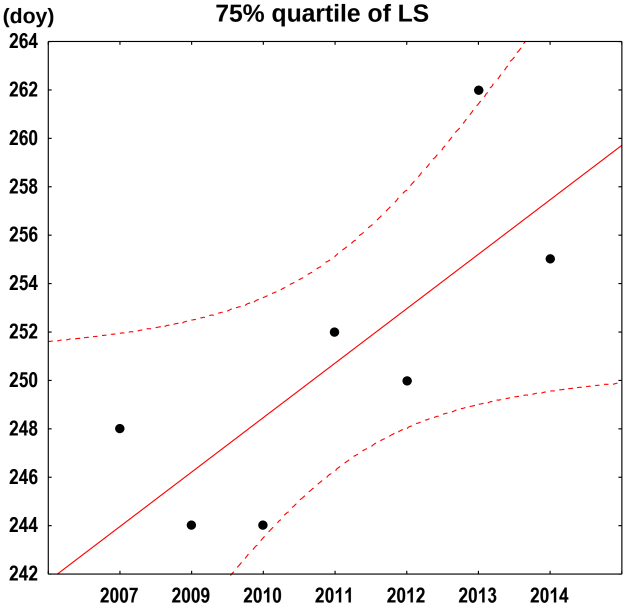


Figure III.5.B.j.12. Trend with time of the latest LS ($\beta=2.3$, $R^2=0.58$, $p<0.01$) of graminoids, as tested by linear regression over the “normal” years (2007-2014).

Comparison of trends among growth forms

Comparing the trends of LS among the selected growth forms at the inter-annual level, we found statistically significant differences (Fig. III.5.B.j.13), as tested by one-way ANOVA (F=14, p<0.01).

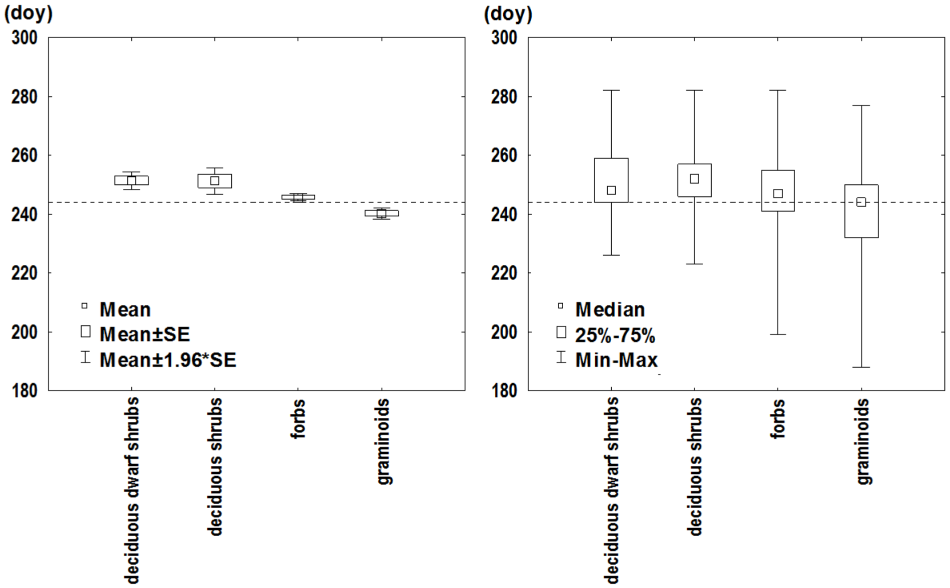


Figure III.5.B.j.13. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf senescence (LS) between the selected growth forms over the period 2007-2015. The dotted black line represents the mean value for the whole period.

Forbs and graminoids exhibited the longest LS duration (respectively 83 and 89 days) while deciduous dwarf shrubs and deciduous shrubs showed shorter LS of almost one month (respectively 56 and 59 days) (Fig. III.5.B.j.13).

The length of LS peak duration ranged from 11 days (deciduous shrubs) to 18 days (graminoids). Graminoids were the first growth form starting LS (188 DOY, beginning of July), followed by forbs, 10 days later. On the contrary, deciduous dwarf shrubs and deciduous shrubs did not start LS until mid-August (226 and 223 DOY).

The completion of LS occurred similarly for all the growth forms, in the first week of October: from 277 DOY for graminoids, to 282 DOY for all the other growth forms, thus indicating a strong signal that regulate the completion of LS and thus the end of the season.

The longer time of LS showed by herbaceous species, could be an adaptation to cope with climate variability, while shrubs appeared more constrained in a lower period and thus less flexible to potential climate variability.

The observed trends with time, confirmed that herbaceous species were able to move their LS, towards later in the season. Therefore, according to our findings, forbs and graminoids could be the most reactive species, concerning LS.

In the following paper (Cannone & Dalle Fratte, 2016 submitted), we investigated in detail the leaf senescence pattern of forbs species, in relation to climate and its impact on growing season lengthening.

Type of article: Original Article

Leaf senescence of high-elevation alpine forbs: sensitivity to climate and carryover effects on growth of the following year

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Running Title: *Climate sensitivity of leaf senescence of alpine forbs*

Abstract

Background and Aims Plant phenology provides robust responses to climate change, but the observation of autumn events, particularly leaf senescence (LS), has been largely neglected, especially that of alpine plants. We investigate the sensitivity of the LS of alpine plants to the climate and hypothesize the following: a) the photoperiod is the most important factor regulating LS, and that b) LS responds to the climate only in extreme conditions when c) LS exerts carryover effects on the vegetative growth the following year.

Methods We show the results of a long-term field observation (2007–2015) of snow melt (SM), LS and growing season length (GSL) of 9 deciduous forb species in a high alpine site above the treeline in the Italian Alps, representative of the European Alps. Field observations were conducted twice per week according to the ITEX protocol.

Key Results a) The photoperiod is the most important factor controlling LS during normal years, with a sufficiently wide photoperiodic window to cope with LS during inter-annual climatic variability; neither SM nor the greening phenological stages exert an influence on LS; b) during normal years, LS has no carryover effects on the greening phenology of the following year; and c) the sensitivity of LS to climate is evident only in years characterized by extreme events (e.g., warming coupled with drought), with a large LS advance and a strong carryover effect that induces an important decrease in the first shoot length the following spring.

Conclusions High-elevation alpine forbs are aplastic species that adopt a defensive strategy for LS that can only be displaced early during the growing season (due to photoperiodic constraints) and in response to extreme events. Therefore, in a climate change context, forbs may be outcompeted by other growth forms, such as grasses, which are able to profit from the potential benefits of an extended growing season in autumn.

Key words: Leaf Senescence; Snow Melt; Growing Season Length; Sensitivity to Climate Variability; Extreme Events; Photoperiod; Plasticity; Carryover Effects; Alpine Plants.

INTRODUCTION

Throughout past decades, vegetation has been changing rapidly in response to recent climate change, particularly in high-elevation and high-latitude regions, and this response provides a robust fingerprint of the effects of climate change (Walther *et al.,* 2002; Parmesan and Yohe, 2003; Settele *et al.*, 2014). In this context, one of the strongest signals originates from recent studies of plant phenology, which have been primarily concentrated on greening and flowering phenomena (Walther *et al.,* 2002; Root *et al.,* 2003; Parmesan and Yohe, 2003; Menzel *et al.,* 2006; Cleland *et al.,* 2007), indicating an average advance of spring events (greening and flowering) in response to earlier snow melt (SM) (Peñuelas *et al.,* 2002; Defila and Clot, 2005; Menzel *et al.,* 2006; Gordo and Sanz, 2009). Conversely, the observation of autumn events has been comparatively neglected (Gallinat *et al.,* 2015), particularly for alpine plants. Among autumn events, leaf senescence (LS) is a key factor in terms of ecosystem functions and processes (Lim *et al.,* 2007) because its potential changes may play an important role in species performance, survival and growth and determine further effects on the productivity and C balance of an ecosystem (Piao *et al.,* 2008; Richardson *et al.,* 2009). During LS, nutrients are transported and remobilized from the aboveground biomass and stored for growth during the following year (Keskitalo *et al.,* 2005; Lim *et al.,* 2007; Fracheboud *et al.,* 2009); therefore, the timing of LS is a trade-off between C acquisition and N storage (Richardson *et al.,* 2010; Estiarte and Peñuelas, 2015). Most studies on LS concentrated on deciduous trees (e.g., Schuster *et al.,* 2014; Estiarte and Peñuelas, 2015; Gill *et al.,* 2015; Panchen *et al.,* 2015, Liu *et al.,* 2016) and identified the photoperiod, air temperature and drought stress as driving factors (e.g., Jolly *et al.,* 2005; Fracheboud *et al.,* 2009; Körner and Basler, 2010; Han *et al.,* 2014; Way and

Montgomery, 2014; Gill *et al.,* 2015), with their interactions producing either advances or delays in LS (Leuzinger *et al.,* 2005; Juknys *et al.,* 2012). For some tree species, an earlier onset of the growing season translated into earlier LS (Fu *et al*., 2014). Importantly, LS may exert carryover effects on the biomass and shoot production of trees during the following year, with effects on nutrient retranslocation and storage, and thus, on future growth (Killingbeck *et al.,* 1990; Niinemets and Tamm, 2005; Weih, 2009). However, to our knowledge, little information on LS is available for herbaceous plants (e.g., Rosa *et al*., 2015), particularly in alpine regions where the growing season is relatively short but could lengthen in response to climate warming, resulting in potential effects on LS and autumn phenology. Indeed, most observations on Arctic and alpine herbaceous plants focused on the first part of the growing season and/or on the flowering and reproductive stages (e.g., Keller and Körner, 2003; Molau *et al.,* 2005; Hulber *et al.,* 2010; Wipf and Rixen, 2010; Cooper *et al.,* 2011; Abeli *et al.,* 2012; Cornelius *et al.,* 2013; Petraglia *et al.,* 2014; Bjorkman *et al.,* 2015; Straka and Starmozski, 2015; Walder and Erschbamer, 2015) because the earlier SM induced by climate warming promoted an earlier onset and longer duration of the growing season (e.g., Hülber *et al.,* 2010; Wipf and Rixen, 2010; Choler, 2015; Rosa *et al.,* 2015). Recent investigations addressed the responses of alpine plants to extreme weather events but primarily focused on germination or reproductive stages (Orsenigo *et al.,* 2014, 2015; Walder and Erschbamer, 2015), whereas only a few studies also involved autumn phenology (Marchand *et al.,* 2004; Shi *et al.,* 2014; Filippa *et al.,* 2015; Rosa *et al.,* 2015; DeBoeck *et al.,* 2016).

The importance of seasonal transitions, particularly of spring and autumn (“shoulder seasons”), has been highlighted for understanding how Arctic and alpine regions will respond to climate change (Ernakovich *et al.,* 2014). Alpine and Arctic ecosystems are similar under historical climate conditions, but based on their different photoperiodic constraints, they have been hypothesized to produce divergent responses to climate change (Ernakovich *et al.,* 2014), particularly in spring and autumn, with consequences and feedbacks on community structure, biotic interactions, and biogeochemistry. Alpine plants are expected to be less capable of adapting to growing season lengthening, particularly if decreased water availability from earlier SM and warmer summers would lead to earlier senescence; by contrast, the lack of photoperiodic constraints will allow Arctic plants to advance their phenology to profit from seasonality changes (Ernakovich *et al.,* 2014). Although photoperiodic limitations have been demonstrated for the reproductive stages of alpine plants (Basler and Körner, 2012; Vitasse *et al*., 2013; Gugger *et al*., 2015), few specific data are available on their LS, and uncertainty remains on which factors drive LS (e.g., SM, temperature, precipitation and photoperiod) and on the effect of inter-annual climate variability, thereby hindering our ability to predict how the timing of LS would shift due to changes in climate (Parmesan and Hanley, 2015).

Here, we analyse the results of a long-term field observation (2007–2015) of the phenological stages, and in particular, of the LS of 9 deciduous forb species in a high alpine site above the treeline over an elevation gradient (250 m) from grasslands to snowbeds in the Italian Central Alps. We hypothesize the following: a) the photoperiod is the most important factor regulating the LS of alpine deciduous forbs, with a sufficiently large photoperiodic window to cope with LS during the inter-annual climate variability; b) alpine forbs are aplastic species following a defensive strategy because their LS responds only to climate extremes (such as the combination of warming and drought); and c) only in extreme conditions does LS exert carryover effects, with advances in LS producing negative effects and reducing the vegetative growth of the following year.

MATERIALS AND METHODS

Study area

The study area was in the Foscagno Valley (46.4°N, 10.2°E), a high-elevation site above the treeline in the Italian Central Alps, which is a region characterized by pronounced warming since 1950, with large effects on vegetation above the treeline (e.g., Cannone *et al*., 2007; Cannone and Pignatti, 2014). The Foscagno Valley includes the subalpine (2200–2400 m), alpine (2400–2800 m) and nival belts (> 2800 m), always on silicate substrate. Here, 40 plots were placed in October 2006 along a 250 m elevation transect (2358–2609 m) (Supplementary Data Fig. S1). The valley is also characterized by the patchy occurrence of mountain permafrost. The most important geomorphological features are the occurrence of the Foscagno rock glacier, which is among the most studied rock glaciers of the Italian Alps (Guglielmin *et al.,* 2001), and some Late Glacial morainic ridges. A continuous alpine grassland (*Caricetum curvulae*) occurs in the lower part of the valley (with patches of subalpine shrub vegetation of *Rhododoreto-Vaccinietum*), whereas discontinuous pioneer and snow bed vegetation are present at higher elevations and in the rock glacier area (Guglielmin *et al.,* 2001).

Phenological Field Monitoring

The phenological monitoring began in May 2007 and remains ongoing. Here, we present the data collected from May 2007 to July 2016 on 9 selected deciduous forb species (Table 1) located across 40 permanent plots (50 x 50 cm) (Supplementary Data Fig. S1). For each species, a minimum of three replicates were monitored each year, resulting in a total of 67 replicates (all species and all plots) for each year (Table 1).

The main phenological stages of each species were analysed during the entire growing season from SM to LS. The phenological observations were conducted in the field twice per week from the start of the spring SM until the beginning of permanent snow cover in autumn, according to the International Tundra Experiment (ITEX) protocol (Webber and Walker, 1991). The field monitoring was initiated by measuring the snow depth in each single plot in the spring to obtain the exact timing of complete SM, characterized by snow absence on the ground (Webber and Walker, 1991). During the entire period (2007–2016), the timing of the greening phenological stages was recorded (day of year – DOY) for first shoot appearance (first shoot) and leaf unfolding (new leaves) (Haggerty and Mazer, 2008). Since 2010, we have also performed quantitative measurements of the first shoot length and number of new leaves on the first day of observation after SM. LS was identified as the date on which at least 50% of the leaves of an individual plant had changed colour (were no longer green) (e.g., Kolářova *et al.,* 2014; Schuster *et al.,* 2014; Panchen *et al.,* 2015).

During the summer of 2008, a masting event of a defoliator lepidopter occurred in the study site *(Zygaena alpina*), which damaged the leaves of many of the analysed deciduous forb species. For this reason, the LS and growing season length (GSL) data recorded in 2008 were excluded from our analyses.

Data elaboration

Preliminary analyses on the quality of our data included the assessment of the effect of the elevation gradient both on SM and LS (tested by linear regression). The climatic representativeness of our study site at the regional scale was tested through a linear regression between the 75% quartile of SM recorded in our area (2007–2015) and those of other automatic weather stations (AWSs) from many locations widespread over the European Alps (Gressoney, Rabbi, Arabba, Val Noana, Pitztaler Gletscher) (Supplementary Data Fig. S2). To test the robustness of SM as an indicator of the very first onset of the growing season, we used a linear regression to assess its relationships with a) the first shoot and b) the new leaves. The GSL was computed as the number of days between the dates of SM and LS (GSL = LS-SM). According to Fu *et al.* (2014), we used a linear regression to assess the relationship between the spring phenological stages (SM, first shoot, new leaves) and LS during the same season. For each variable (SM, LS, GSL), we computed non-parametric statistics at an inter-specific level (Maggini *et al.,* 2011). We also computed the inter-quartile difference (i.e., 75 – 25% quartile) to provide the mid-phenophase duration (Jentsch *et al.,* 2009) or the duration of the phenophase peak. Advances or delays of each phenophase were computed by the anomaly of the 75% quartile of each year with respect to the 75% quartile of the entire monitoring period. T-tests allowed statistically significant differences to be identified between different years (VanVliet *et al.,* 2014) and extreme years. The degree of phenotypic plasticity of LS was calculated as a phenotypic plasticity index (Pi_v) (Valladares et al., 2006), computed as the difference between the maximum and minimum mean values divided by the maximum mean, which serves to standardize the index ranging from 0 (no plasticity) to 1 (maximum plasticity).

To assess the influence of climate on LS, we selected the climatic data provided by the closest AWS (http://www2.arpalombardia.it/siti/arpalombardia/meteo) located at La Foppa, which was less than 1 km from our study site and at a comparable elevation (2650 m a.s.l.) with our study area. For each year, the following climatic factors were available: a) monthly mean air temperature; air thawing degree days (TDD, cumulative sum of temperature above 0°C); air freezing degree days (FDD, cumulative sum of temperature below 0°C); monthly mean and total values of daily liquid precipitation (mm); b) for the GSL period (the period between SM and LS): air TDD, air FDD, mean air temperature, mean and total rain, and total incoming radiation were available. The TDD and FDD provide the cumulative effects of air temperature and its consequences on biota (Molau and Mølgaard, 1996; Klene *et al.,* 2001; Cannone *et al.,* 2006; Cannone and Guglielmin, 2009). We also considered the following factors: the photoperiod (number of hours of light per day) at the LS date and SM. Preliminary analyses (through linear regression) allowed us to avoid redundancy in selecting the climatic variables (Supplementary Data Table S1). Based on these results, we performed generalized linear/nonlinear models (GLZ) and selected the model with the best fit based on Akaike's information criterion (AIC). GLZ was performed to a) identify the factors driving LS at an inter-annual level during "normal years" (period 2009–2014); b) assess which factors between the spring climate and the LS of the previous year (LS^{-1Y}) influenced the greening stages (date of the first shoot, date of new leaves, length of the first shoot, number of new leaves) to identify potential carryover effects of LS^{-1Y} on growth the following year; and c) identify the factors driving LS at an intra-annual level, including the extreme years. Because the quantitative measurements of the greening phenophases started in 2010, when performing these analyses for the "normal years", we selected the period of 2009–2014 for LS^{-1y} and 2010-2015 for the greening phases. All computations were performed using the software program Statistica®.

RESULTS

Snow melt, Leaf Senescence and Growing Season Length

Preliminary analyses allowed us to determine (as tested by linear regression) that the elevation gradient exerted an almost negligible effect on both SM ($p < 0.01$, $R^2 = 0.19$) and LS ($p < 0.01$, $R^2 = 0.15$); although these relationships were statistically significant, the explained variance was very low. We then tested the quality of our SM data and assessed whether they were representative of the European Alps (Supplementary Data Table S2, Fig. S2). We also assessed whether SM was a robust indicator of the very first onset of the growing season, based on the strong and statistically significant relationship between SM and first shoot development ($R^2 = 0.98$, $p < 0.01$, $\beta = +1$) and between SM and leaf unfolding ($R^2 = 0.9$, $p < 0.01$, $\beta = +0.89$) (as tested by linear regression at inter-specific and inter-annual levels). According to Fu *et al.* (2014), we also used a linear regression to assess the relationship between the spring phenological stages (SM, first shoot and new leaves) and LS of the same year (e.g., SM2009, first shoot 2009, new leaves 2009, LS2009) both at the inter-annual level (for the entire period of 2009–2014) and for each single year. In contrast to deciduous trees, although statistically significant at the inter-annual level, we did not detect any important relationship with LS because of the very low explained variance (SM vs LS: $p < 0.01$, $R^2 = 0.15$; first shoot vs LS: $p < 0.01$, $R^2 = 0.14$; new leaves vs LS: $p < 0.01$, $R^2 = 0.12$). Similar results were also obtained by analysing each year separately: indeed, even when statistically significant, the relationships were always very poor (data not shown).

SM exhibited a large inter-annual variability (Fig. 1a, b; Supplementary Data Table S3), but only 2007 could be considered an extreme year (confirmed by t-test, $p < 0.01$) characterized by an extreme SM advance, which was identified for all the Alps (data not shown). In addition, LS exhibited large inter-annual variability (Fig. 1c, d; Supplementary Data Table S3), with the largest advance occurring in 2015, which was identified as an extreme year ($p < 0.01$, t-test). As expected, the GSL was also characterized by large inter-annual variability (Fig. 1e, f, Supplementary Data Table S3), with both 2007 and 2015 being extreme years ($p < 0.01$, t-test). Notably, the extreme year of 2007, characterized by advanced SM, lengthened the GSL by only 4 days beyond its upper range limits, whereas the extreme year 2015, characterized by an advanced LS, produced a more than three-fold effect on GSL, shortening it by 13 days less than the lower range.

LS relationship with phenological and climatic factors: normal years

LS relationships with biotic and abiotic factors were first tested by during the “normal years” (2009–2014). Preliminary analyses allowed redundancy to be avoided and appropriate climatic variables to be selected (Supplementary Data Table S1) to perform a GLZ, for which we selected the model with the best fit based on the AIC (Table 2). The photoperiod was the most important factor affecting LS in a statistically significant way ($p < 0.01$), whereas the other factors exerted only a very limited influence (Table 3). According to these results, we quantified the range of natural variability of the photoperiod associated with LS to be between 14.5 and 11.2 h; indeed, the onset of LS occurred between 14.5 and 13.9 h of light, and LS completion was achieved between 12.3 and 11.2 h of light.

A GLZ was performed to assess whether the LS exerted carryover effects on plant growth during the following year. Specifically, the GLZ assessed whether the LS of the previous year (LS^{-1Y}) could be a more effective factor than climate in driving the greening phenological stages (DOY of first shoot and of new leaves, length of the first shoot, number of new leaves) at the beginning of the growing season during the following year. For this aim, the best GLZ model was selected based on the AIC (Table 4 and Supplementary Data Table S4). According to our analyses, LS^{-1Y} did not exert any significant effects on the greening stages of the following year, whereas SM was the most important factor, with the exception of the number of new leaves, for which the most important factor was the TDD in June, followed by SM (Table 4).

LS relationship with other phenological and climatic factors: extreme years

To explain the large advance in LS observed during the extreme year of 2015 and to identify its driving factors, a GLZ was performed for each year, with the best model selection based on the AIC (Table 5). In all years, the photoperiod was the prevailing factor affecting LS except for 2015, when the influence of the photoperiod drastically decreased and was comparable to the $TDD_{SM\text{-}LS}$ (Table 5, Supplementary Data Table S5). The 2015 growing season was characterized by the hottest and driest July (the hottest of the last twenty years) (Supplementary Data Fig. S3), which could have triggered a significant advance of LS; remarkably, 2015 was characterized only by an anomalous LS onset occurring well outside the photoperiodic range (15.3 vs 14.5 h), whereas LS completion was fully within the range of natural variability during normal years (11.8 h). Furthermore, the large advance in LS recorded in 2015 corresponded to an important decrease of the first shoot length measured in 2016, analysing both their maximum (Fig. 2a) and mean values (Fig. 2b): in spring 2016, the first shoot length exhibited the smallest size over the entire study period, with a mean length of 7.7 mm against the mean length of 13.3 mm for the period of 2010–2016.

DISCUSSION

Our results contributed to the knowledge gap of the LS of alpine plants. They provide quantitative data on the range of variation in the LS of deciduous forbs in response to inter-annual climate variability, which climatic and environmental factors drive LS, and the potential carryover effects of LS on the vegetative growth of the following year.

LS relationship with SM and implications for GSL

Earlier onset of the greening vegetative stages may influence the LS of trees (e.g., Fu *et al.*, 2014), but few data are available for herbaceous plants. Indeed, particularly in the Arctic, it is still discussed whether plant growth may begin earlier but not necessarily last longer (Rosa *et al.*, 2015). Considering the importance of SM in regulating the greening vegetative stages in alpine and Arctic regions, we first focused on our SM data, and prior to testing their relationship with LS, we assessed their representativeness and exportability within the alpine context. According to our results, we confirmed the importance of SM in providing the onset of the growing season and its large inter-annual variability, which is consistent with previous observations in other alpine areas (e.g., Beniston, 2012). Manipulative experiments (e.g., snow additions and/or removals) were performed to disentangle whether an earlier onset of the growing season would imply consequences on LS but resulted in contrasting responses: in some cases, SM advances induced earlier LS (and no changes of GSL) (e.g., Rosa *et al.,* 2015), while in other cases, SM delays induced an accelerated development across the growing season (and a shortened GSL) (e.g., Cooper *et al.,* 2011). Our data provided evidence that SM did not exert any influence on LS, and therefore, an earlier SM did not imply an earlier LS. This fact was obvious during “normal years” (Fig. 1a–d, Supplementary Data Table S3) and became even more evident when considering extreme years. The advanced SM in 2007, the earliest of the last two decades (1996–

2015), triggered the earliest onset of the growing season but not the earliest LS. Indeed, in 2007, despite the large SM advance, LS slightly delayed both its onset and completion, and in this extreme year, the GSL was lengthened by only 4 days more than that in its upper range (Fig. 1e, f; Supplementary Data Table S3). Conversely, the advanced LS in 2015 was not triggered by an earlier SM and produced a larger effect on GSL, shortening it by 13 days less than its lower range of variation.

According to Schuster *et al.* (2014), senescence phases could have been underestimated in terms of their influence on the lengthening of the growing season. Our data allowed us to assess whether LS exhibits an inter-annual variability, corresponding to a relatively wide photoperiodic range and allowing coping with the inter-annual climate variability during normal years. However, given the length of our monitoring period, we preferred to focus our analyses on the relationships of LS with the main environmental and climatic factors instead of its trends with time.

Driving factors of LS and its sensitivity to climate extremes

Our analyses provided evidence that the photoperiod is the most important factor affecting the LS of high-elevation alpine forbs. The smaller inter-annual variability, shorter duration and peak of LS compared to SM (Supplementary Data Table 3S) confirm the hypothesis that for Arctic and alpine environments, the timing of senescence is more conservative than the onset of growth (Shaver and Billings, 1977; Körner, 2003; Körner *et al.,* 2003**)**. Our data indicate that during normal years, alpine forbs do not respond primarily to climate in developing their LS but instead to the photoperiod, in agreement with previous observations that plants of regions characterized by severe winters exhibit a strong photoperiodic regulation of LS (e.g., Estiarte and Peñuelas, 2015; Rosa *et al.,* 2015). Moreover, our results provide support for the hypothesis of potentially divergent responses to climate change between alpine and Arctic ecosystems (Ernakovich *et al.,* 2014) because of their different photoperiodic constraints, particularly in spring and autumn. The need to account for photoperiod constraints has also been emphasized by Keller and Körner (2003) to evaluate climate change effects on alpine plants because warming could be too rapid to track the change in the photoperiod by evolutionary adjustment in many alpine and Arctic species. In this frame, the knowledge of the natural variability of LS with respect to the photoperiod in the climate background is indispensable. According to our data, during normal years, the range of natural variability of LS corresponds to a relatively wide photoperiod window (11.2–14.5 h of light), allowing LS to cope with inter-annual climatic variation.

However, to assess LS sensitivity to climate and predict its potential responses to climate change, it is important to identify which environmental cues can induce deviations from its normal behaviour and the size of that deviation because this provides information on how strongly the species are tied to the photoperiod. Anomalous years characterized by extreme climatic events have been shown to have large effects on other phenological events (i.e., flowering), and these effects can be greater than the background variability to climate warming (Jentsch *et al.,* 2009). Therefore, the climate sensitivity of the LS of alpine forbs could be tested by examining the years characterized by extreme climatic events. LS is a process that begins at the end of leaf growth (Estiarte and Peñuelas, 2015), a phenophase that occurs at the beginning of July in our case. Senescence implies a radical change in foliar metabolism that shifts from assimilation to the remobilization of resources and the transition from anabolism to catabolism, and these processes require several weeks before the external signals of LS are visible (Estiarte and Peñuelas, 2015). The GLZ performed at an intra-annual level (Table 5) demonstrated that unlike normal years, both the photoperiod and the $\mathrm{TDD}_{\mathrm{SM\text{-}LS}}$ in the extreme year of 2015 controlled LS: therefore, the large advance in LS observed in 2015 could be the result of the extreme climatic conditions in July 2015, characterized by the highest air temperature of the last 20 years coupled with the lowest liquid precipitation. Our data also agree with the results of a recent manipulation experiment performed on an alpine grassland (De Boeck *et al.,* 2016) showing that the combination of warming and drought advanced LS, with more pronounced impacts detected on forbs than on graminoids (DeBoeck *et al.,* 2011, 2016). The large LS advance observed in 2015 in response to the combination of warming and drought could support the hypothesis by Ernakovich *et al.* (2014) that in the future, decreased water availability (in our case due to low precipitation; in Ernakovich *et al*. (2014) hypothesized in relation to earlier SM) and warmer summer temperatures would lead to earlier senescence of alpine plants, making them more vulnerable to climate change than Arctic plants. The observed behaviour of alpine forbs in response to extreme events resembles that of some winter deciduous tree species for which the photoperiod and temperature were recognized to be the main cues controlling LS, with water stress imposing an additional influence (Estiarte and Peñuelas, 2015).

Given their dependency on the photoperiod, high-elevation alpine forbs should be considered "periodic" (or species that have a genetically fixed growth strategy) or "aplastic" species because they are unable to adapt their growth strategy to changing climatic conditions and are potentially out-competed by species with plastic growth strategies (Sørensen, 1941; Rosa *et al.,* 2015). We quantified the plasticity of LS of alpine forbs in response to the natural inter-annual climate variability by computing the index of phenotypic plasticity (Pi_v) according to Valladares *et al.* (2006). We obtained a low Pi_v value (0.16), indicating a low plasticity of LS, similar to the value obtained by Gugger *et al*. (2015) when comparing the reproductive phenology of high-elevation

($Pi_v = 0.15$) vs mid-elevation ($Pi_v = 0.19$) plants in response to climate manipulations. Although Gugger *et al*. (2015) selected a species pool, including different growth forms in addition to forbs, focused on the reproductive stages (and not on LS), and tested the plasticity of plants in response to experimental warming and drought (and not to natural inter-annual climate variability), we found important similarities between our work and their study. Gugger *et al*. (2015) concluded that given the photoperiod constraints on their reproductive stages, alpine species adopt a conservative strategy, allowing them to profit from growing season lengthening only at the beginning of the growing season and with drought stress inducing advances in the frame of this "escape" strategy. In addition, in our case, we observed that alpine forbs adopted a defensive strategy for LS, involving plasticity only in response to extreme climatic conditions, and that can only be displaced early during the growing season, as shown by the large LS advance in 2015.

Relationship between LS and greening phenological stages

For some winter deciduous trees, autumn phenology was demonstrated to exert feedback on the biomass production and plant growth of the next year (e.g., Weih, 2009). However, few studies have followed the carryover effects of autumnal conditions on the following spring across multiple years, and this knowledge gap has been recently recognized to be a research priority (Gallinat *et al.,* 2015). Our results indicate that for high-elevation alpine forbs during normal years, there was no carryover effect of LS of the previous year (LS^{-1Y}) on the spring greening phenophases of the following year (first shoot, new leaves) or on the quantitative growth of the first shoot. Therefore, no carryover effects mirroring the LS conditions of the previous year were detected for high-elevation alpine forbs. However, the exceptional advance in LS detected in the extreme year of 2015 resulted in a strong decrease in the size of the first shoot during the spring of 2016, implying that the large LS advance partially prevented proper nutrient storage and bud preformation at the end of the growing season in 2015. Indeed, late-falling leaves have likely senesced slowly and have had more time to achieve the most complete resorption from all foliage (Estiarte and Peñuelas, 2015), whereas the opposite is likely to occur in early senescing leaves. Moreover, our data agree with the observation that the premature LS caused by water stress is associated with a reduction in nutrient resorption (Killingbeck, 2004).

In conclusion, according to the results of this study, high-elevation alpine forbs are mainly aplastic species, and their LS is controlled by the photoperiod, with a window wide enough to cope with the inter-annual climate variability during normal years. The sensitivity of LS to climate becomes evident only in extreme years, when alpine forbs show relatively low plasticity, adopting a defensive strategy that can be displaced only early during the growing season (due to photoperiodic constraints), with large LS advances only in response to extreme climatic events (e.g., combination of warming and drought). This defensive strategy also involves the capability of LS to affect growth the following year: indeed, only in response to extreme (adverse) climatic conditions does LS exert carryover effects, with LS advances producing negative effects on the vegetative growth of the following year. The consequences of this behaviour may imply that in a climate change context, forbs could be out-competed by other growth forms, such as grasses, which may be able to profit from the potential benefits of an extended growing season in autumn.

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Figure Captions

FIG. 1. Nonparametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snow melt (a, b), leaf senescence (c, d) and growing season length (e, f) from 2007 to 2015 (except 2008 for leaf senescence and growing season length; see methods). The mean value for the entire period of each parameter is represented by the dotted black line.

FIG. 2. Relationship between LS of the previous year and a) maximum first shoot length and b) mean first shoot length recorded during the following years since 2010 (e.g., LS2009 vs FS2010, LS2010 vs FS2011, etc.).

TABLE 1: *List of the winter deciduous alpine forb species selected for phenological monitoring (2007–2015), the number of replicates (n), and their distribution according to elevation (m a.s.l.).*

Species	**n**	**Elevation min**	**Elevation max**
Cardamine resedifolia	4	2429	2516
Cerastium uniflorum	9	2494	2576
Doronicum clusii	3	2505	2516
Geum reptans	14	2486	2537
Leucanthemopsis alpina	15	2493	2609
Oxyria digyna	7	2486	2598
Ranunculus glacialis	3	2518	2597
Senecio carniolicus	9	2384	2516
Veronica alpina	3	2357	2516
All Species	67	2357	2609

***Table 2**. ΔAIC values of linear/nonlinear models for the selection of the best model concerning LS (dependent variable). ΔAIC is calculated as $(AIC)_{best\ model} - (AIC)_{other\ models}$. Legend: LS-SM: factor computed for the period between SM and LS but not for specific months; LS-Photo = the photoperiod (hours of light per day) at LS.*

Environmental Factors	**ΔAIC**
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + RainJuly + RainAug + RainSept + Elev	0.000
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + RainJuly + RainAug + RainSept	-0.718
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + RainJuly + RainAug + RainSept + FDD$_{SM\text{-}LS}$ + Elev	-1.594
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + RainJune + RainJuly + RainAug + RainSept + Elev	-1.730
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + AirTempJuly + RainJuly + RainAug + RainSept + Elev	-1.796
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + AirTempAug + RainJuly + RainAug + RainSept + Elev	-1.999
SM + LS-Photo + TDDSM-LS + MeanRainJuly + MeanRainAug + RainSept + FDD$_{SM\text{-}LS}$	-2.070
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + AirTempAug + RainJuly + RainAug + RainSept	-2.696
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + AirTempJuly + RainJuly + RainAug + RainSept	-2.706
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + RainJune + RainJuly + RainAug + RainSept	-2.713
SM + LS-Photo + TDD$_{SM\text{-}LS}$ + FDD$_{SM\text{-}LS}$ + AirTemp$_{SM\text{-}LS}$ + Rain$_{SM\text{-}LS}$ + Year +	-45.899

AirTempJune + AirTempJuly + AirTempSept	
SM + LS-Photo + TDD$_{\text{SM-LS}}$ + FDD$_{\text{SM-LS}}$ + AirTemp$_{\text{SM-LS}}$ + Rain$_{\text{SM-LS}}$ + Year	-167.907
SM + LS-Photo +TDDJune + TDDJuly + TDDAug + TDDSept + RainJune + RainJuly + RainAug + RainSept + Elevation	-412.83

***Table 3**. Effect of the main climate factors on LS (dependent variable) during the "normal years" (2009–2014), using the factors selected by the best model (ΔAIC = 0; see Table 2) and tested by GLZ. Legend: LS-SM: factor computed for the period between SM and LS but not for specific months; *** = $p < 0.01$.*

	Wald Stat.	**p**
Elevation (m)	2.7	0.098
SM	479.3	***
LS-Phoot	16675.8	***
$TDD_{LS\text{-}SM}$	618.1	***
RainJuly	437.8	***
RainAug	660.6	***
RainSept	290.8	***
	ΔAIC	**p**
Full Model	0.0	***

TABLE 4. *Influence of the previous year's LS (*LS^{-1Y}*) and of the main climate factors on the greening phenological stages (first shoot, new leaves, first shoot length, number of new leaves) of the following year, using the factors selected by the best model (*$\Delta AIC = 0$*; see Supplementary Data Table S4) as tested by GLZ in the period 2010–2014 (normal years). Legend: *** =* $p < 0.001$.

FIRST SHOOT	**Wald Stat**	**p**	**NEW LEAVES**	**Wald Stat**	**p**
Year	33.42	***	Year	17.22	***
LS^{-1Y}			LS^{-1Y}	2.44	0.12
SM	26224	***	SM	10783	***
TDDMay	38.48	***	TDDMay	35.76	***
RainMay	69.20	***	RainMay	18.38	***
TDDJune	53.07	***	TDDJune	0.76	0.38
RainJune	19.52	***	RainJune	25.66	***
Full Model	**ΔAIC**	**p**	**Full Model**	**ΔAIC**	**p**
First Shoot	0	***	**New Leaves**	0	***
FIRST SHOOT LENGTH	**Wald Stat**	**p**	**NUMBER NEW LEAVES**	**Wald Stat**	**p**
Year			Year	3.15	0.07
LS^{-1Y}			LS^{-1Y}	2.84	0.09
SM	10.92	***	SM	11.21	***
TDDMay	2.76	0.096	TDDMay	2.25	0.13

RainMay			RainMay	4.04	0.04
TDDJune	4.96	0.025	TDDJune	29.1	***
RainJune	0.46	0.49	RainJune		
Full Model	**ΔAIC**	**p**	**Full Model**	**ΔAIC**	**p**
First Shoot Length	0	***	**Number New Leaves**	0	***

TABLE 5*. Effect of the main climate factors on LS computed separately for each year using the factors selected by the best model ($\Delta AIC = 0$; see Supplementary Data Table S5) as tested by GLZ. Legend: LS-SM: factor computed for the period between SM and LS but not for specific months; *** = $p < 0.001$.*

	2007		**2009**		**2010**		**2011**		**2012**		**2013**		**2014**		**2015**	
	Wald Stat.	**p**	**Wald Stat.**	**p**	**Wald Stat.**	**p**	**Wald Stat.**	**p**	**Wald Stat.**	**p**	**Wald Stat.**	**p**	**Wald Stat.**	**p**	**Wald Stat.**	**p**
Elevation	5.05	0.02									4.8	0.03			2.8	0.09
SM	25.4	***	23.2	***	2.8	0.09	3.4	***	10.8	***	73.4	***	6.1	0.01	23.4	***
LS-Photo	13022	***	5953	***	5432	***	2009	***	1152	***	1269.2	***	739.6	***	86.1	***
TDD$_{SM-LS}$	10.5	***	166	***	7.75	***	25.4	***	13.8	***	58.5	***			52	***
FDD$_{SM-LS}$	12.29	***			37.9	***	19.3	***	4.5	0.03	15.7	***				
Rain$_{SM-LS}$	110	***	8.2	***	23.5	***					84.6	***	154.2	***	7.6	***
	Delta AIC	**p**	**Delta AIC**	**p**	**Delta AIC**	**p**	**Delta AIC**	**p**	**Delta AIC**	**p**	**Delta AIC**	**p**	**Delta AIC**	**p**	**Delta AIC**	**p**
Full model	0	***	0	***	0	***	0	***	0	***	0	***	0	***	0	***

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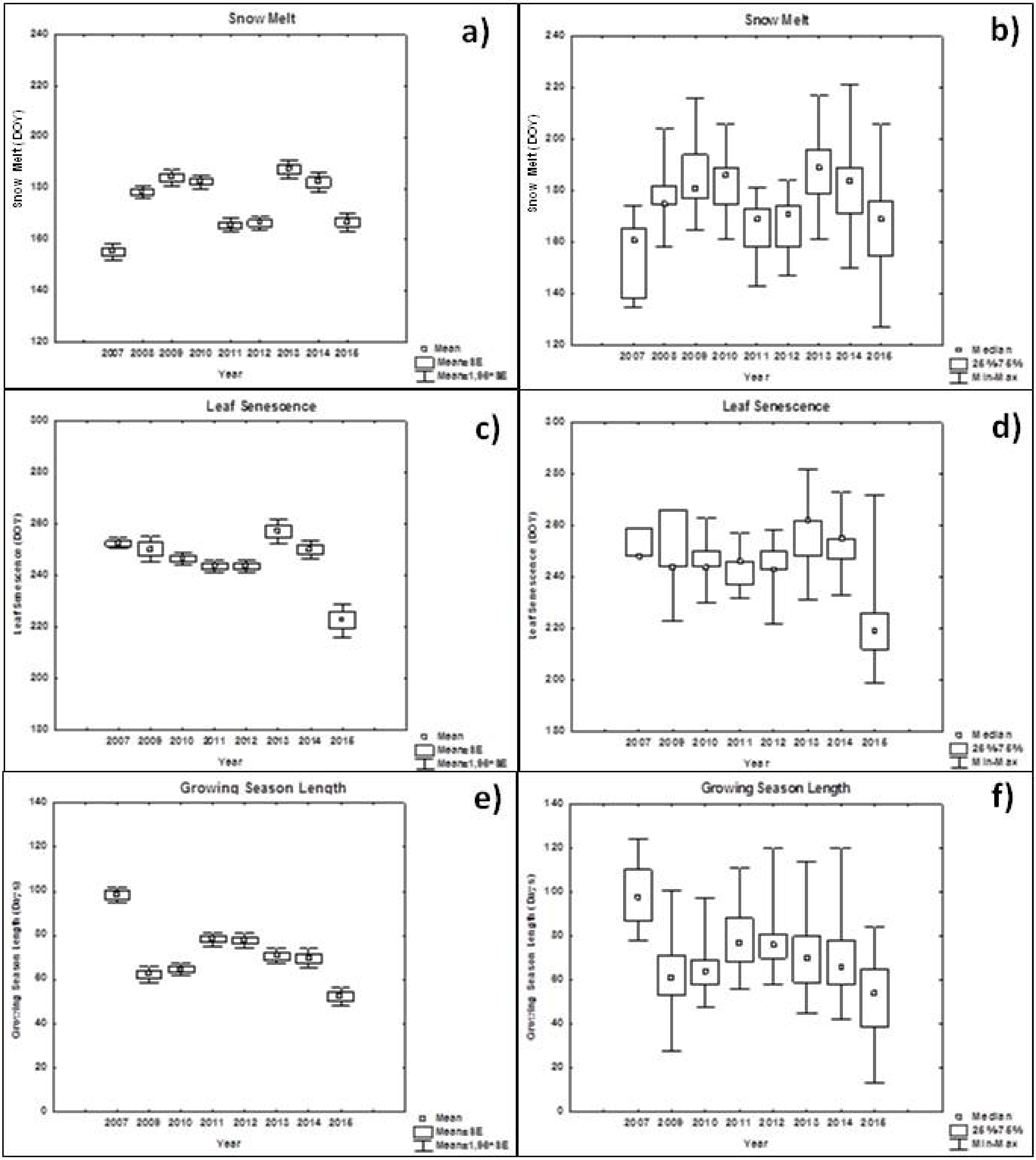
a)
Snow Melt
240
220
200
180
160
140
120
Snow Melt (DOY)
2007
2008
2009
2010
2011
2012
2013
2014
2016
Year
Mean
Mean±SE
Mean±1,96*SE
b)
Snow Melt
240
220
200
180
160
140
120
Snow Melt (DOY)
2007
2008
2009
2010
2011
2012
2013
2014
2016
Year
Median
25%-75%
Min-Max
c)
Leaf Senescence
300
280
260
240
220
200
180
Leaf Senescence (DOY)
2007
2009
2010
2011
2012
2013
2014
2016
Year
Mean
Mean±SE
Mean±1,96*SE
d)
Leaf Senescence
300
280
260
240
220
200
180
Leaf Senescence (DOY)
2007
2009
2010
2011
2012
2013
2014
2016
Year
Median
25%-75%
Min-Max
e)
Growing Season Length
140
120
100
80
60
40
20
0
Growing Season Length (Days)
2007
2009
2010
2011
2012
2013
2014
2016
Year
Mean
Mean±SE
Mean±1,96*SE
f)
Growing Season Length
140
120
100
80
60
40
20
0
Growing Season Length (Days)
2007
2009
2010
2011
2012
2013
2014
2016
Year
Median
25%-75%
Min-Max

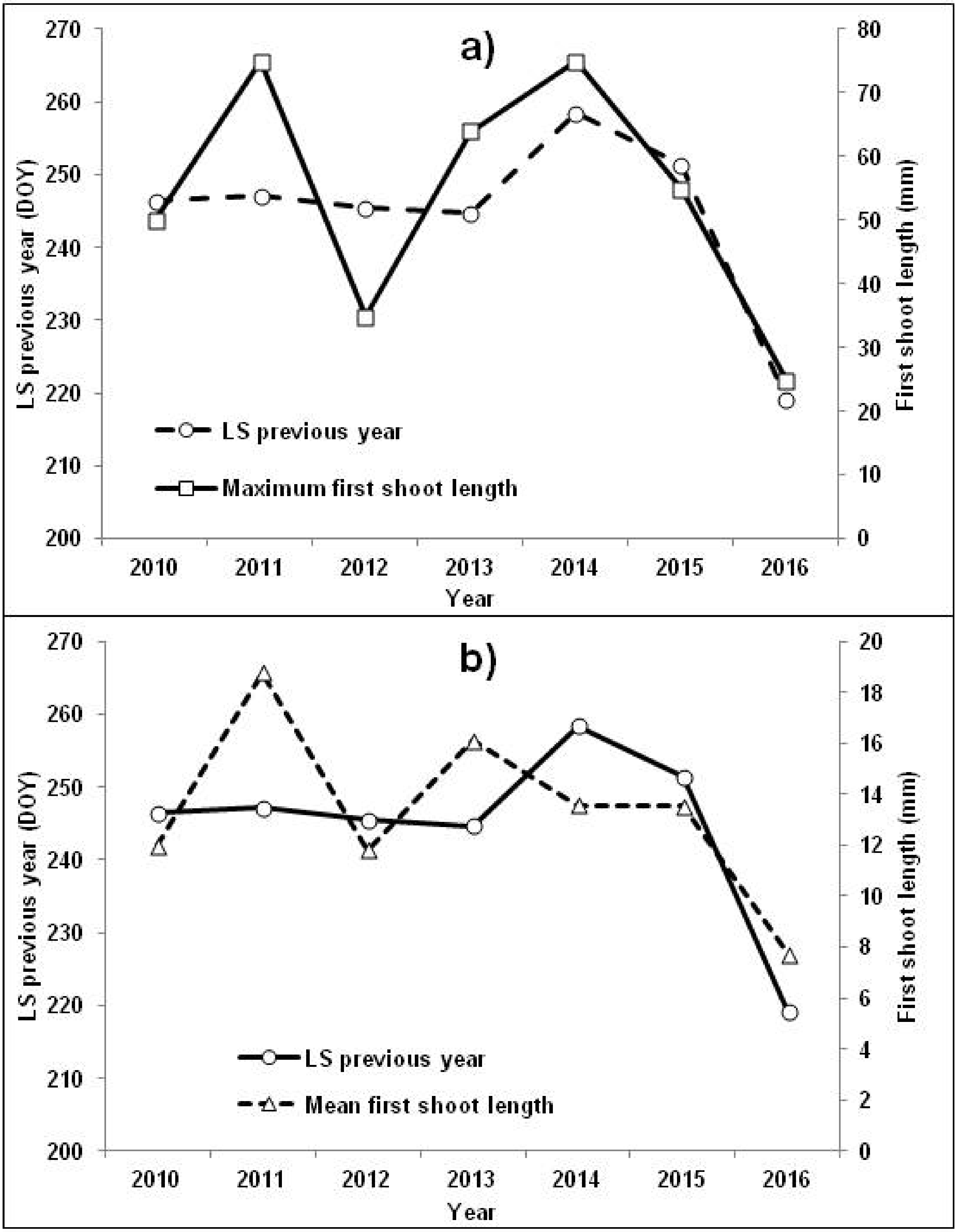
a)
LS previous year (DOY)
First shoot length (mm)
270
260
250
240
230
220
210
200
80
70
60
50
40
30
20
10
0
2010
2011
2012
2013
2014
2015
2016
Year
LS previous year
Maximum first shoot length
b)
LS previous year (DOY)
First shoot length (mm)
270
260
250
240
230
220
210
200
20
18
16
14
12
10
8
6
4
2
0
2010
2011
2012
2013
2014
2015
2016
Year
LS previous year
Mean first shoot length

Figure S1. Location of the phenological monitoring plots in the study area of the Foscagno valley (aerial photograph 2012 AGEA).

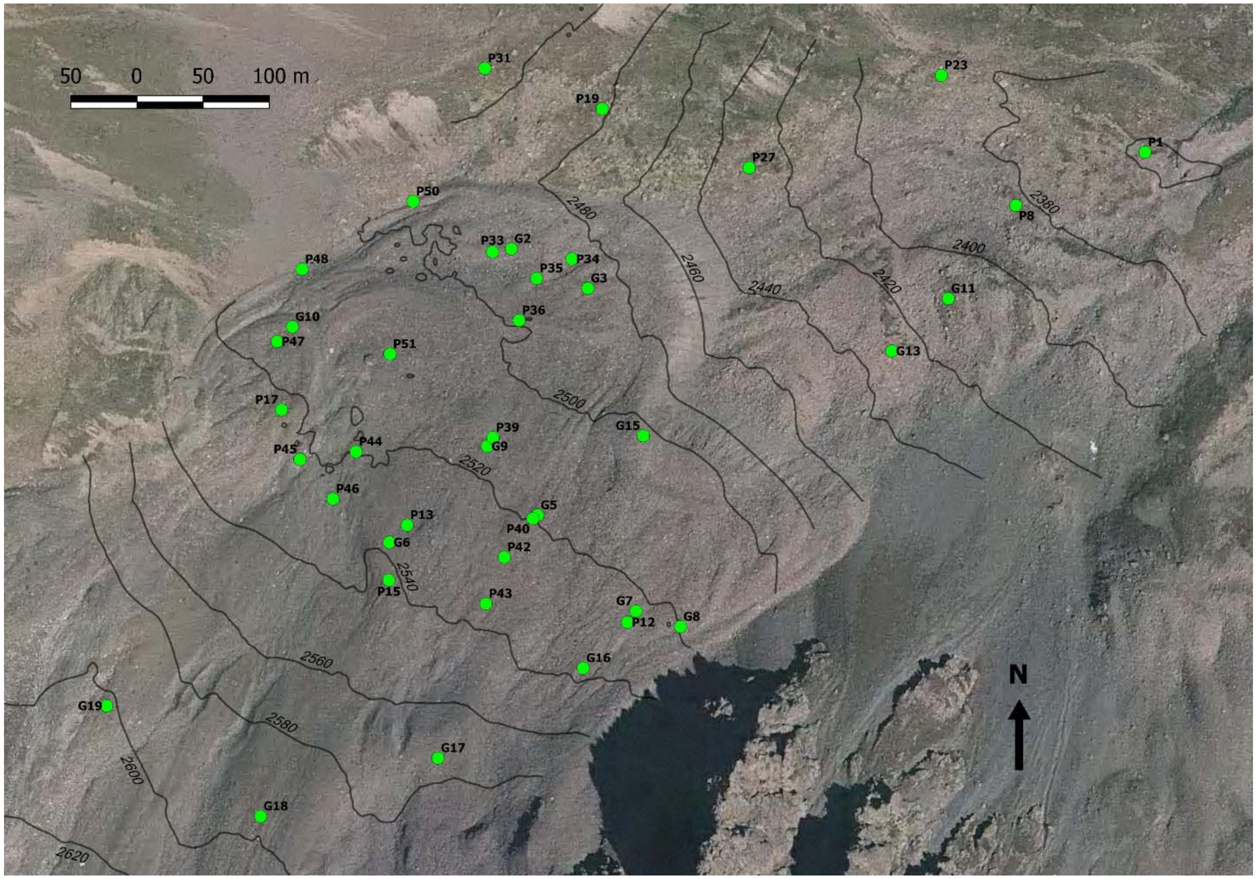

Figure S2. Location of the Automatic Weather Stations (AWS, red dots) used to assess the representativeness of the snow melt data from our study site (yellow star, Foscagno valley).

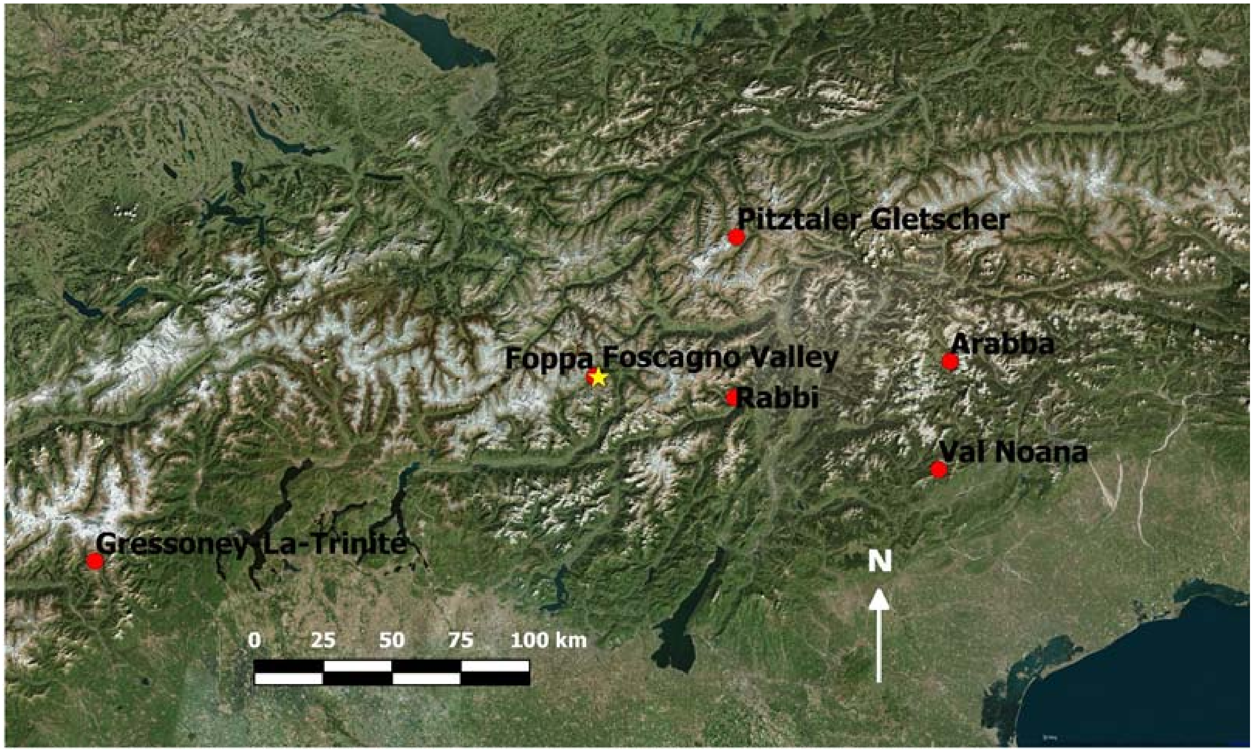

Figure S3. Air temperature of July (mean ± standard error) in the period 2007-2015. The mean value for the whole period of each parameter is represented by the dotted black line.

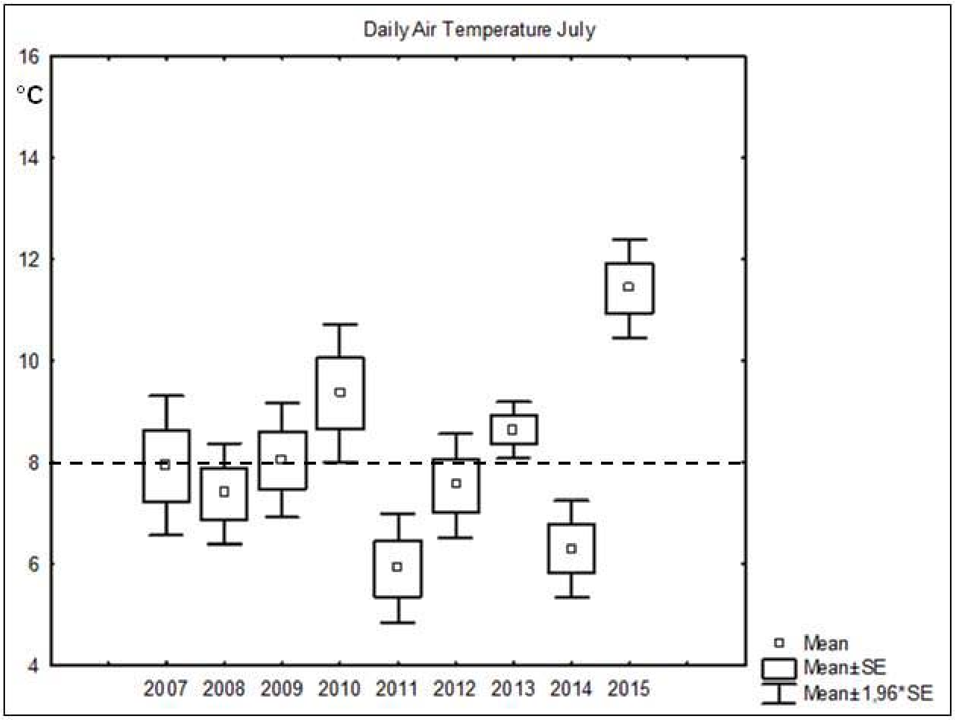

Table S1. Assessment of eventual redundancy, as tested by linear regression, among the main environmental, phenological and climatic variables.

Variable 1	**Variable 2**	**R^2**	**p**
Elevation	SM	0.19	< 0.001
Elevation	LS	0.0004	0.66
Elevation	First Shoot	0.17	< 0.001
Elevation	New Leaves	0.18	< 0.001
SM	LS	0.15	< 0.001
TDD_{SM-LS}	RadSM-LS	0.8	< 0.001
$Rain_{SM-LS}$	RadSM-LS	0.48	< 0.001
TDD_{SM-LS}	TDDJune	0.077	< 0.001
TDD_{SM-LS}	TDDJuy	0.024	< 0.001
TDD_{SM-LS}	TDDAug	0.25	< 0.001
TDD_{SM-LS}	TDDSept	0.24	< 0.001
TDD_{SM-LS}	AirJune	0.07	< 0.001
TDD_{SM-LS}	AirJuly	0.0009	0.52
TDD_{SM-LS}	AirAug	0.067	< 0.001
TDD_{SM-LS}	AirSept	0.09	< 0.001
$Rain_{SM-LS}$	RainJune	0.3	< 0.001
$Rain_{SM-LS}$	RainJuly	0.32	< 0.001
$Rain_{SM-LS}$	RainAug	0.01	0.033
$Rain_{SM-LS}$	RainSept	0.11	< 0.001

Table S2. Elevation of the AWS outside from different locations of the European Alps used for the snow melt comparison with our study area (75% quartile) and their statistical significance as tested by linear regression with La Foppa AWS (2650 m a.s.l.).

AWS	**Elevation (m a.s.l.)**	**R^2**	**p**
Gressoney-La Trinité	2379	0.85	< 0.01
Rabbi	1335	0.80	0.02
Arabba	2265	0.90	< 0.01
Val Noana	1020	0.83	< 0.01
Pitztaler	2850	0.97	0.02

Table S3. Non parametric statistics of snow melt (SM), leaf senescence (LS) and growing season length (GSL) computed for each single year, as well as for the entire monitoring period (2007-2015), and for the restricted period 2009-2014 as representative of "normal years" (excluding extreme years for SM and LS, see methods). Legend: DOY Day Of Year; NC = not considered (see methods).

	Snow Melt (DOY)							
	Mean	**Minimum**	**25% quartile**	**Median**	**75% quartile**	**Maximum**	**St. Dev.**	**n**
2007	155	135	138	161	166	174	12.78	64
2008	179	158	175	175	182	204	9.70	63
2009	184	165	177	181	194	216	12.56	65
2010	183	161	175	186	189	206	10.91	67
2011	166	143	158	169	173	181	10.84	67
2012	166	147	158	171	174	184	10.93	67
2013	188	161	179	189	196	217	14.46	67
2014	182	150	171	184	189	221	15.44	67
2015	167	127	155	169	176	206	14.89	67

2007-2015	174	127	165	175	185	221	16.36	594
2009-2014	178	143	169	177	189	221	15.2	383

Leaf Senescence (DOY)

	Mean	**Minimum**	**25% quartile**	**Median**	**75% quartile**	**Maximum**	**St. Dev.**	**N**
2007	253	248	248	248	259	259	5.54	63
2008	NC	NC	NC	NC	NC	NC	NC	NC
2009	247	223	244	244	254	266	11.73	64
2010	247	230	244	244	250	263	7.09	67
2011	245	232	237	246	246	263	8.09	61
2012	245	222	243	243	250	270	8.60	65
2013	258	224	248	262	262	282	11.69	63
2014	251	233	247	255	255	281	11.20	63
2015	219	199	212	216	226	272	15.54	63
2007-2015	245	199	241	247	255	282	15.00	509
2009-2014	249	222	244	246	255	282	10.9	383

Growing Season Length (Days)

	Mean	**Minimum**	**25% quartile**	**Median**	**75% quartile**	**Maximum**	**St. Dev.**	**N**
2007	98	78	87	98	110	124	14.21	63
2008	NC	NC	NC	NC	NC	NC	NC	NC
2009	62	28	53	61	71	101	14.56	64
2010	65	48	58	64	69	97	10.72	67
2011	78	56	68	77	88	111	12.16	61
2012	78	58	70	76	81	120	13.38	65
2013	71	45	59	70	80	114	14.27	63
2014	70	42	58	66	78	120	17.24	63
2015	52	13	39	54	65	84	15.81	63
2007-2015	71	13	59	70	83	124	18.96	516
2009-2014	71	36	60	69	79	120	14.9	383

Table S4. ΔAIC values of linear/non linear models for the selection of the best model concerning the greening phenological stages of the following year (first shoot; new leaves; first shoot length; number of new leaves, as dependent variables). ΔAIC is calculated as : $(\text{AIC})_{\text{best model}} – (\text{AIC})_{\text{other models}}$. Legend: LS-SM: factor computed for the period between SM and LS and not for specific months; LS-Photo = photoperiod (hours of light per day) at LS.

Dep Var	**Factors**	**Delta AIC**
First Shoot	Year + SM + TDDMay + RainMay + TDDJune + RainJune	0
First Shoot	Year + $\text{LS}^{-1\text{Y}}$ + SM + TDDMay + RainMay + TDDJune + RainJune	-1,704
First Shoot	Year + SM + TDDMay + RainMay + TDDJune	-17,578
First Shoot	Year + LS-1Y + SM + TDDMay + RainMay + TDDJune	-18,755
First Shoot	SM + TDDMay + RainMay + TDDJune	-28,331
First Shoot	SM + TDDMay + RainMay + TDDJune + RainJune	-29,803
First Shoot	$\text{LS}^{-1\text{Y}}$ + SM + TDDMay + RainMay + TDDJune	-30,331
First Shoot	$\text{LS}^{-1\text{Y}}$ + SM + TDDMay + RainMay + TDDJune + RainJune	-31,701
First Shoot	Year + SM + RainMay + TDDJune	-33,948

First Shoot	Year + LS^{-1Y} + SM + RainMay + TDDJune	-34,800

Dep Var	**Factors**	**Delta AIC**
New Leaves	Year + LS^{-1Y} + SM + TDDMay + RainMay + RainJune	0
New Leaves	Year + SM + TDDMay + RainMay + RainJune	-0,077
New Leaves	Year + LS^{-1Y} + SM + TDDMay + RainMay + TDDJune + RainJune	-1,243
New Leaves	Year + SM + TDDMay + RainMay + TDDJune + RainJune	-1,670
New Leaves	Year + SM + TDDMay + TDDJune + RainJune	-15,169
New Leaves	LS^{-1Y} + SM + TDDMay + RainMay + RainJune	-15,565
New Leaves	SM + TDDMay + RainMay + TDDJune + RainJune	-15,976
New Leaves	LS^{-1Y} + SM + TDDMay + RainMay + TDDJune + RainJune	-16,067
New Leaves	SM + TDDMay + RainMay + RainJune	-16,083
New Leaves	Year + LS^{-1Y} + SM + TDDMay + TDDJune + RainJune	-17,167

Dep Var	**Factors**	**Delta AIC**
First Shoot Length	SM + TDDMay + TDDJune + RainJune	0
First Shoot Length	SM + TDDMay + TDDJune	-1,045
First Shoot Length	SM + TDDMay + RainMay + TDDJune	-1,110

First Shoot Length	LS^{-1Y} + SM + TDDMay + TDDJune + RainJune	-1,475
First Shoot Length	LS^{-1Y} + SM + TDDMay + RainMay + TDDJune	-1,887
First Shoot Length	Year + SM + TDDMay + TDDJune + RainJune	-1,927
First Shoot Length	SM + TDDMay + RainMay + TDDJune + RainJune	-1,990
First Shoot Length	LS^{-1Y} + SM + TDDMay + TDDJune	-2,238
First Shoot Length	SM + TDDJUne + RainJune	-2,390
First Shoot Length	Year + SM + TDDMay + TDDJune	-2,512

Dep Var	**Factors**	**Delta AIC**
Number New Leaves	Year + LS^{-1Y} + SM + TDDMay + RainMay + TDDJune	0
Number New Leaves	SM + TDDJUne + RainJune	-0,401
Number New Leaves	LS^{-1Y} + SM + TDDJune + RainJune	-0,590
Number New Leaves	Year + SM + TDDMay + RainMay + TDDJune	-1,063
Number New Leaves	Year + SM + TDDJune + RainJune	-1,519
Number New Leaves	LS^{-1Y} + SM + RainMay + TDDJune + RainJune	-1,657
Number New Leaves	Year + LS^{-1Y} + SM + TDDMay + RainMay + TDDJune + RainJune	-1,855
Number New Leaves	LS^{-1Y} + SM +TDDMay + RainMay + TDDJune	-2,107

Number New Leaves	Year + LS^{-1Y} + SM + TDDJune + RainJune	-2,166
Number New Leaves	SM + RainMay + TDDJUne + RainJune	-2,175

Table S5. ΔAIC values of linear/non linear models for the selection of the best generalized linear/non linear models computed through ΔAIC values on LS for each year. Each best model has ΔAIC = 0. Legend: LS-SM: factor computed for the period between SM and LS and not for specific months; LS-Photo = photoperiod (hours of light per day) at LS.

Dep. Var.	**Year**	**Factors**	**ΔAIC**
LS	2007	Elev + SM + LS-Photo + TDDSM-LS + FDDSM-LS + RainSM-LS	0
LS	2009	SM + LS-Photo + TDDSM-LS + RainSM-LS	0
LS	2010	SM + LS-Photo + TDDSM-LS + FDDSM-LS + RainSM-LS	0
LS	2011	SM + LS-Photo + TDDSM-LS + FDDSM-LS	0
LS	2012	SM + LS-Photo + TDDSM-LS + FDDSM-LS	0
LS	2013	Elev + SM + LS-Photo + TDDSM-LS + FDDSM-LS + RainSM-LS	0
LS	2014	SM + LS-Photo + RainSM-LS	0
LS	2015	Elev + SM + LS-Photo + TDDSM-LS + RainSM-LS	0

III.5.B.k. *Relations between phenology and climatic factors*

We tested by GRMs the relation between phenology and climatic factors. For each of the analyzed phenophases, our analyses have been carried out at the inter-specific level by following two steps: I) considering only climatic factors and II) including also biotic factors (i.e. previous phenological stages).

Influence of climatic factors

First shoot (FS)

The most important factor affecting FS in a statistically significant way ($p<0.01$) was the SM, considering both all the study period (F=191913) or only the “normal” years of FS (thus excluding 2007) (F=81662) (Table III.5.B.k.1).

Only the TDD cumulated since SM showed also some significant influence on FS (even if not comparable with SM) on both all the study period (2007-2016) and excluding the “extreme” year of FS (2007).

Table III.5.B.k.1. Influence of the main climate factors on FS (dependent variable) during the whole study period (2007-2016), and excluding the “extreme” years of FS (2007), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: FS-SM: factor computed for the period between SM and FS.

	2007-2016			**2008-2016**		
	F	**p**	**R^2**	**F**	**p**	**R^2**
full model	46740.4	<0.01	1.00	21799.0	<0.01	1.00
elevation				4.2	0.04	
year						
SM	191912.7	<0.01		81661.7	<0.01	
FS_phot	13.4	<0.01		41.6	<0.01	
airTDD_FS-SM	1879.2	<0.01		1472.9	<0.01	
airMEAN_FS-SM	473.9	<0.01		463.4	<0.01	
rainTOT_FS-SM	126.7	<0.01		80.3	<0.01	
airMEAN_APRIL				19.3	<0.01	
rainTOT_APRIL						
radTOT_APRIL						
airMEAN_MAY	28.4	<0.01		38.2	<0.01	
rainTOT_MAY	113.5	<0.01		44.6	<0.01	
radTOT_MAY				8.4	<0.01	
airMEAN_JUNE				10.6	<0.01	
rainTOT_JUNE	28.9	<0.01		12.5	<0.01	
radTOT_JUNE				20.5	<0.01	

New leaf (NL)

Among the abiotic factors, SM was the most important factor in affecting the inter-specific responses of NL in a statistically significant way ($p<0.01$) ($F=13425$), while the other factors exerted only limited influence (Table III.5.B.k.2), thus highlighting the important role of the start of growing season on leaves unfolding.

Table III.5.B.k.2. Influence of the main climate factors on NL (dependent variable) during the whole period (2007-2016), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: NL-SM: factor computed for the period between SM and NL.

	F	**p**	**R^2**
full model	1862.0	<0.01	0.95
elevation			
year	48.1	<0.01	
SM	13424.6	<0.01	
NL_phot			
airTDD_NL-SM	382.9	<0.01	
airMEAN_NL-SM	103.6	<0.01	
rainTOT_NL-SM	19.4	<0.01	
airMEAN_APRIL	71.2	<0.01	
rainTOT_APRIL	104.2	<0.01	
radTOT_APRIL			
airMEAN_MAY	76.9	<0.01	
rainTOT_MAY	55.4	<0.01	
radTOT_MAY			
airMEAN_JUNE	103.0	<0.01	
rainTOT_JUNE	107.9	<0.01	
radTOT_JUNE	86.3	<0.01	

Pre-unfolding period (NL-SM)

Considering all the study period (2007-2016), the main climatic factors affecting NL-SM duration in a statistically significant way (p<0.01) was the air TDD cumulated since SM, both on all the study period (F=383) and on the normal years of NL-SM (F=281) (Table III.5.B.k.3).

Table III.5.B.k.3. Influence of the main climate factors on NL-SM (dependent variable) during the whole study period (2007-2016), and excluding the "extreme" years of NL-SM (2007), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: NL-SM: factor computed for the period between SM and NL.

	2007-2016			**2008-2016**		
	F	**p**	**R^2**	**F**	**p**	**R^2**
full model	173.8	<0.01	0.66	118.1	<0.01	0.59
elevation						
year	48.1	<0.01				
SM	25.3	<0.01		59.9	0.00	
NL_phot				35.8	0.00	
airTDD_NL-SM	382.9	<0.01		280.8	0.00	
airMEAN_NL-SM	103.6	<0.01		100.1	0.00	
rainTOT_NL-SM	19.4	<0.01		4.6	0.03	
airMEAN_APRIL	71.2	<0.01		14.2	0.00	
rainTOT_APRIL	104.2	<0.01				
radTOT_APRIL				20.5	0.00	
airMEAN_MAY	76.9	<0.01		16.7	0.00	
rainTOT_MAY	55.4	<0.01		27.4	0.00	
radTOT_MAY				22.3	0.00	
airMEAN_JUNE	103.0	<0.01		14.2	0.00	
rainTOT_JUNE	107.9	<0.01		21.6	0.00	
radTOT_JUNE	86.3	<0.01				

Flower bud (FB)

The most important abiotic factor affecting inter-specific responses of FB in a statistically significant way (p<0.01) was the SM (F = 3944), coupled with the air TDD cumulated from SM to FB (F=2199) (Table III.5.B.k.4).

Table III.5.B.k.4. Influence of the main climate factors on FF (dependent variable) during the whole period (2007-2016), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: FB-SM: factor computed for the period between SM and FB.

	F	**p**	**R^2**
full model	2558.6	<0.01	0.99
elevation			
year	13.4	<0.01	
SM	3943.8	<0.01	
FB_phot	64.4	<0.01	
airTDD_FB-SM	2199.2	<0.01	
airFDD_FB-SM	10.3	<0.01	
airMEAN_FB-SM	102.4	<0.01	
rainTOT_FB-SM	242.0	<0.01	
airMEAN_MAY			
rainTOT_MAY	22.8	<0.01	
radTOT_MAY	20.2	<0.01	
airMEAN_JUNE	12.9	<0.01	
rainTOT_JUNE	93.1	<0.01	
radTOT_JUNE	19.6	<0.01	
airMEAN_JULY	138.6	<0.01	
rainTOT_JULY	98.2	<0.01	
radTOT_JULY			

First flowering day (FF)

The most important abiotic factor affecting inter-specific responses of FF in a statistically significant way ($p<0.01$) was the SM (F=1579) (Table III.5.B.k.5), coupled with the air TDD cumulated since SM (F=1405) (Table III.5.B.k.5). The photoperiod exerted here a small influence (F=639).

Table III.5.B.k.5. Influence of the main climate factors on FF (dependent variable) during the whole period (2007-2016), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: FF-SM: factor computed for the period between SM and FF.

	F	**p**	**R^2**
full model	3761.1	<0.01	0.99
elevation	13.0	<0.01	
year			
SM	1579.0	<0.01	
FF_phot	639.4	<0.01	
airTDD_FF-SM	1405.0	<0.01	
airFDD_FF-SM	49.7	<0.01	
airMEAN_FF-SM	57.6	<0.01	
rainTOT_FF-SM	277.3	<0.01	
airMEAN_MAY	7.9	<0.01	
rainTOT_MAY			
radTOT_MAY			
airMEAN_JUNE	35.9	<0.01	
rainTOT_JUNE	7.1	0.01	
radTOT_JUNE	57.1	<0.01	
airMEAN_JULY	119.1	<0.01	
rainTOT_JULY	163.7	<0.01	
radTOT_JULY	44.8	<0.01	

Main flowering day (MF)

Among the abiotic factors influencing the responses of MF in a statistically significant way ($p<0.01$) the photoperiod (MF_phot) involved the largest influence (F=1257) (Table III.5.B.k.6), thus highlighting a conservative strategy of alpine plants.

The SM and the TDD cumulated since SM exerted comparable influence (respectively F=796 and F=761), however compared to photoperiod they exerted lower influence.

Table III.5.B.k.6. Influence of the main climate factors on MF (dependent variable) during the whole period (2007-2016), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: MF-SM: factor computed for the period between SM and MF.

	F	**p**	**R^2**
full model	3810.7	<0.01	0.99
elevation	10.8	<0.01	
year	12.6	<0.01	
SM	796.4	<0.01	
MF_phot	1255.6	<0.01	
airTDD_MF-SM	761.1	<0.01	
airFDD_MF-SM	21.5	<0.01	
airMEAN_MF-SM	18.5	<0.01	
rainTOT_MF-SM	146.7	<0.01	
airMEAN_MAY			
rainTOT_MAY	9.3	<0.01	
radTOT_MAY			
airMEAN_JUNE	26.8	<0.01	
rainTOT_JUNE			
radTOT_JUNE	24.7	<0.01	
airMEAN_JULY	173.2	<0.01	
rainTOT_JULY	215.4	<0.01	
radTOT_JULY			

Seed development (SD)

The most important abiotic factor affecting inter-specific responses of SD in a statistically significant way (p<0.01) was the photoperiod (F=2416), with the other factors exerting only limited influence (Table III.5.B.k.7). The importance of the photoperiod limitation on seeds development highlights again the conservative strategy of alpine plants to start their SD with safer climatic condition.

Table III.5.B.k.7. Influence of the main climate factors on SD (dependent variable) during the whole period (2007-2015), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: SD-SM: factor computed for the period between SM and SD.

	F	**p**	**R2**
full model	5362.1	<0.01	0.99
elevation	12.1	<0.01	
year			
SM	402.6	<0.01	
SD_phot	2416.3	<0.01	
airTDD_SD-SM	405.8	<0.01	
airFDD_SD-SM	9.5	<0.01	
airMEAN_SD-SM	7.0	<0.01	
rainTOT_SD-SM	66.7	<0.01	
airMEAN_MAY	17.1	<0.01	
rainTOT_MAY	10.2	<0.01	
radTOT_MAY			
airMEAN_JUNE	42.2	<0.01	
rainTOT_JUNE	16.7	<0.01	
radTOT_JUNE	28.4	<0.01	
airMEAN_JULY	127.2	<0.01	
rainTOT_JULY	148.1	<0.01	
radTOT_JULY			

Seed ripening (SR)

Similarly to SD, the most important factor affecting inter-specific responses of SR in a statistically significant way ($p<0.01$) was the photoperiod ($F = 25917$), coupled with the SM and the air TDD cumulated since SM, even if they exerted lower influence (respectively $F=460$ and $F=472$) compared to photoperiod. All the other factors showed only very limited influence (Table III.5.B.k.8).

As observed for SD, the photoperiodic limitation could be a conservative strategy, resulted from the adaptation to the alpine severe climate, preventing plants to ripen and disperse seeds in non-favorable climatic condition, thus improving the reproductive success.

Table III.5.B.k.8. Influence of the main climate factors on SR (dependent variable) during the whole period (2007-2015), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: SR-SM: factor computed for the period between SM and SR.

	F	**p**	**R^2**
full model	59791.6	<0.01	1.00
elevation			
year			
SM	460.3	<0.01	
SR_phot	25916.7	<0.01	
airTDD_SR-SM	472.4	<0.01	
airFDD_SR-SM			
airMEAN_SR-SM	22.6	<0.01	
rainTOT_SR-SM	89.0	<0.01	
airMEAN_JUNE			
rainTOT_JUNE			
radTOT_JUNE	4.0	<0.01	
airMEAN_JULY	155.5	<0.01	
rainTOT_JULY	94.8	<0.01	
radTOT_JULY	32.2	<0.01	
airMEAN_AUG	161.9	<0.01	
airTDD_AUG	328.4	<0.01	
rainTOT_AUG			

Leaf Senescence (LS)

The most important factor affecting inter-specific response of LS in a statistically significant way ($p<0.01$) was the photoperiod (LS_phot) on either the "normal" years of LS (2007-2014) (F = 8414) or when considering all the years of the dataset (2007-2015) (F = 8910) (Table III.5.B.k.9).

Among the secondary factors, the model run on the whole period of LS identified the SM and the TDD cumulated since SM, even if their effects was lower compared to photoperiod (respectively F=624 and F=637). On the contrary, the other factors, considering only the normal years, exerted very restricted influence (Table III.5.B.k.9).

Table III.5.B.k.9. Influence of the main climate factors on LS (dependent variable) during the whole period (2007-2015) and only for the "normal" years of LS (thus excluding 2015), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: LS-SM: factor computed for the period between SM and LS.

	2007-2015			**2007-2014**		
	F	**p**	**R^2**	**F**	**p**	**R^2**
full model	5362.1	<0.01	0.99	20303.8	<0.01	1.00
elevation	4.6	0.03			0.03	
YEAR						
SM	624.2	<0.01		158.0	<0.01	
LS_phot	8902.9	<0.01		8413.5	<0.01	
TDD_LS-SM	636.7	<0.01		148.0	<0.01	
FDD_LS-SM	13.9	<0.01		13.2	<0.01	
TMED_LS-SM	57.3	<0.01		29.4	<0.01	
pioggia_LS-SM	117.8	<0.01		32.0	<0.01	
airMEAN_JUNE	176.2	<0.01		144.8	<0.01	
rainTOT_JUNE	76.1	<0.01				
radTOT_JUNE	258.8	<0.01		121.0	<0.01	
airMEAN_JULY	151.5	<0.01		98.0	<0.01	
rainTOT_JULY	127.1	<0.01		80.2	<0.01	
radTOT_JULY						
airMEAN_AUG						
airTDD_AUG	78.5	<0.01				
rainTOT_AUG						

Influence of biotic and abiotic factors

New leaf (NL)

Including also the biotic forcing (in this case timing of FS), FS was the most important factor affecting the inter-specific responses of NL in a statistically significant way (p<0.01) (F=561) (Table III.5.B.k.10).

However, the effect of FS was coupled with other climatic factors exerting statistically significant influence on NL, among which the airTDD cumulated since SM exerted the largest influence (F=256) (Table III.5.B.k.10).

Table III.5.B.k.10. Influence of the main climate factors and of FS on NL (dependent variable) during the whole period (2007-2016), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: NL-SM: factor computed for the period between SM and NL.

	F	**p**	**R^2**
full model	2639.6	<0.01	0.97
elevation			
year	68.1	<0.01	
SM	95.2	<0.01	
FS	560.7	<0.01	
NL_phot			
airTDD_NL-SM	256.1	<0.01	
airMEAN_NL-SM	66.6	<0.01	
rainTOT_NL-SM	11.6	<0.01	
airMEAN_APRIL	140.4	<0.01	
rainTOT_APRIL	145.3	<0.01	
radTOT_APRIL			
airMEAN_MAY	91.9	<0.01	
rainTOT_MAY	49.1	<0.01	
radTOT_MAY			
airMEAN_JUNE	158.9	<0.01	
rainTOT_JUNE	149.4	<0.01	
radTOT_JUNE	115.8	<0.01	

Pre-unfolding period (NL-SM)

Considering the biotic forcing on NL-SM (in this case NL) for the whole study period, the total heat cumulated since SM was again the main factor influencing the pattern of NL-SM in a statistically significant way (p<0.01) on both all the study period (F=397) and only the normal years of NL-SM (F=300) (Table III.5.B.k.11).

Table III.5.B.k.11. Influence of the main climate and biotic factors on NL-SM (dependent variable) during the whole study period (2007-2016), and excluding the "extreme" years of NL-SM (2007), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: NL-SM: factor computed for the period between SM and NL.

	2007-2016			**no 2007**		
	F	**p**	**R^2**	**F**	**p**	**R^2**
full model	228.8	<0.01	0.81	140.1	<0.01	0.59
elevation						
year				10.7	<0.01	
SM	35.0	<0.01		59.5	<0.01	
NL						
NL_phot				36.0	<0.01	
airTDD_NL-SM	396.5	<0.01		299.6	<0.01	
airMEAN_NL-SM	109.2	<0.01		103.3	<0.01	
rainTOT_NL-SM	13.6	<0.01		6.6	<0.01	
airMEAN_APRIL						
rainTOT_APRIL	43.4	<0.01				
radTOT_APRIL	111.8	<0.01		53.8	<0.01	
airMEAN_MAY	8.4	<0.01				
rainTOT_MAY	54.9	<0.01		89.2	<0.01	
radTOT_MAY				55.4	<0.01	
airMEAN_JUNE						
rainTOT_JUNE	32.2	<0.01		31.4	<0.01	
radTOT_JUNE						

First flowering day (FF)

Including also the biotic factors (in this case the timing of FB), the air TDD cumulated since SM was again the main factor (F=1146) affecting inter-specific responses of FF in a statistically significant way (p<0.01) (Table III.5.B.k.12).

However also the SM and photoperiod (FF_phot) exerted a strong influence on FF (respectively F=979 and F=608). The FF showed a statistically significant relation with FB, as tested by linear regression at the inter-annual and inter-specific level (see chap. III.5.B.f.). This analysis demonstrated that the effect of the climate coupled with the photoperiodic limitation overwhelmed the effect of FB (Table III.5.B.k.12).

Table III.5.B.k.12. Influence of the main climate factors and of previous phenological stage on FF (dependent variable) during the whole period (2007-2016), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: FF-SM: factor computed for the period between SM and FF.

	F	**p**	**R^2**
full model	3781.5	<0.01	0.99
elevation	20.1	<0.01	
year	15.7	<0.01	
SM	979.1	<0.01	
FB	99.1	<0.01	
FF_phot	608.3	<0.01	
airTDD_FF-SM	1145.8	<0.01	
airFDD_FF-SM	51.0	<0.01	
airMEAN_FF-SM	43.4	<0.01	
rainTOT_FF-SM	229.0	<0.01	
airMEAN_MAY			
rainTOT_MAY	3.8	<0.01	
radTOT_MAY			
airMEAN_JUNE	24.6	<0.01	
rainTOT_JUNE			
radTOT_JUNE	77.8	<0.01	
airMEAN_JULY	123.7	<0.01	
rainTOT_JULY	200.0	<0.01	
radTOT_JULY	43.9	<0.01	

Main flowering day (MF)

Considering also the previous phenological stage (in this case the FF), the most important factor affecting the patterns of MF in a statistically significant way ($p<0.01$) was again the photoperiod ($F=877$) (Table III.5.B.k.13).

Other variables were identified as influencing the MF, even if with limited effect compared to photoperiod: the SM ($F=275$), the FF ($F=283$) and the air TDD cumulated since SM ($F=330$).

Table III.5.B.k.13. Influence of the main climate factors and of previous phenological stage on MF (dependent variable) during the whole period (2007-2016), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: MF-SM: factor computed for the period between SM and MF.

	F	**p**	**R^2**
full model	3943.0	<0.01	0.99
elevation	4.5	0.03	
year			
SM	275.1	<0.01	
FF	283.5	<0.01	
MF_phot	876.5	<0.01	
airTDD_MF-SM	329.6	<0.01	
airFDD_MF-SM	8.0	<0.01	
airMEAN_MF-SM	6.8	<0.01	
rainTOT_MF-SM	68.6	<0.01	
airMEAN_MAY			
rainTOT_MAY	44.3	<0.01	
radTOT_MAY	43.8	<0.01	
airMEAN_JUNE	6.0	<0.01	
rainTOT_JUNE	32.4	<0.01	
radTOT_JUNE	33.9	<0.01	
airMEAN_JULY	26.6	<0.01	
rainTOT_JULY	13.7	<0.01	
radTOT_JULY	33.1	<0.01	

Seed development (SD)

Including in our analysis also the previous phenological stage (i.e. MF) the photoperiod persisted as the main environmental cue regulating the patterns of MF (F=1752) (Table III.5.B.k.14).

The MF affected the SD in a statistically significant way (p<0.01) (F=233), with an effect comparable to the SM (F=318) or to the air TDD (F=384). The other variables exerted instead only limited influence.

Table III.5.B.k.14. Influence of the main climate factors on SD (dependent variable) during the whole period (2007-2015), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: SD-SM: factor computed for the period between SM and SD.

	F	**p**	**R^2**
full model	6570.9	<0.01	0.99
elevation	11.2	<0.01	
year			
SM	318.6	<0.01	
MF	233.4	<0.01	
SD_phot	1752.0	<0.01	
airTDD_SD-SM	384.0	<0.01	
airFDD_SD-SM			
airMEAN_SD-SM	10.5	<0.01	
rainTOT_SD-SM	47.2	<0.01	
airMEAN_MAY	107.1	<0.01	
rainTOT_MAY	87.3	<0.01	
radTOT_MAY	45.4	<0.01	
airMEAN_JUNE			
rainTOT_JUNE	92.2	<0.01	
radTOT_JUNE	112.2	<0.01	
airMEAN_JULY	174.9	<0.01	
rainTOT_JULY	131.8	<0.01	
radTOT_JULY			

Seed ripening (SR)

Including in our analysis the previous phenological stage (in this case the SD), the most important factor affecting inter-specific responses of SR in a statistically significant way (p<0.01) was again the photoperiod (F = 35118) (Table III.5.B.k.15).

The SM exerted only a limited influence (F=525) coupled with the air TDD cumulated since SM (F=487) (Table III.5.B.k.15).

The SD did not affect the pattern of SR, thus confirming previous hypothesis that SR is not affected by previous reproductive phenology. Due to this reason, the SR responses could be different to changes in growing season lengthening scenario, respect previous reproductive phenology.

Table III.5.B.k.15. Influence of the main climate factors on SR (dependent variable) during the whole period (2007-2015), as tested by backward stepwise GRM at the inter-specific and inter-annual level. Legend: SR-SM: factor computed for the period between SM and SR.

	F	p	R^2
full model	59815.2	<0.01	1.00
elevation			
year			
SM	524.6	<0.01	
SD	4.4	0.04	
SR_phot	35117.8	<0.01	
airTDD_SR-SM	486.6	<0.01	
airFDD_SR-SM			
airMEAN_SR-SM	18.8	<0.01	
rainTOT_SR-SM	102.5	<0.01	
airMEAN_JUNE			
rainTOT_JUNE			
radTOT_JUNE			
airMEAN_JULY	238.4	<0.01	
rainTOT_JULY	83.0	<0.01	
radTOT_JULY	37.1	<0.01	
airMEAN_AUG	200.6	<0.01	
airTDD_AUG	356.5	<0.01	
rainTOT_AUG			

III.5.B.l. Patterns of first shoot length (FS_beg_n)

Analogously to the other phenophases, our analyses have been carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2010-2016) at the inter-specific level, FS_beg_n exhibited statistically significant differences, as tested by one-way ANOVA (F=9, p<0.01) (Fig. III.5.B.l.1).

Table III.5.B.l.1. Non-parametric statistics of first shoot length (FS_beg_n) computed for each single year, as well as for the entire monitoring period (2010-2016), at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	132	12	2	5	8	15	50	10.5
2011	133	17	2	6	14	20	80	14.7
2012	133	11	2	5	10	15	35	6.7
2013	132	16	2	5	13	21	64	13.2
2014	130	13	1	5	10	18	75	12.4
2015	131	12	1	4	10	15	55	10.1
2016	131	9	1	4	8	10	25	5.6
20010-2016	922	13	1	5	10	16	80	11.2

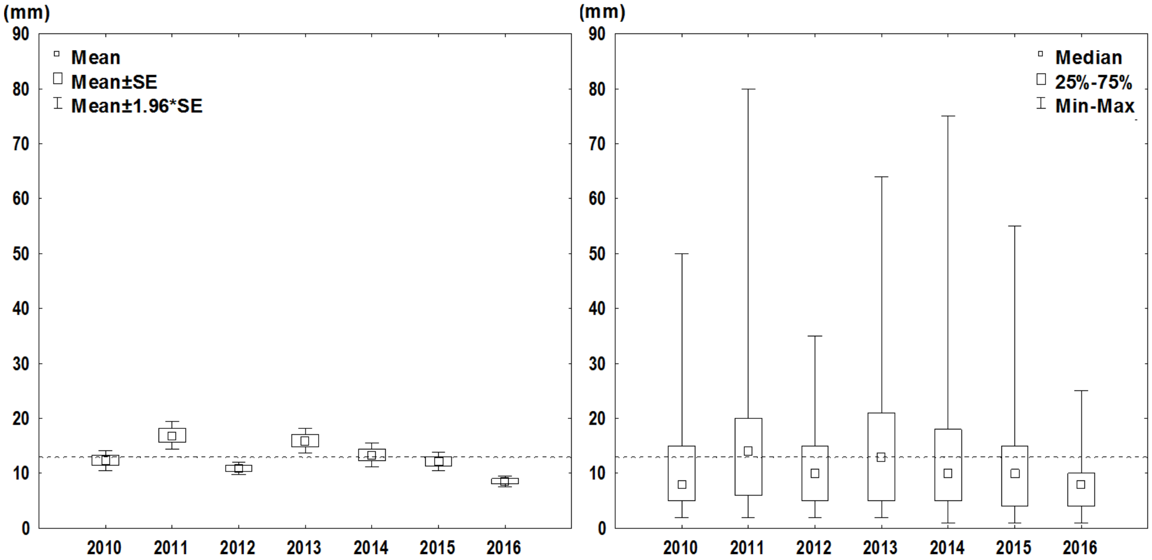

Figure III.5.B.l.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot length (FS_beg_n) from 2010 to 2016 at the inter-specific level. The dotted black line represents the mean value for the whole period.

During the entire monitoring period (2010-2016) (Table III.5.B.l.1), the mean and median values of FS_beg_n were almost coincident (respectively 13 and 10 mm) and its 75% quartile coincided with 16 mm.

Analyzing each year separately (Table III.5.B.l.1), the shortest FS_beg_n ranged between 1 and 2 mm (thus ranging only of the accuracy of our measure), while the longest FS_beg_n spanned from 25 mm (in 2016) to 80 mm (in 2011).

Considering the 75% quartiles anomalies, the longest FS_beg_n were measured in 2011 and 2013 (respectively + 4 and + 5 mm), while the shortest in 2016 (-6 mm), although all years without statistically significant differences ($p>0.05$).

Investigating thus all the dataset (2010-2016), we did not find statistically significant trends of FS_beg_n with time.

As the timing of FS is strongly affected by the SM (see chap III.5.B.a and III.5.B.k), we tested by linear regression at the inter-annual and inter-specific level whether SM could influence the size of FS. However, our analyses indicated a lack of relation with SM timing ($\beta=0.02$, $R^2=0.06$, $p<0.01$).

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2010-2016) the FS_beg_n of deciduous dwarf shrubs (i.e. *Salix herbacea*) did not exhibit statistically significant differences among years ($p>0.05$) (Fig. III.5.B.l.2).

Table III.5.B.l.2. Non-parametric statistics of first shoot length (FS_beg_n) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	7	7	4	5	7	8	9	1.9
2011	7	6	4	4	6	8	12	2.9
2012	7	5	3	3	4	6	11	2.8
2013	7	6	4	5	5	9	10	2.3
2014	7	7	4	4	6	10	10	2.5
2015	7	6	4	4	6	6	9	1.7
2016	7	8	5	6	8	10	10	2.0
2010-2016	49	6	3	4	6	8	12	2.4

Over the study period (2010-2016), mean and median values were coincident (6 mm) while the 75% indicated FS_beg_n of 10 mm (Table III.5.B.l.2).

The shortest FS_beg_n ranged from 3 (in 2012) to 5 mm (in 2016), while the longest FS_beg_n spanned from 9 mm (in 2010 and 2015) to 12 mm (in 2011) (Table III.5.B.l.2).

According to the anomalies of the 75% quartiles over the whole dataset, the shortest FS_beg_n was recorded in 2011 and 2015 (-2 mm), and the longest in 2014 and 2016 (+2 mm) (Fig. III.5.B.l.2), although all without statistically significance, as tested by t-test (p>0.05).

Considering thus the whole period (2010-2016) the analysis of FS_beg_n with time did not reveal any statistically significant trend, as tested by linear regression (p>0.05).
As tested by linear regression at the inter-annual level, we have not found any statistically significant relation between FS_beg_n and SM (p>0.05).

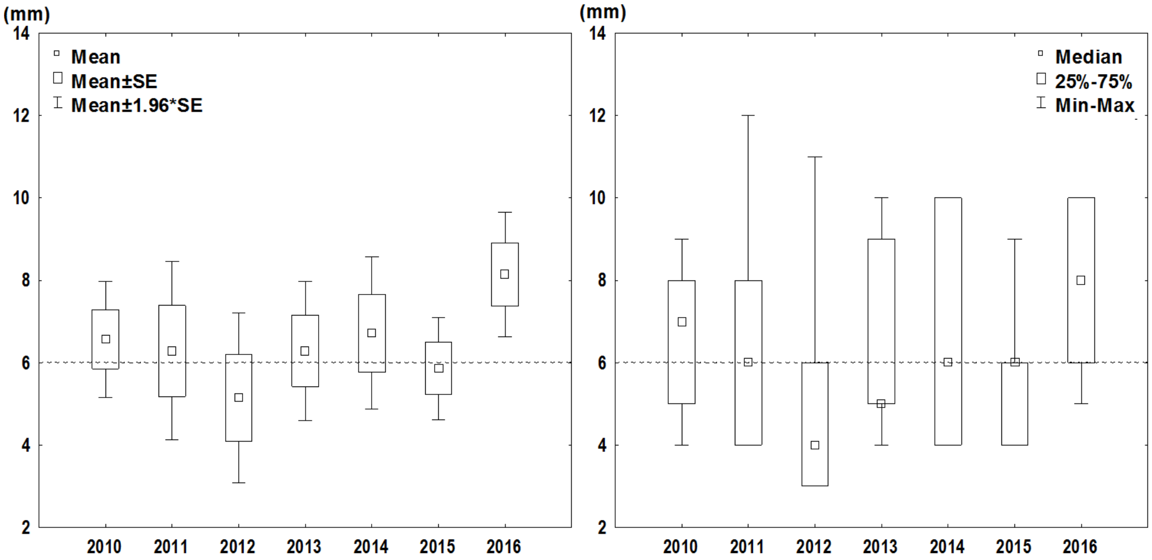

Figure III.5.B.l.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot length (FS_beg_n) for deciduous dwarf shrubs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

Deciduous shrubs

As tested by one-way ANOVA, overall the study period (2010-2016) the FS_beg_n of deciduous shrubs (i.e. *Vaccinium uliginosum*) exhibited statistically significant differences among years (F=4, p<0.01) (Fig. III.5.B.l.3).

Over the study period (2010-2016), the mean values of FS_beg_n corresponded to 5 mm, while the median and 75% quartile were coincident (6 mm) (Table III.5.B.l.3). The shortest FS_beg_n ranged from 2 mm (in 2011 and 2013) to 6 mm (in 2014), while the longest FS_beg_n spanned from 4 mm (in 2011) to 10 mm (in 2016) (Table III.5.B.l.3).

Analyzing the anomalies of the 75% quartiles, the shortest FS_beg_n was recorded in 2011 (-3 mm) while the longest in 2016 (+8 mm) (Fig. III.5.B.l.3), although all without statistically significant differences, as tested by t-test (p>0.05).

Table III.5.B.l.3. Non-parametric statistics of first shoot length (FS_beg_n) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	4	6	5	5	6	6	6	0.6
2011	4	3	2	3	3	4	4	0.8
2012	4	5	4	5	5	5	5	0.5
2013	4	5	2	4	6	7	8	2.5
2014	4	6	6	6	6	6	6	
2015	4	6	4	5	6	7	7	1.3
2016	4	8	5	6	8	9	10	2.1
2010-2016	28	5	2	5	6	6	10	1.8

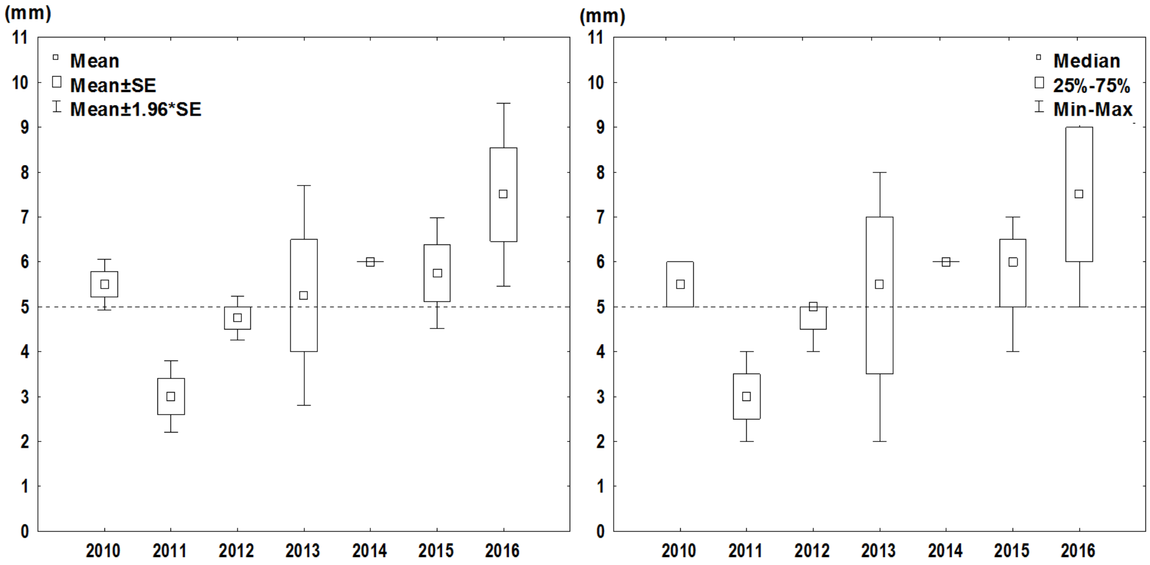

Figure III.5.B.l.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot length (FS_beg_n) for deciduous shrubs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

Considering thus all the dataset, we did not find any statistically significant trend of FS_beg_n with time, as tested by linear regression ($p>0.05$). Moreover, as tested by linear regression at the inter-annual level, we have not found any statistically significant relation between FS_beg_n and SM ($p>0.05$).

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2010-2016) the FS_beg_n of evergreen dwarf shrubs (i.e. *Empetrum hermaphroditum* and *Kalmia procumbens*) did not exhibit statistically significant differences among years ($p>0.05$) (Fig. III.5.B.l.4).

Over all the study period (2010-2016), mean and median values were coincident, indicating FS_beg_n of 3 mm, while the 75% quartile coincided with 4 mm (Table III.5.B.l.4).
The shortest FS_beg_n ranged from 1 to 2 mm, while the longest FS_beg_n spanned from 4 mm (in 2011) to 9 mm (in 2016) (Table III.5.B.l.4).

Analyzing the anomalies of the 75% quartiles, the longest FS_beg_n war recorded in 2010 (+4 mm) and was identified as statistically significant different, as tested by t-test ($p<0.01$) (Fig. III.5.B. l.4).

Table III.5.B.l.4. Non-parametric statistics of first shoot length (FS_beg_n) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev..
2010	9	5	2	2	5	8	8	2.7
2011	9	3	2	3	3	3	4	0.6
2012	9	4	2	3	3	4	6	1.5
2013	9	3	2	2	3	4	5	1.3
2014	9	3	1	2	2	3	7	1.8
2015	9	3	1	2	3	3	5	1.2
2016	9	4	2	2	3	4	9	2.2
2010-2016	63	3	1	2	3	4	8	1.6

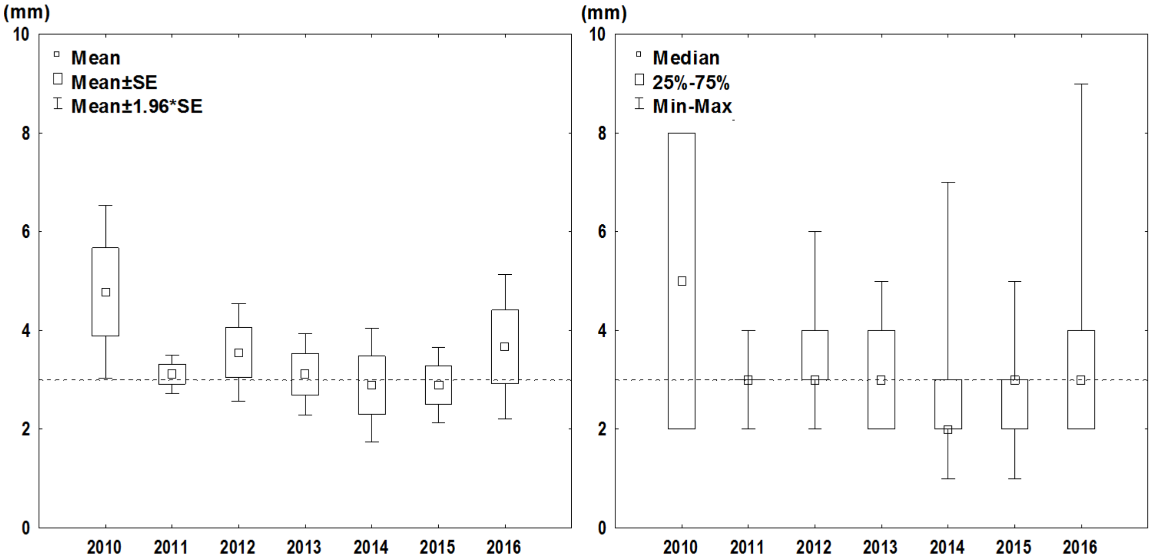

Figure III.5.B.l.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot length (FS_beg_n) for evergreen dwarf shrubs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

However, considering only "normal" years (2011-2016) the evergreen dwarf shrubs did not show any statistically significant trend of the FS_beg_n with time ($p>0.05$). Moreover, as tested by linear regression at the inter-annual level, we have not found any statistically significant relation between FS_beg_n and SM ($p>0.05$).

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2010-2016) the FS_beg_n of evergreen shrubs (i.e. *Rhododendron ferrugineum* and *Juniperus communis*) did not exhibit statistically significant differences among years (p>0.05) (Fig. III.5.B.l.5).

Table III.5.B.l.5. Non-parametric statistics of first shoot length (FS_beg_n) for evergreen shrubs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	8	9	4	5	9	12	14	4.0
2011	8	11	3	4	10	18	21	7.5
2012	8	9	4	5	7	13	14	4.2
2013	8	13	3	5	13	21	23	8.1
2014	8	10	2	6	10	15	18	5.7
2015	8	10	2	6	11	13	17	4.9
2016	8	8	2	6	10	10	14	3.8
2010-2016	56	9	2	5	8	14	23	5.7

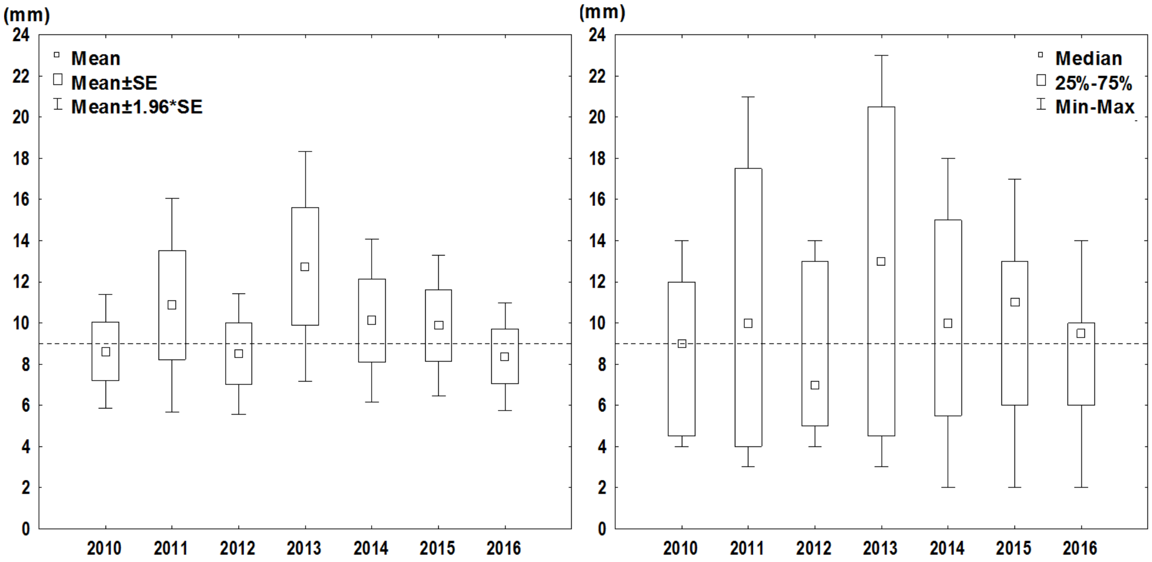

Figure III.5.B.l.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot length (FS_beg_n) for evergreen shrubs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

Over all the study period (2010-2016), according to the mean and median values, the FS_beg_n coincided respectively with 9 and 8 mm, while the 75% corresponded to 14 mm (Table III.5.B.l.5). The shortest FS_beg_n ranged from 2 to 5 mm, while the longest from 14 mm (in 2016 and 2007) to 23 mm (in 2013).

Considering the anomalies of the 75% quartiles, the longest FS_beg_n was recorded in 2013 (+7 mm), even without any statistically significance, according to t-test (p>0.05) (Fig. III.5.B.l.5).

Considering thus all the study period (2010-2016) we did not find any statistically significant trend of the FS_beg_n with time for evergreen shrubs, as tested by linear regression ($p>0.05$).

As tested by linear regression at the inter-annual level, the SM did not explain any proportion of the FS_beg_n variance ($\beta=0.2$, $R^2=0.07$, $p=0.05$), indicating a lack of relation with the timing of SM.

Forbs

Considering all the study period, also forbs exhibited statistically significant differences among years, as tested by one-way ANOVA ($F=6$, $p<0.01$) (Fig III.5.B.l.6).

The mean and median values of FS_beg_n over the whole period (2010-2016) coincided respectively to 13 and 10 mm, while the 75% quartile corresponded to 18 mm (Table III.5.B.l.6). The shortest FS_beg_n ranged from 1 to 2 mm, while the longest from 25 mm (in 2016) to 75 mm (in 2011 and 2014) (Table III.5.B.l.6).

Comparing the 75% anomalies, forbs showed the longest FS_beg_n in 2011 (+5 mm) and the shortest FS_beg_n in 2016 (-8 mm). The year 2016 was the only one identified as statistically significant, as tested by t-test ($p=0.04$) (Fig. III.5.B.l.6).

However, we did not observe any statistically significant trend with time for the forbs FS_beg_n, considering the period (2010-2015), as tested by linear regression ($p>0.05$).

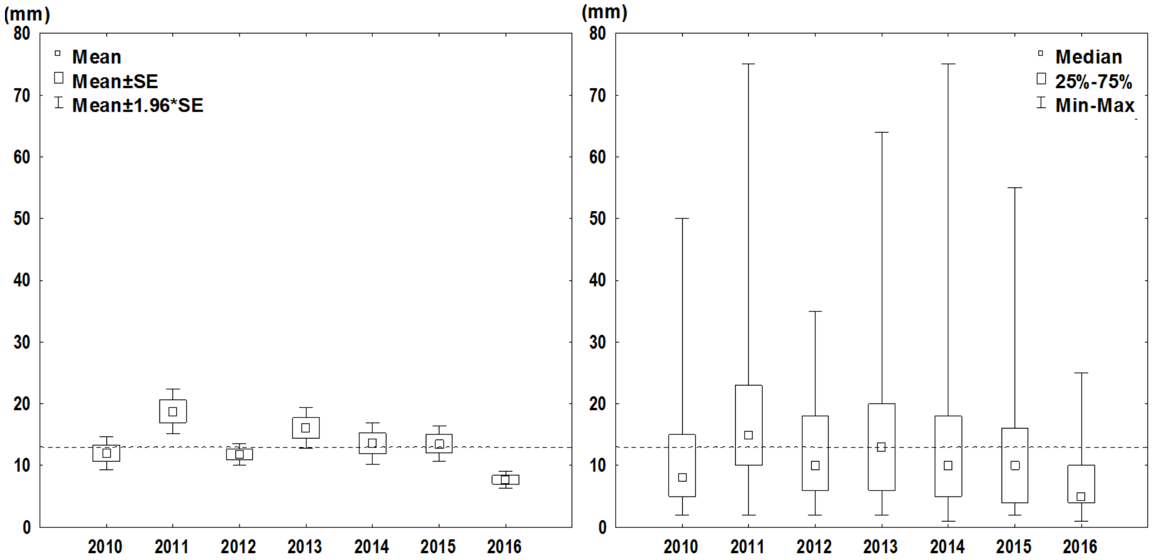

Figure III.5.B.l.6. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot length (FS_beg_n) of forbs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

Table III.5.B.l.6. Non-parametric statistics of first shoot length (FS_beg_n) of forbs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	67	12	2	5	8	15	50	11.1
2011	67	19	2	10	15	23	75	15.0
2012	67	12	2	6	10	18	35	7.4
2013	66	16	2	6	13	20	64	13.5
2014	65	14	1	5	10	18	75	13.6
2015	66	14	2	4	10	16	55	11.9
2016	66	8	1	4	5	10	25	5.8
2010-2016	464	13	1	5	10	18	75	12.0

As tested by linear regression at the inter-annual level, the SM did not explain any proportion of the FS_beg_n variance (β=0.1, R^2=0.03, p<0.01), indicating a lack of relation with the timing of SM.

Graminoids

As tested by one-way ANOVA, overall the study period (2010-2016) the FS_beg_n of graminoids exhibited statistically significant differences among years (F=6, p<0.01) (Fig. III.5.B.l.7).

Over the study period (2010-2016), according to the mean and median values, the FS_beg_n corresponded respectively to 17 and 15 mm, while the 75% coincided with 20 mm (Table III.5.B.l.7).

Considering the intra-annual variability, the shortest FS ranged from 4 mm to 8 mm (in 2013), while the longest FS spanned from 25 mm (in 2012 and 2016) to 80 mm (in 2011) (Table III.5.B.l.7).

Considering the anomalies of the 75% quartiles, the longest FS_beg_n was recorded in 2011 and 2013 (+ 8 mm), while the shortest FS_beg_n in 2016 (-5 mm) (Fig. III.5.B.l.7), although without any statistically significant differences, as tested by t-test (p>0.05). Moreover, concerning the maximum values, in 2011 it was recorded an anomalous FS_beg_n up to 80 mm.

Table III.5.B.l.7 Non-parametric statistics of first shoot length (FS_beg_n) for graminoids computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	37	17	4	10	12	25	50	10.9
2011	38	22	5	10	15	28	80	15.4
2012	38	13	6	10	12	18	25	4.9
2013	38	22	8	11	20	28	60	12.8
2014	37	18	4	10	16	23	65	12.0
2015	37	14	4	10	14	16	40	7.9
2016	37	11	3	8	10	15	25	5.6
2010-2016	262	17	3	10	15	20	80	11.2

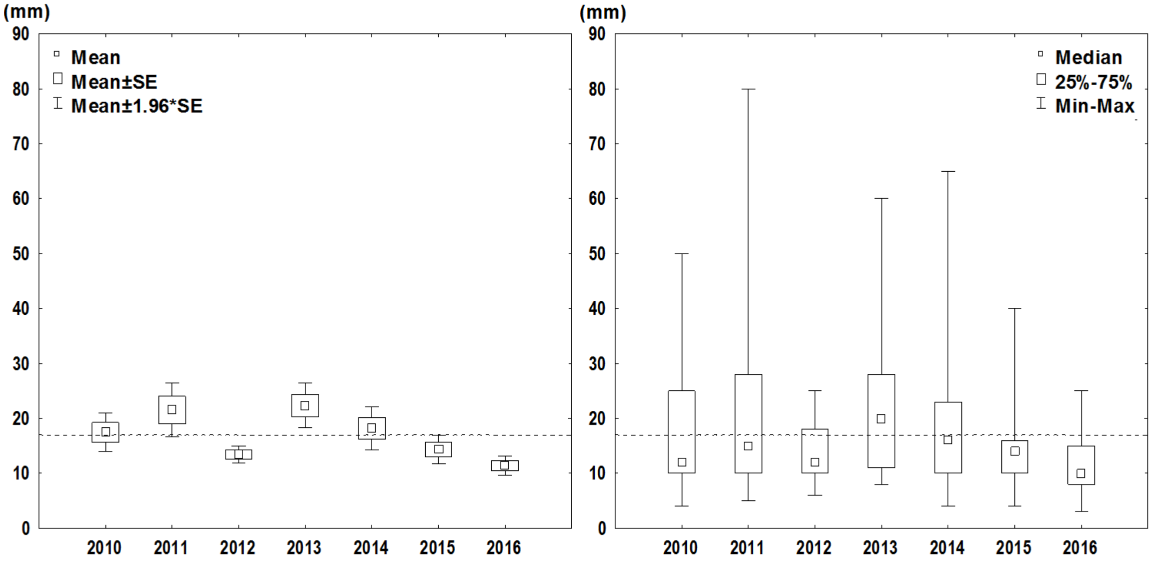

Figure III.5.B.l.7. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot length (FS_beg_n) of graminoids from 2010 to 2016. The dotted black line represents the mean value for the whole period.

Considering all the study period (2010-2016) we did not find any statistically significant trend of the FS_beg_n with time for graminoids, as tested by linear regression ($p>0.05$).

As tested by linear regression at the inter-annual level, the SM explained a very small amount of the FS_beg_n variance ($\beta=0.3$, $R^2=0.12$, $p<0.01$), indicating a lack of relation with the timing of SM.

Comparison of trends among growth forms

Deciduous dwarf shrubs, deciduous shrubs and evergreen dwarf shrubs showed the shortest FS_beg_n respect the other growth forms (Fig. III.5.B.l.8). Indeed, according to the 75% quartiles anomalies over all the dataset, the FS for these growth forms was shorter respectively of -8, -10 and -12 mm, while graminoids showed the longest FS_beg_n (+4 mm).

Graminoids were the growth form most sensitive at the FS stage, showing an advance of FS over the study period (see chap. III.5.B.b).
Comparing the FS_beg_n with the pattern of FS, we could therefore hypothesize that the growth forms with higher values of FS_beg_n (i.e. longer shoot after SM and thus potentially growing under thin snow cover) such as graminoids, are the most responsive and potentially adaptable to earlier SM. Indeed, graminoids were the only one growth form advancing their FS timing in response to earlier SM (see chap. III.5.B.b)

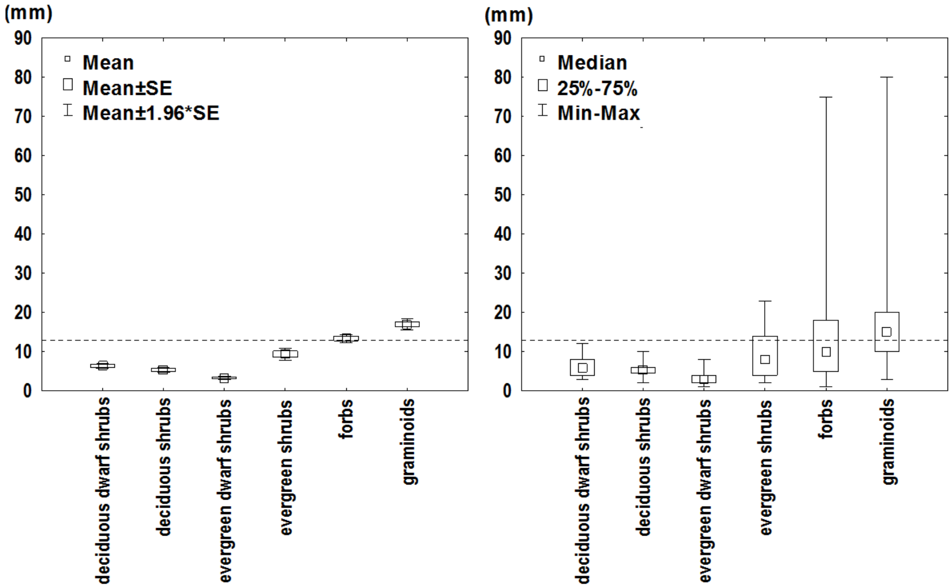

Figure III.5.B.l.8. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoot length (FS_beg_n) between different growth forms over the period 2010-2016. The dotted black line represents the mean value for the whole period.

For all the growth forms, we did not found any variance of FS_beg_n explained by SM, meaning that this performance at the beginning of the new season was influenced by other factors, such as climate but also nutrient limitation.

III.5.B.m. *Patterns of maximum plant height (Hmax)*

Analogously to the other phenophases, our analyses have been carried out following two steps: I) inter-specific level; II) intra-growth forms level.

Inter-specific level

Overall the study period (2010-2016) at the inter-specific level, Hmax (Fig. III.5.B.m.1) exhibited statistically significant differences, as tested by one-way ANOVA (F=6, $p<0.01$) (Fig. III.5.B.m.2).

Figure III.5.B.m.1. Example of plant height sampling.

During the entire monitoring period (2010-2016) (Table III.5.B.m.1), the mean and median values of Hmax coincided respectively to 74 and 50 mm, and its 75% quartile coincided with 90 mm.

Analyzing each year separately (Table III.5.B.m.1), the lowest plant height ranged between 7 mm (in 2016) and 15 mm (in 2013), while the maximum plant height spanned from 370 mm (in 2010) to 420 mm (in 2016).

Considering the 75% quartiles anomalies, the highest plant height was measured in 2013 (+25 mm), while the lowest in 2016 (-40 mm). The year 2016 was the only one identified as "extreme", as tested by t-test (p=0.04).

Table III.5.B.m.1. Non-parametric statistics of plant height (Hmax) computed for each single year, as well as for the entire monitoring period (2010-2016), at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	133	73	10	35	50	90	370	65.7
2011	133	77	14	32	55	90	390	70.7
2012	133	76	14	30	60	90	400	71.3
2013	132	100	15	59	89	115	403	70.8
2014	130	63	10	25	45	70	405	70.7
2015	130	79	10	35	56	100	410	74.2
2016	131	53	7	20	40	50	420	70.0
20010-2016	922	74	6	30	50	90	420	71.6

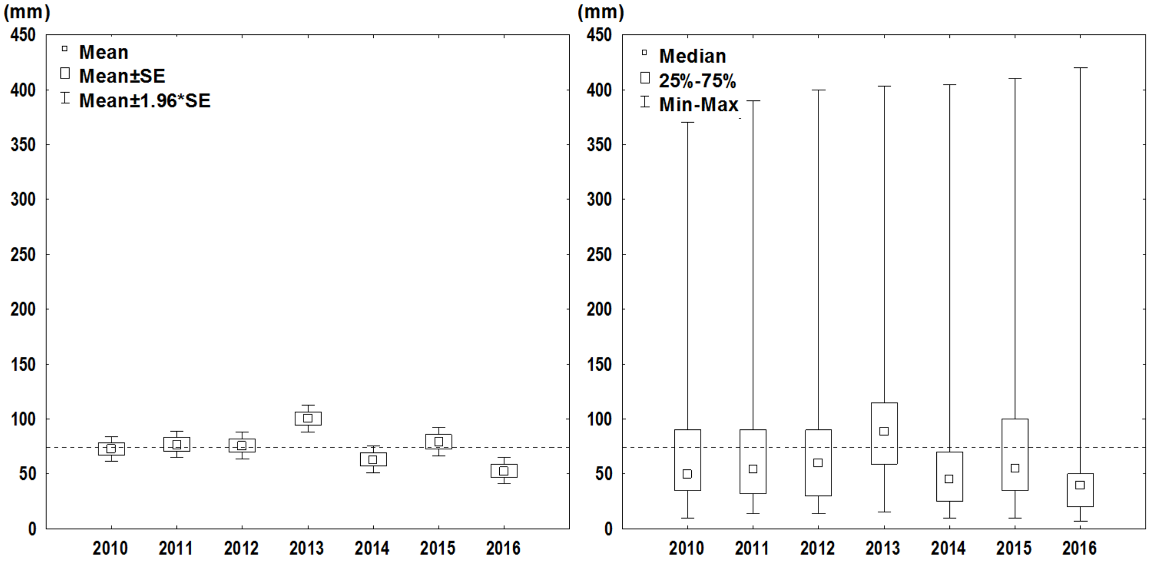

Figure III.5.B.m.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) from 2010 to 2016 at the inter-specific level. The dotted black line represents the mean value for the whole period.

Investigating thus only the "normal" years (2010-2015), we did not find statistically significant trends of Hmax with time. However, we observed a statistically significant increase of the maximum plant height, as tested by linear regression (β=7.1, R^2=0.83, p=0.01) (Fig. III.5.B.m.3).

We tested by linear regression at the inter-annual and inter-specific level whether SM could influence the Hmax. Our analyses indicated a lack of relation with SM timing (β=-1.0, R^2=0.05, p<0.01).

Similarly we tested by linear regression at inter-annual and inter-specific level whether FS_beg_n could affect the Hmax. Also in this case we did not find a relation with the first shoots length ($\beta=1.6$, $R^2=0.07$, $p<0.01$).

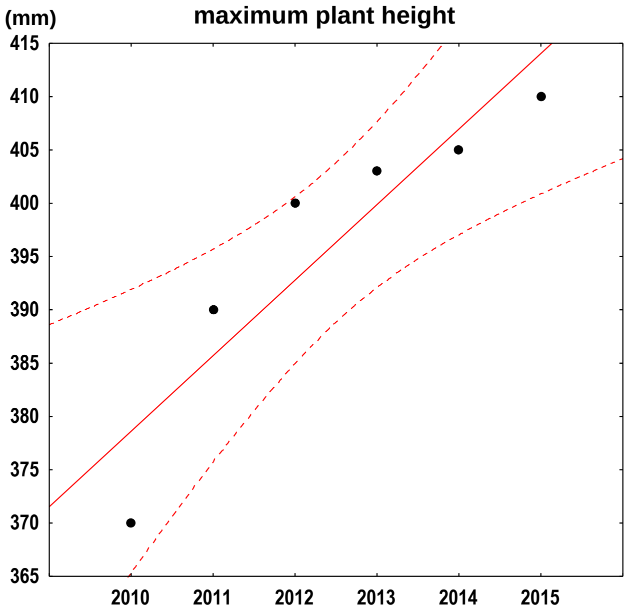

Figure III.5.B.m2. Trend with time of the maximum plant height, as tested by linear regression at the inter-specific level ($\beta=7.1$, $R^2=0.83$, $p=0.01$).

Intra-growth forms level

Deciduous dwarf shrubs

As tested by one-way ANOVA, overall the study period (2010-2016) the Hmax of deciduous dwarf shrubs (i.e. *Salix herbacea*) did not exhibit statistically significant differences among years ($p>0.05$) (Fig III.5.B.m.3).

Over the study period (2010-2016), mean and median values were almost coincident (respectively 27 and 25 mm) while the 75% quartile coincided with 33 mm (Table III.5.B.m.2).

The lowest plant height ranged from 10 mm (in 2016) to 27 mm (in 2013), while the highest plant height spanned from 30 mm (in 2012) to 55 mm (in 2011) (Table III.5.B.m.2).

According to the anomalies of the 75% quartiles over the whole dataset, the lowest Hmax was recorded in 2014 (-7 mm), and the highest in 2011 (+9 mm) (Fig. III.5.B.m.3), although all without statistically significant differences, as tested by t-test ($p>0.05$).

Considering thus the whole period (2010-2016) the analysis of Hmax with time did not reveal any statistically significant trend, as tested by linear regression ($p>0.05$).

Moreover, as tested by linear regression at the inter-annual level we observed a lack of relation with both SM timing and FS_beg_n ($p>0.05$).

Table III.5.B.m.2. Non-parametric statistics of plant height (Hmax) for deciduous dwarf shrubs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	7	29	15	15	25	40	50	12.8
2011	7	31	18	18	30	42	55	14.0
2012	7	23	15	15	25	28	30	6.3
2013	7	34	27	28	33	39	44	6.3
2014	7	23	18	18	22	26	35	6.0
2015	7	27	20	20	25	30	42	7.6
2016	7	21	10	15	15	35	40	11.4
2010-2016	49	27	10	20	25	33	55	10.1

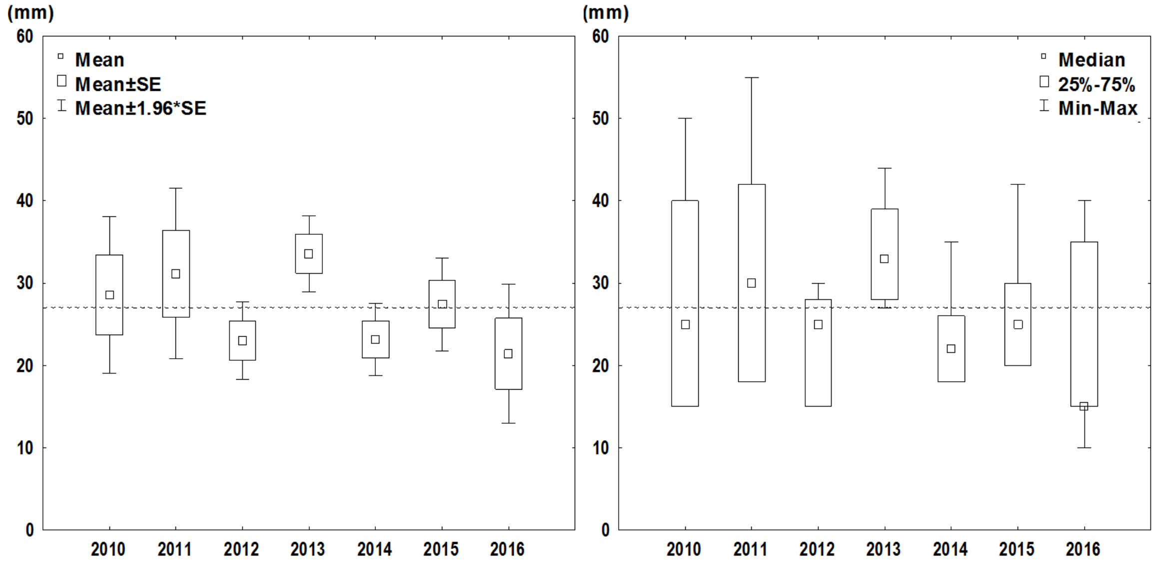

Figure III.5.B.m.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) for deciduous dwarf shrubs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

Deciduous shrubs

As tested by one-way ANOVA, overall the study period (2010-2016) the Hmax of deciduous shrubs (i.e. *Vaccinium uliginosum*) did not exhibit statistically significant differences among years ($p>0.05$) (Fig III.5.B.m.4).

Over the study period (2010-2016), the mean and median values were almost coincident (respectively 60 and 56 mm), while the 75% quartile coincided with 77 mm (Table III.5.B.m.3).

Table III.5.B.m.3. Non-parametric statistics of plant height (Hmax) for deciduous shrubs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	4	55	35	38	55	73	75	20.4
2011	4	57	36	41	53	73	85	21.4
2012	4	61	40	45	58	78	90	21.7
2013	4	79	56	56	73	102	114	28.2
2014	4	51	30	38	48	64	78	20.1
2015	4	56	35	43	55	70	80	18.9
2016	4	61	40	48	58	75	90	21.0
2010-2016	28	60	30	43	56	77	114	21.1

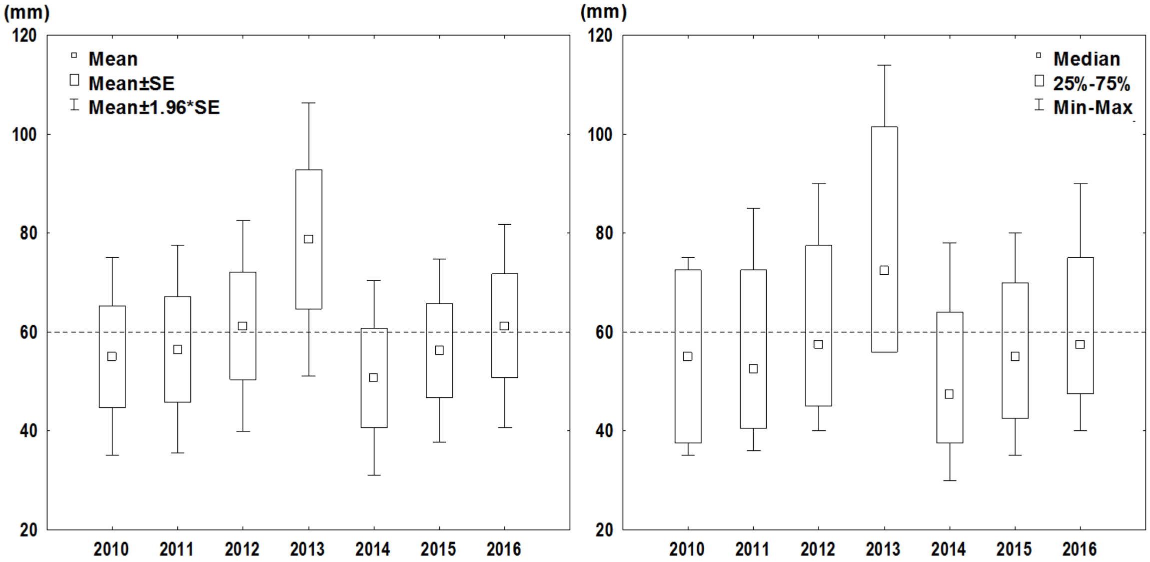

Figure III.5.B.m.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) for deciduous shrubs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

The lowest plant height ranged from 30 mm (in 2014) to 56 mm (in 2013), while the highest spanned from 75 mm (in 2010) to 114 mm (in 2013) (Table III.5.B.m.3).

Analyzing the anomalies of the 75% quartiles, the lowest Hmax was recorded in 2014 (-13 mm) while the highest in 2013 (+25 mm) (Fig. III.5.B.m.4). The 2013 was identified as statistically significant different, as tested by t-test ($p<0.01$).

Considering thus only the “normal” years (excluding 2013 as “extreme” plant height), we did not find any statistically significant trend of Hmax with time, as tested by linear regression ($p>0.05$).

Moreover, as tested by linear regression at the inter-annual level we observed a lack of relation with both SM timing ($\beta=0.9$, $R^2=0.18$, $p=0.03$) and FS_beg_n ($p>0.05$).

Evergreen dwarf shrubs

As tested by one-way ANOVA, overall the study period (2010-2016) the Hmax of evergreen dwarf shrubs (i.e. *Empetrum hermaphroditum* and *Kalmia procumbens*) did not exhibit statistically significant differences among years ($p>0.05$) (Fig. III.5.B.m.5).

Over all the study period (2010-2016), mean and median values were almost coincident (respectively 33 and 30 mm), while the 75% quartile indicated plant height of 45 mm (Table III.5.B.m.4).

The lowest plant height ranged from 15 mm (in 2010 and 2016), while the highest spanned from 45 mm (in 2016) to 65 mm (in 2013) (Table III.5.B.m.4).

Table III.5.B.m.4. Non-parametric statistics of plant height (Hmax) for evergreen dwarf shrubs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev..
2010	9	32	15	20	30	40	55	13.9
2011	9	32	18	25	30	40	55	12.6
2012	9	32	18	20	30	40	60	14.4
2013	9	41	23	30	37	53	65	15.7
2014	9	31	20	22	25	45	50	12.6
2015	9	31	20	20	25	35	56	12.7
2016	9	29	15	25	25	35	45	10.5
2010-2016	63	33	15	22	30	45	65	13.4

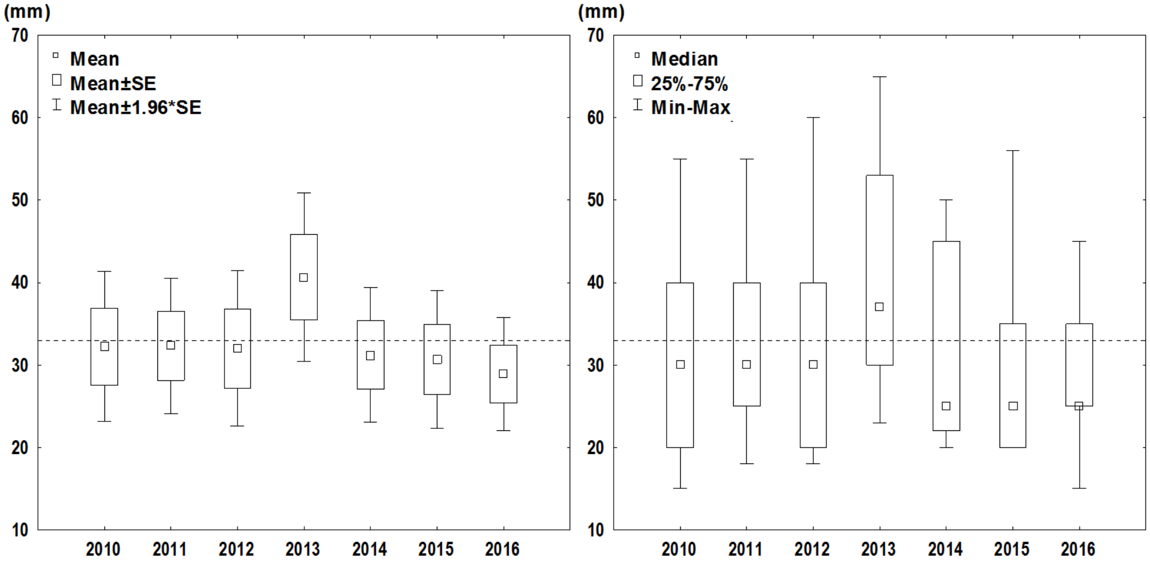

Figure III.5.B.m.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) for evergreen dwarf shrubs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

Analyzing the anomalies of the 75% quartiles, the highest Hmax was recorded in 2013 (+8 mm), while the lowest in 2015 and 2016 (both -10 mm). The 2013 was the only one year identified as statistically significant different, as tested by t-test ($p=0.02$) (Fig. III.5.B.m.5).

Considering only "normal" years (excluding 2013) the evergreen dwarf shrubs showed a statistically significant decrease of the Hmax with time ($\beta=-1.1$, $R^2=0.86$, $p<0.01$) (Fig. III.5.B.m.6).

As tested by linear regression at the inter-annual level, we have not found any statistically significant relation between both SM and FS_beg_n with Hmax ($p>0.05$).

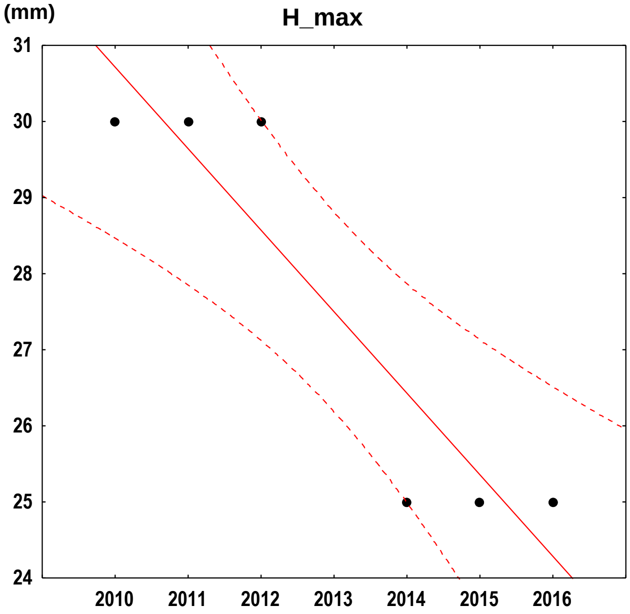

Figure III.5.B.m.6. Trend with time of the plant height, as tested by linear regression for evergreen dwarf shrubs ($\beta=7.1$, $R^2=0.83$, $p=0.01$).

Evergreen shrubs

As tested by one-way ANOVA, overall the study period (2010-2016) the FS length of evergreen shrubs (i.e. *Rhododendron ferrugineum* and *Juniperus communis*) did not exhibit statistically significant differences among years ($p>0.05$) (Fig. III.5.B.m.7).

Over all the study period (2010-2016), according to the mean and median values, the Hmax coincided respectively with 283 and 302 mm, while the 75% corresponded to 358 mm (Table III.5.B.m.5).
The lowest plant height ranged from 85 mm (in 2011) to 110 mm (in 2015), while the highest from 370 mm (in 2010) to 420 mm (in 2016).

Table III.5.B.m.5. Non-parametric statistics of plant height (Hmax) for evergreen shrubs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	8	267	100	198	295	340	370	100.9
2011	8	273	85	213	298	345	390	104.1
2012	8	278	90	209	300	358	400	108.1
2013	8	282	100	215	301	362	403	106.5
2014	8	289	105	223	310	368	405	105.5
2015	8	295	110	230	309	380	410	106.4
2016	8	298	108	230	314	383	420	109.3
2010-2016	56	283	85	220	302	358	420	100.5

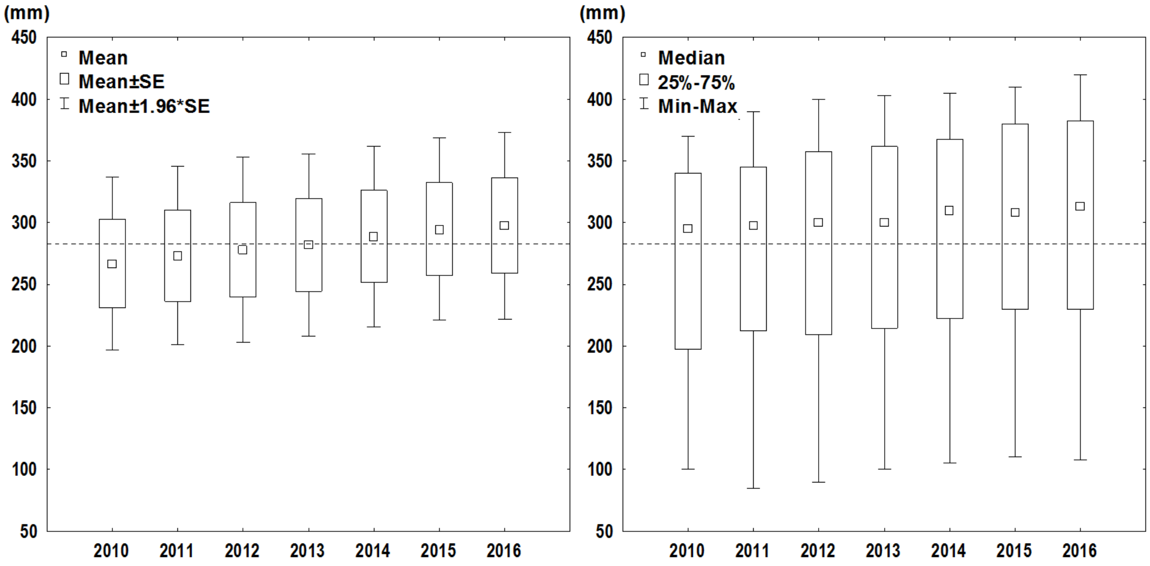

Figure III.5.B.m.7. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) for evergreen shrubs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

Considering the anomalies of the 75% quartiles, the highest Hmax was recorded in 2016 (+25 mm), and the lowest in 2010 (-18 mm) (Fig. III.5.B.m.7), even all without statistically significant differences, according to t-test ($p>0.05$).

The evergreen shrubs showed the highest plant height (see below – comparison among growth forms) and statistically significant different compared to all the others. Therefore, the values of maximum plant height observed at the inter-specific level corresponded to the evergreen shrubs Hmax. Indeed the observed trend of increasing of the maximum plant height was observed for evergreen shrubs. Moreover, considering thus all the study period, we observed a statistically significant increase of the Hmax, as tested by linear regression ($\beta=3.1$, $R^2=0.92$, $p<0.01$) (Fig. III.5.B.m.8).

As tested by linear regression at the inter-annual level, both the SM ($\beta=-3.1$, $R^2=0.09$, $p=0.03$) and the FS_beg_n ($\beta=6.7$, $R^2=0.14$, $p<0.01$) did not explain any proportion of the Hmax variance.

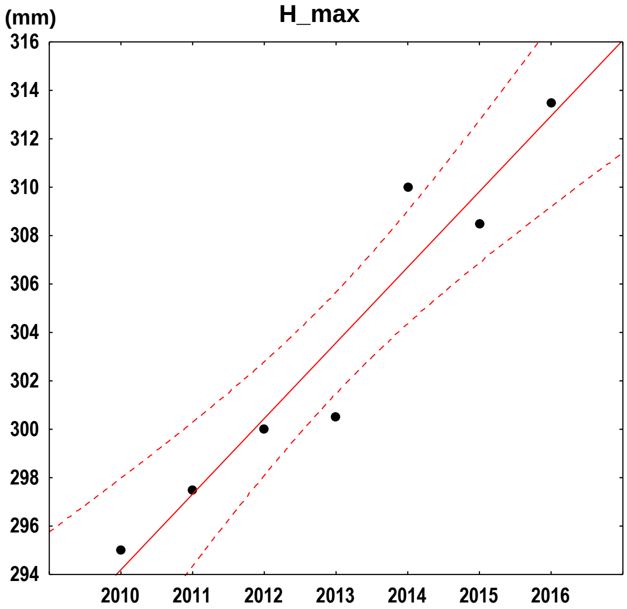

Figure III.5.B.m.8. Trend with time of the plant height, as tested by linear regression for evergreen shrubs (β=7.1, R^2=0.83, p=0.01).

Forbs

Considering all the study period, also forbs exhibited statistically significant differences among years, as tested by one-way ANOVA (F=13, p<0.01) (Fig. III.5.B.m.9).

Table III.5.B.m.6. Non-parametric statistics of plant height (Hmax) of forbs computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	67	54	10	30	45	70	170	33.2
2011	67	58	14	28	40	85	210	41.3
2012	67	56	14	25	50	80	240	39.7
2013	66	82	15	66	82	95	190	36.2
2014	65	41	10	20	32	50	130	27.1
2015	65	64	10	30	45	80	250	47.5
2016	66	32	7	15	35	45	70	17.2
2010-2016	463	55	6	25	45	80	250	38.6

The mean and median values of Hmax over the whole period (2010-2016) coincided respectively to 55 and 45 mm, while the 75% quartile corresponded to 80 mm (Table III.5.B.m.6).

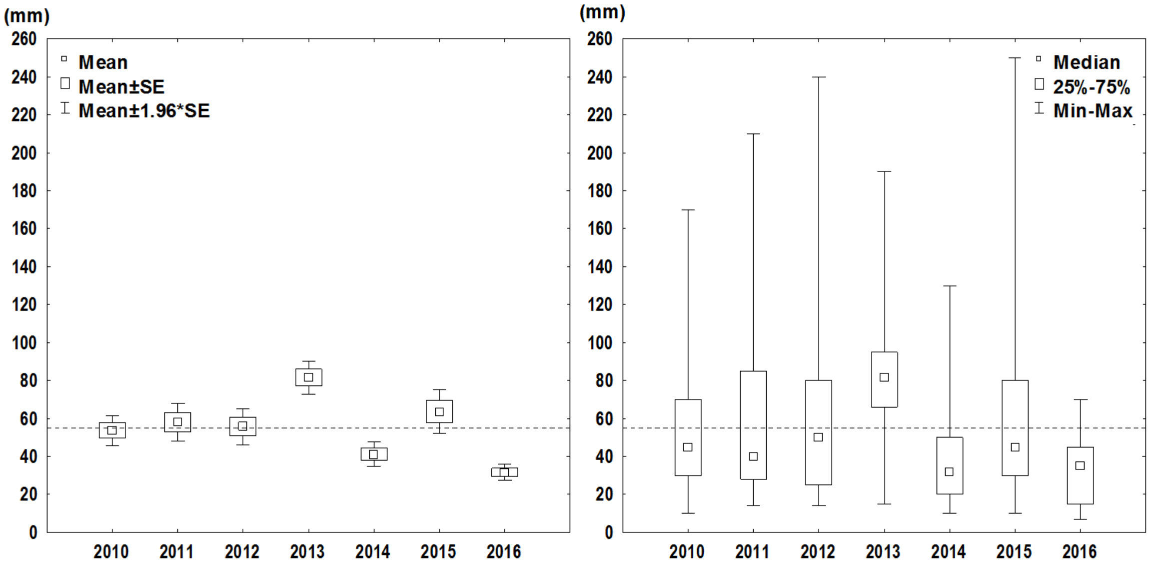

Figure III.5.B.m.9. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) of forbs from 2010 to 2016. The dotted black line represents the mean value for the whole period.

The lowest plant height ranged from 7 mm (in 2016) to 15 mm (in 2013), while the highest spanned from 70 mm (in 2016) to 250 mm (in 2015) (Table III.5.B.m.6).

Comparing the 75% anomalies, forbs showed the highest Hmax in 2015 (+15 mm) and the lowest in 2014 and 2016 (respectively -30 and -35 mm). However, we did not find any statistically significant difference, as tested by t-test (Fig. III.5.B.m.6).
Considering thus all the study period, we did not observe any statistically significant trend with time for the forbs Hmax, as tested by linear regression ($p>0.05$).

As tested by linear regression at the inter-annual level, the SM did not explain any proportion of the Hmax variance ($p>0.05$), while we found a statistically significant relation between Hmax and FS_beg_n, even if proportion of variance of Hmax explained was low ($\beta=1.8$, $R^2=0.31$, $p<0.01$).

Graminoids

As tested by one-way ANOVA, overall the study period (2010-2016) the Hmax of graminoids exhibited statistically significant differences among years ($F=10$, $p<0.01$) (Fig. III.5.B.m.10).

Over the study period (2010-2016), according to the mean and median values, the Hmax corresponded respectively to 85 and 75 mm, while the 75% coincided with 100 mm (Table III.5.B.m.7).

Considering the intra-annual variability, the lowest plant height ranged from 15 mm (in 2016) to 40 mm (in 2010 and 2012), while the highest spanned from 100 mm (in 2016) to 320 mm (in 2013) (Table III.5.B.m.7).

Table III.5.B.m.7 Non-parametric statistics of plant height (Hmax) for graminoids computed for each single year, as well as for the entire monitoring period (2010-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
2010	38	85	40	55	78	100	240	40.6
2011	38	90	31	60	81	90	280	50.9
2012	38	90	40	65	80	100	300	47.1
2013	38	123	38	90	110	145	320	55.9
2014	37	70	35	45	56	80	220	39.4
2015	37	84	35	55	80	100	200	38.3
2016	37	49	15	40	50	60	100	16.6
2010-2016	263	85	15	50	75	100	320	47.3

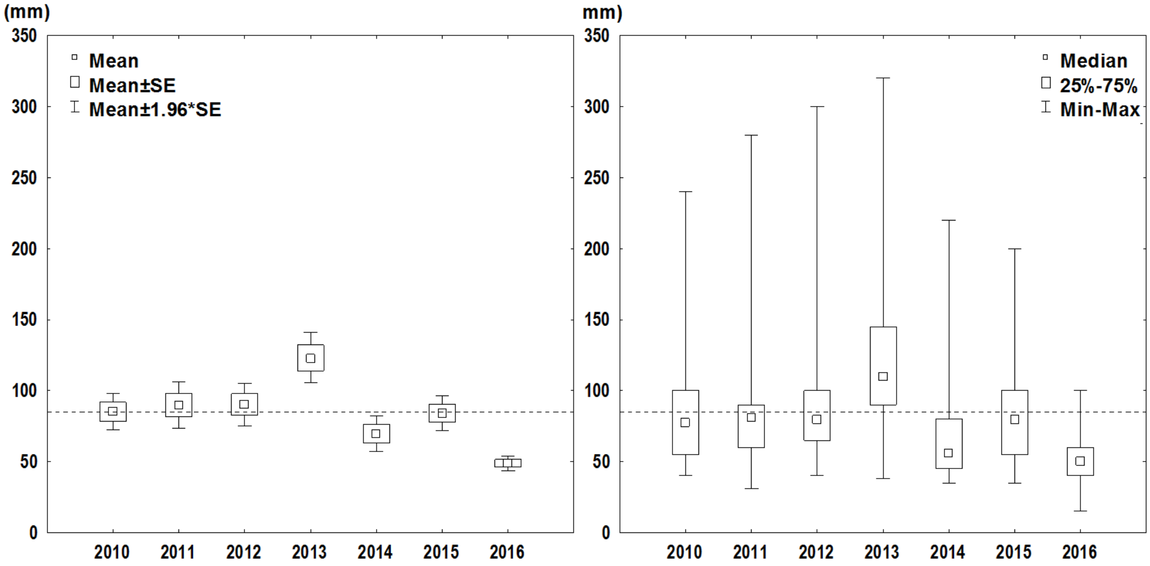

Figure III.5.B.m.10. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) of graminoids from 2010 to 2016. The dotted black line represents the mean value for the whole period.

According to the anomalies of the 75% quartiles, the highest Hmax was recorded in 2013 (+ 45 mm), while the lowest in 2016 (-40 mm) (Fig. III.5.B.m.10). The year 2013 was identified as statistically significant different, as tested by t-test ($p=0.02$).

We did not find any statistically significant trend of the Hmax with time for graminoids, as tested by linear regression ($p>0.05$) over the “normal” years (excluding 2013).
As tested by linear regression at the inter-annual level, the SM ($\beta=-0.6$, $R^2=0.04$, $p<0.01$) and the FS_beg_n ($\beta=1.5$, $R^2=0.13$, $p<0.01$) explained a very small amount of the Hmax variance.

Comparison of trends among growth forms

As tested by one-way ANOVA on the whole dataset, we found high variability among the selected growth forms ($F=282$, $p<0.01$) (Fig. III.5.B.m.11).

As could be expected, the evergreen shrubs showed the highest Hmax (Fig. III.5.B.m.11), that was identified as statistically significant, as tested by t-test (p<0.01).

Since we observed an increasing trend of Hmax only for evergreen shrubs, we could hypothesize that they were the most competitive growth forms in terms of biomass production. Our findings thus confirm results from close sites from Italian Alps (e.g. Cannone et al., 2007) where an increase of shrublands was observed in response to climate warming, since the 1950s.

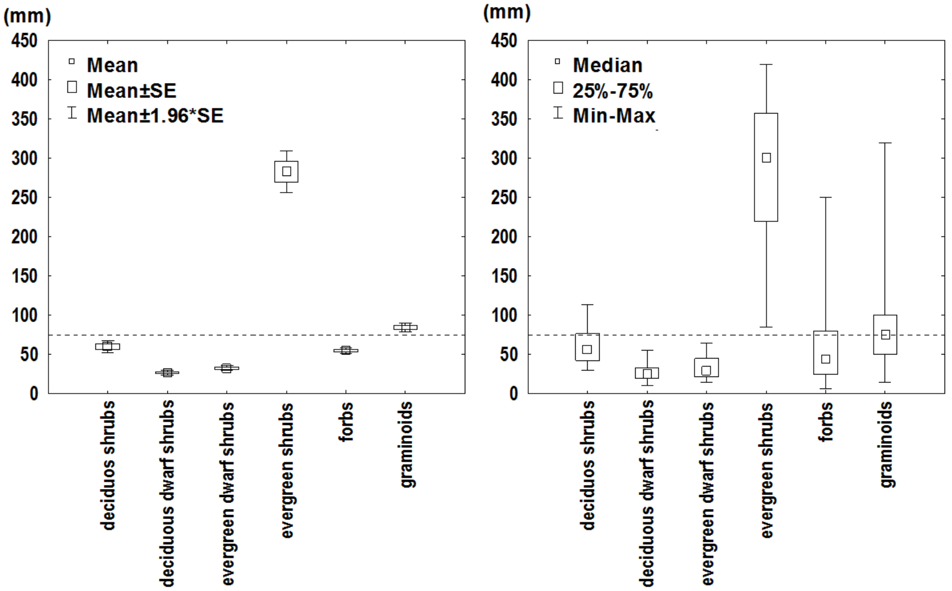

Figure III.5.B.m.11. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) between different growth forms over the period 2010-2016. The dotted black line represents the mean value for the whole period.

However, for all the growth forms, we did not found any variance of Hmax explained by SM, indicating a lack of relation with SM timing and Hmax. Therefore, we could hypothesize that other factors (climate or nutrients) regulate the seasonal development of alpine plants, in terms of biomass production.

III.5.C. Ground surface temperature monitoring

III.5.C.a. *Spatial distribution and temporal evolution of MAGST*

Our analyses have been carried out following two steps: I) inter-site and II) intra-surface types level.

Inter-site level

Overall the study period (2009-2016), the mean annual ground surface temperature (MAGST) showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=3, p<0.01) (Fig. III.5.C.a.1).

The MAGST over all the study period at the inter-site level coincided with 2.4 °C (Table III.5.C.a.1).

Table III.5.C.a.1. Non-parametric statistics of mean annual ground surface temperature (MAGST) computed for each single year, as well as for the entire monitoring period (2009-2016), at the inter-site level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	St.Dev.
2009	3	2.8	1.8	1.8	2.9	3.8	3.8	1.0
2010	11	2.1	0.2	1.2	2.4	2.9	3.2	1.0
2011	11	2.9	1.3	2.0	3.4	3.7	4.0	0.9
2012	13	2.5	0.9	2.0	2.8	3.1	3.6	0.9
2013	12	2.3	1.2	1.6	2.3	3.0	3.5	0.8
2014	13	2.0	0.6	1.5	1.9	2.8	3.1	0.8
2015	13	3.1	1.9	2.4	3.1	4.0	4.2	0.8
2016	13	1.7	0.4	1.3	1.8	2.3	2.8	0.7
2009-2016	89	2.4	0.2	1.7	2.4	3.1	4.2	0.9

The minimum MAGST ranged from 0.2 °C (in 2010) to 1.8 °C (in 2009), while the maximum MAGST ranged from 2.8 °C (in 2016) to 4.2 °C (in 2015) (Table III.5.C.a.1).

Considering the anomalies respect the mean of all the study period, the warmest MAGST was recorded in 2015 (+0.7 °C) while the coldest MAGST occurred in 2016 (-0.7 °C) (Fig. III.5.C.a.1).

As tested by t-test at the inter-sites level we did not observe any year with statistically significant differences (p>0.05).

Analyzing thus all the dataset (2009-2016), we did not identify any statistically significant trend with time, as tested by linear regression (p>0.05).

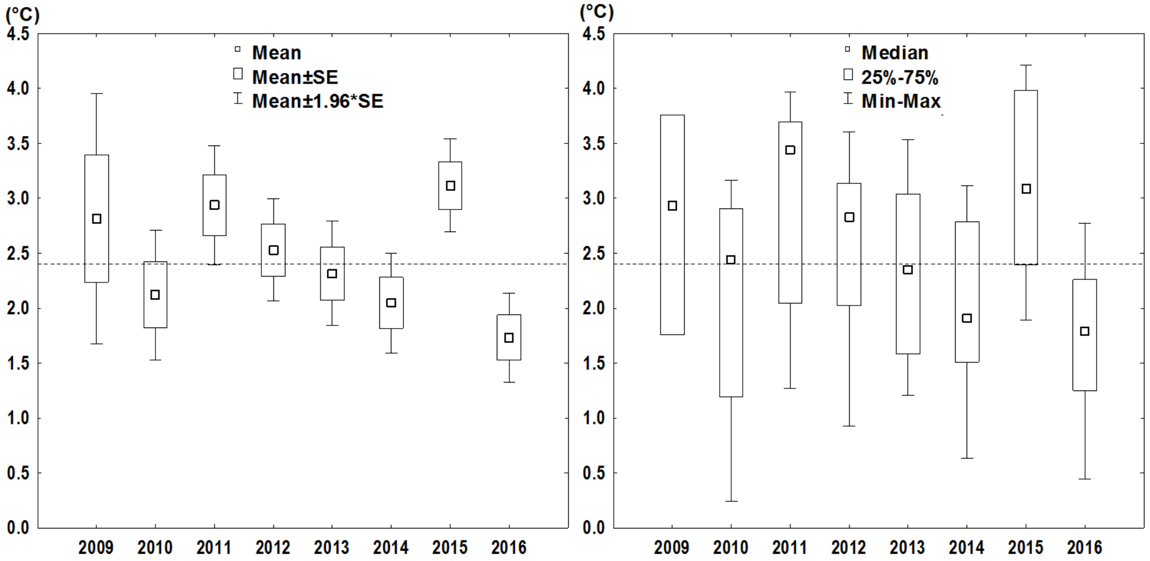

Figure III.5.C.a.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of mean annual ground surface temperature (MAGST) from 2009 to 2016, at inter-sites level. The dotted black line represents the mean value for the whole period.

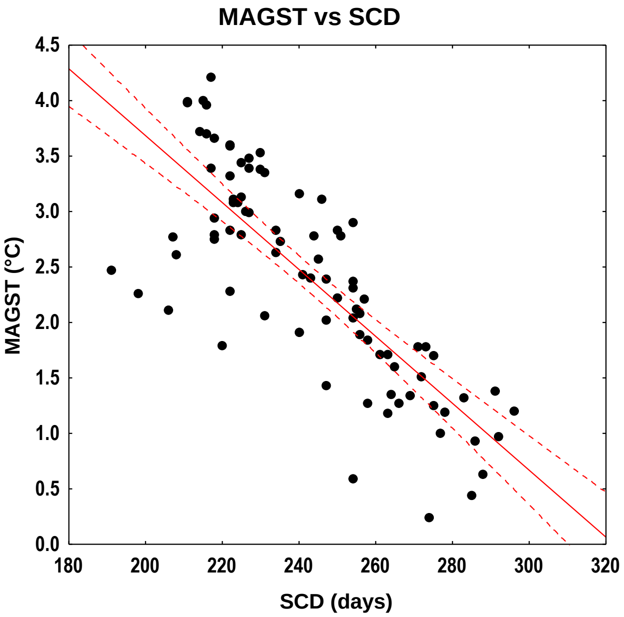

Figure III.5.C.a.2. Relation between MAGST and SCD as tested by linear regression at the inter-sites level (β=-0.03, R^2=0.63, $p<0.01$).

As tested by linear regression at the inter-sites, the MAGST displayed a statistically significant relation with the snow cover duration (SCD) computed from the daily GST (see methods) (β=-0.03, R^2=0.63, $p<0.01$) (Fig. III.5.C.a.2).

Intra-surface types level

According to the observed inter-annual and intra-annual evolution of MAGST for each surface type, we could divide the patterns of MAGST in two subgroups.

The first group involves the evergreen shrubs (both *Kalmia procumbens* and *Rhododendron ferrugineum*): they showed an important cooling of MAGST only during the last year (2016), with a cooling of -0.8 °C in *K.procumbens* while *R.ferrugineum* showed an even greater value (-0.9 °C see Fig. III.5.C.a.3).

However, as tested by t-test, only the *R.ferrugineum* cover displayed a statistically significant cooling in 2016 (p=0.04).

Tested by linear regression we did not observe any MAGST trend with time for both *R.ferrugineum* (only "normal" years) and *K.procumbens* (all years).

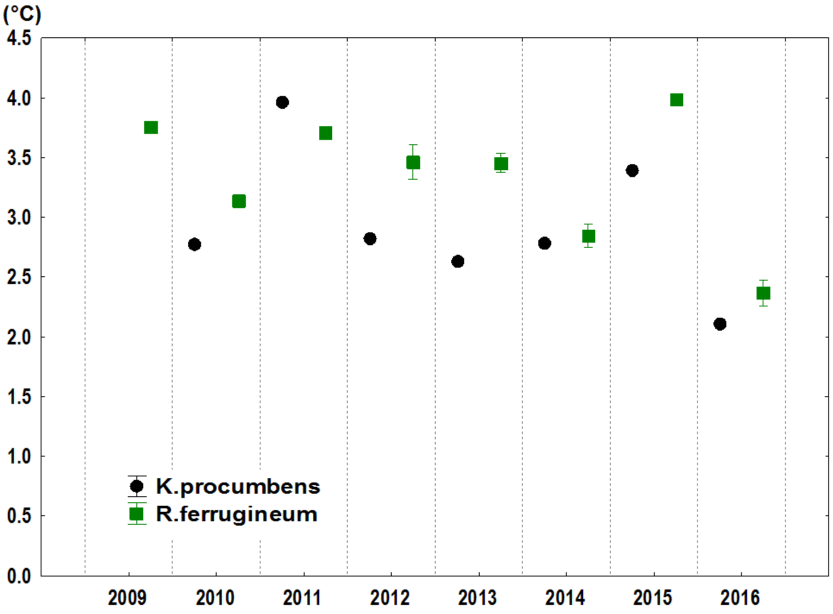

Figure III.5.C.a.3. MAGST (mean, minimum and maximum) of *Kalmia procumbens* and *Rhododendron ferrugineum* from 2009 to 2016.

On the contrary, all the other surface types showed a more variable behavior with several years of low temperature (2010, 2013, 2014 and 2016) alternated to higher values in the other years and, with little differences according to the surface types (Fig. III.5.C.a.4).

For all these surface types the 2015 showed the warmest MAGST, but only for *C.uniflorum* was observed a statistically significant warming, as tested by t-test (p=0.02).

Tested by linear regression for each surface type (excluding the "extreme" 2015 for *C.uniflorum*), we did not find any statistically significant trend of MAGST with time ($p>0.05$).

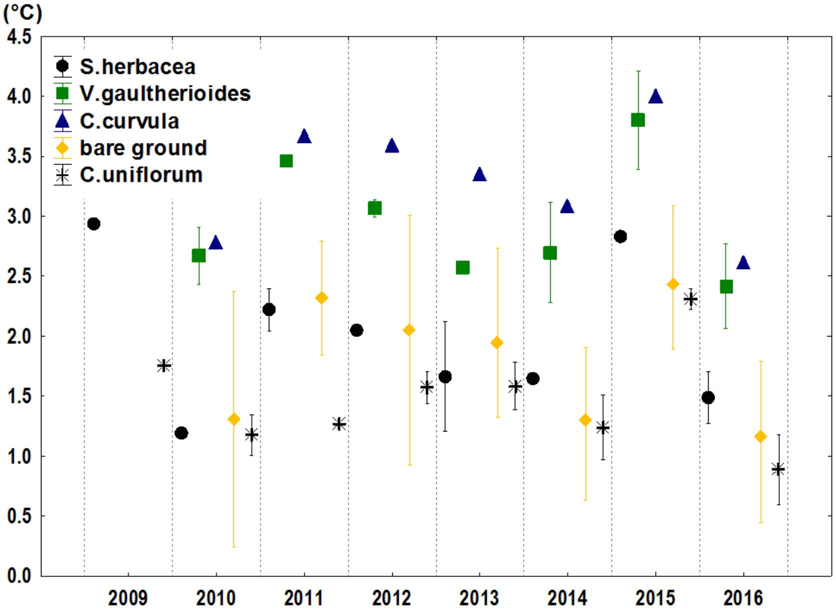

Figure III.5.C.a.4 MAGST (mean, minimum and maximum) of *Salix herbacea, Vaccinium uliginosum, Carex curvula*, bare ground and *Cerastium uniflorum* from 2009 to 2016.

Comparison of trends among surface types

As tested by one-way ANOVA, we observed statistically significant differences among the selected surface types ($F=20$, $p<0.01$) (Fig. III.5.C.a.5), thus indicating that the variability of the MAGST could be a result of the different coverage types.

Considering all our dataset (2009-2016) the MAGST was warmer for *Rhododendron ferrugineum* and *Carex curvula* (in both cases 3.3 °C). Also *Kalmia procumbens* and *Vaccinium uliginosum* showed warm temperature (respectively 2.9°C and 3.0°C) (Fig. III.5.C.a.5). Unexpectedly, the coldest MAGST was found for *Cerastium uniflorum* (1.5°C), which was few decimals colder of bare ground (1.8°C) and *Salix.herbacea* (2.0°C).

Comparing the maximum MAGST for each surface type over all the dataset (2009-2016), it spanned from 4.2°C (with *V.uiliginosum*) to 2.4°C (with *C.uniflorum*), while considering the minimum MAGST, it ranged from 0.2°C (bare ground) to 2.6°C (*C.curvula*) (Fig. III.5.C.a.5).

Considering the whole range exhibited by the MAGST for the different surface types (Fig. III.5.C.a.5), the largest variability was observed for bare ground surface types that ranged from 0.2

to 3.1 °C, while the *C.curvula* exhibited the lowest variability of MAGST, ranging from 2.6 to 4 °C.

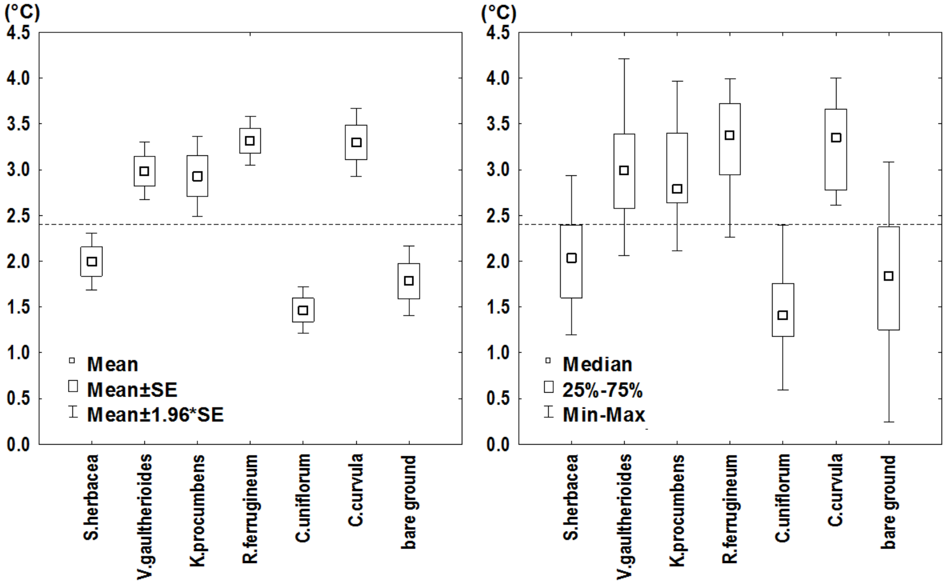

Figure III.5.C.a.5. Non-parametric statistics of mean annual ground surface temperature (MAGST) computed for each single surface type on the entire monitoring period (2009-2016).

It was relevant the “extreme” cold MAGST in 2016 that was recorded only for *R.ferrugineum* and *K.procumbens*, most likely because of the low temperature recorded during winter 2016 (see next chap. III.5.C.b).

On the contrary, in 2015 a warmer summer occurred (see chap III.5.C.d). This influenced the MAGST for almost all the surface types (Fig. III.5.C.a.3 and Fig. III.5.C.a.4), even if *C.uniflorum* was the only one surface type that exhibited an “extreme” warming in 2015, as tested by t-test (p=0.02), which was thus attributable to the warmer temperatures occurred in summer 2015 (see chap. III.5.C.d).

In addition to the previous classification of MAGST among surface types (see Fig III.5.C.a.3 and Fig. III.5.C.a.4), we could also divide our surface types, according to their patterns respect to the bare ground soils. In this case we have two groups: vegetated soils warmer than bare ground soils (i.e. *V.uliginosum, K.procumbens, R.ferrugineum* and *S.herbacea*), and vegetated soils cooler or with similar temperature to bare ground soils (i.e. *S.herbacea* and *C.uniflorum*) (Fig. III.5.C.a.5).

In our case, the response of MAGST was more related to the ecology of the selected species rather than to the growth form types. Indeed, shrublands species (*R.ferrugineum* and *V.gaultherioides*), dwarf shrublands (*K.procumbens*) and grasslands (*C.curvula*) showed the highest MAGST, while snowbed (*S.herbacea*) and pioneers (*C.uniflorum*) showed temperature more similar to bare ground (Fig. III.5.C.a.5).

However, the importance of the vegetation structure (thus the growth form types) was also relevant. The warmest vegetated soils (e.g. *R.ferrugineum*) were those showing lower variability of mean daily GST from one day to another, compared to bare ground and *C.uniflorum* (Fig. III.5.C.a.6).

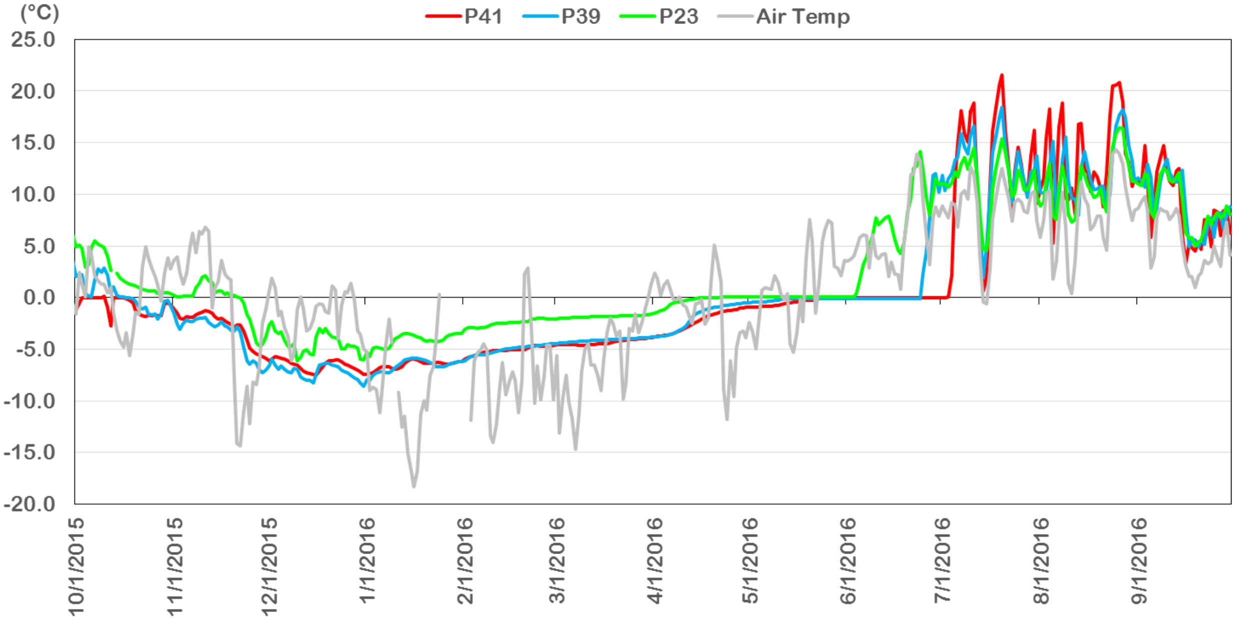

Figure III.5.C.a.6. Comparison of mean daily GST under different surface types: P41 (bare ground), P39 (*Cerastium uniflorum*), P23 (*Rhododendron ferrugineum*) and mean daily air temperature, during the last hydrologic year (10/01/2015 – 09/30/2016).

On the contrary, the coldest vegetated soils (i.e. *C.uniflorum*) showed lower buffering effect respect the air temperature (like the bare ground site), thus showing larger daily GST variability compared to *R.ferrugineum* (Fig.III.5.C.a.6).

If comparing only the temperature during the summer season for example, it was quite clear that vegetated soils were colder respect the bare ground site (Fig. III.5.C.a.6). However, with vegetated soils the snow melted earlier (almost one month when comparing *R.ferrugineum* and bare ground), thus allowing vegetated surface types to accumulate higher temperatures.

The snow cover (and thus the ecology of the selected plots) was strongly related to the surface types (Fig. III.5.C.a.7) and its role was relevant in determining the MAGST (Fig. III.5.C.a.2 and Fig. III.5.C.a.6).

Indeed, as tested by one-way ANOVA the SCD showed statistically significant differences among the selected surface types (F=18, p<0.01) (Fig. III.5.C.a.7).

Over all our dataset, we observed lower MAGST in correspondence of longer SCD (Fig. III.5.C.a.5 and Fig. III.5.C.a.7).

As tested by linear regression, the MAGST displayed statistically significant relation with the duration of snow cover (SCD) only for two of selected surface types: *S.herbacea* ($\beta=-0.03$, $R^2=0.79$, $p<0.01$) and bare ground ($\beta=-0.03$, $R^2=0.69$, $p<0.01$).

The other vegetated soils (*V.uliginosum*, *R.ferrugineum*, *K.procumbens*, *C.uniflorum* and *C.curvula*) did not exhibit statistically significant relation between MAGST and SCD, as tested by linear regression (p>0.05), thus stressing the importance of other factors (biotic or abiotic). For example the shading effect due to the variability of the topography (that could influence the incident radiation received by the soil surface and thus the surface temperatures), or the different quantity and/or quality of organic matter accumulated in the litter and in the A horizon, and the local soil moisture.

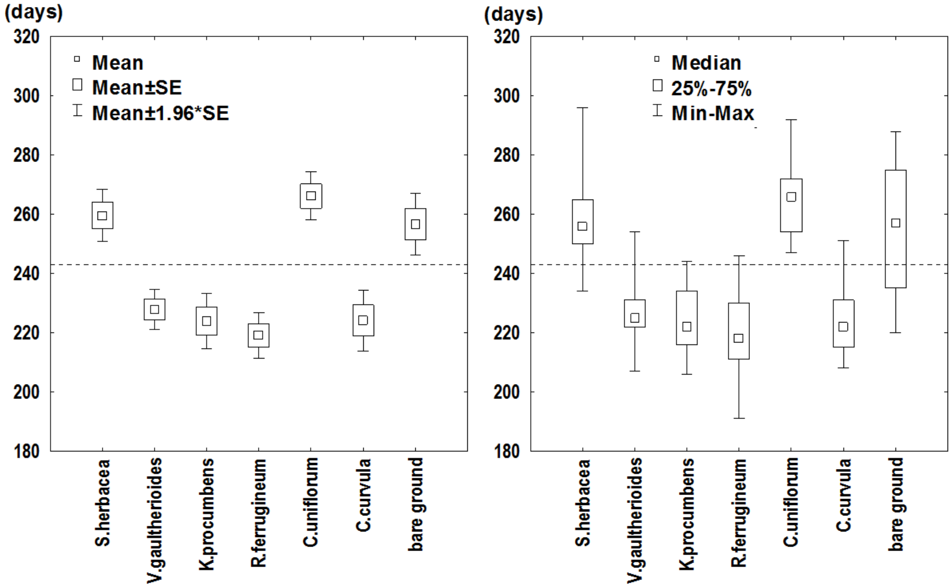

Figure III.5.C.a.7. Non-parametric statistics of snow cover duration (SCD) computed for each surface types on the entire monitoring period (2009-2016).

III.5.C.b. *Bottom temperature of winter snow cover (BTS)*

Our analyses have been carried out following two steps: I) inter-site and II) intra-surface types level.

Inter-site level

Overall the study period (2009-2016), the BTS showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=112, p<0.01) (Fig. V.1.a.1) and exhibited a mean value of -0.8 °C (Table III.5.C.b.1).

Table III.5.C.b.1. Non-parametric statistics of bottom temperature of winter snow cover (BTS) computed for each single year, as well as for the entire monitoring period (2009-2016).

	Valid N	**Mean**	**Minimum**	**Median**	**Maximum**
2009	93	-0.3	-1.2	0.2	0.3
2010	341	-1.0	-3.1	-0.6	0.0
2011	341	-0.3	-1.3	-0.2	0.9
2012	403	-1.0	-4.1	-0.6	0.2
2013	372	-0.6	-2.3	-0.5	0.2
2014	403	-0.5	-2.0	-0.4	0.2
2015	403	-0.6	-2.7	-0.3	0.2
2016	403	-1.8	-4.7	-1.6	-0.2
2009-2016	2759	-0.8	-4.7	-0.6	0.9

The minimum BTS ranged from -4.7 °C (in 2016) to -1.2 °C (in 2009), while the maximum BTS spanned from -0.2°C (in 2016) to 0.9 °C (in 2011) (Table III.5.C.b.1).

At the inter-site level, the mean values of BTS indicated absence of permafrost in the period 2009-2015, but possible permafrost occurrence in the last winter (2016) (Table III.5.C.b.1).

Considering the anomalies respect the mean of all the study period, the warmest BTS was recorded in 2009 and 2011 (+0.5 °C) while the coldest BTS occurred in 2016 (-1.0 °C) (Fig. III.5.C.b.1).

The year 2016 was the only one that showed statistically significant differences, as tested by t-test (p<0.01) and could be identified as "extreme" year of BTS, and was thus removed from further analysis of BTS trend with time.

Analyzing thus only the "normal" years, we did not identify any statistically significant trend with time, as tested by linear regression (p>0.05).

The analysis of the record of snow depth at La Foppa AWS indicated a large delay of the beginning date of snow cover (BD) in 2016, which was the only one identified as statistically significant over the period 2009-2016, as tested by t-test (p<0.01).

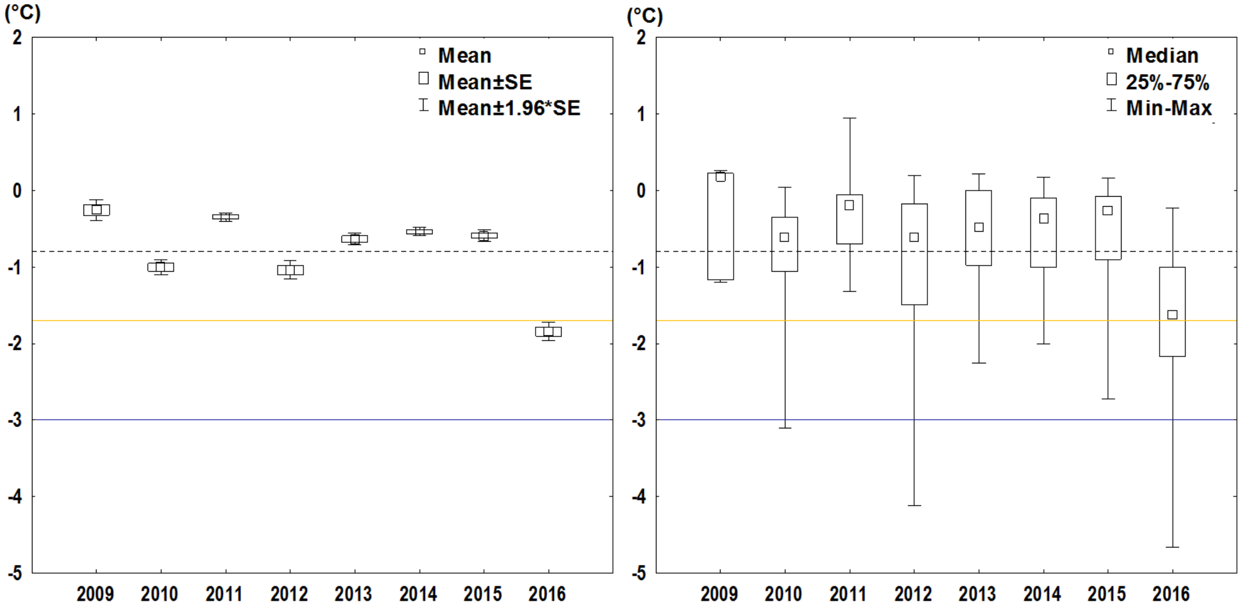

Figure III.5.C.b.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of bottom temperature of winter snow cover (BTS) from 2009 to 2016, at inter-site level. The dotted black line represents the mean value for the whole period, while the orange and blue line represents respectively the possible and probable permafrost occurrence (according to Guglielmin & Tellini, 1994).

However, we did not find any statistically significant trend of BD with time, as tested by linear regression over the "normal" years ($p>0.05$).

As tested by linear regression at the inter-annual level on the whole period (2009-2016), we did not find any statistically significant relation between the BD and BTS (mean values).

At La Foppa AWS we observed also a statistically significant delay of the beginning date of snow cover deeper than 80 cm (BD>80) (+47 days respect the mean of the whole period) (Fig. III.5.C.b.2), as tested by t-test ($p<0.01$).

We did not identify any statistically significant trend with time of the BD>80, as tested by linear regression over the "normal" years ($p>0.05$).

However, as tested by linear regression at the inter-annual level, we found a statistically significant relation between the BD>80 and the BTS (mean values), considering the whole dataset 2009-2016 ($\beta=-0.02$, $R^2=0.95$, $p<0.01$) (Fig. III.5.C.b.2), thus highlighting the strong relation between the snow depth and the BTS values (and thus permafrost occurrence).

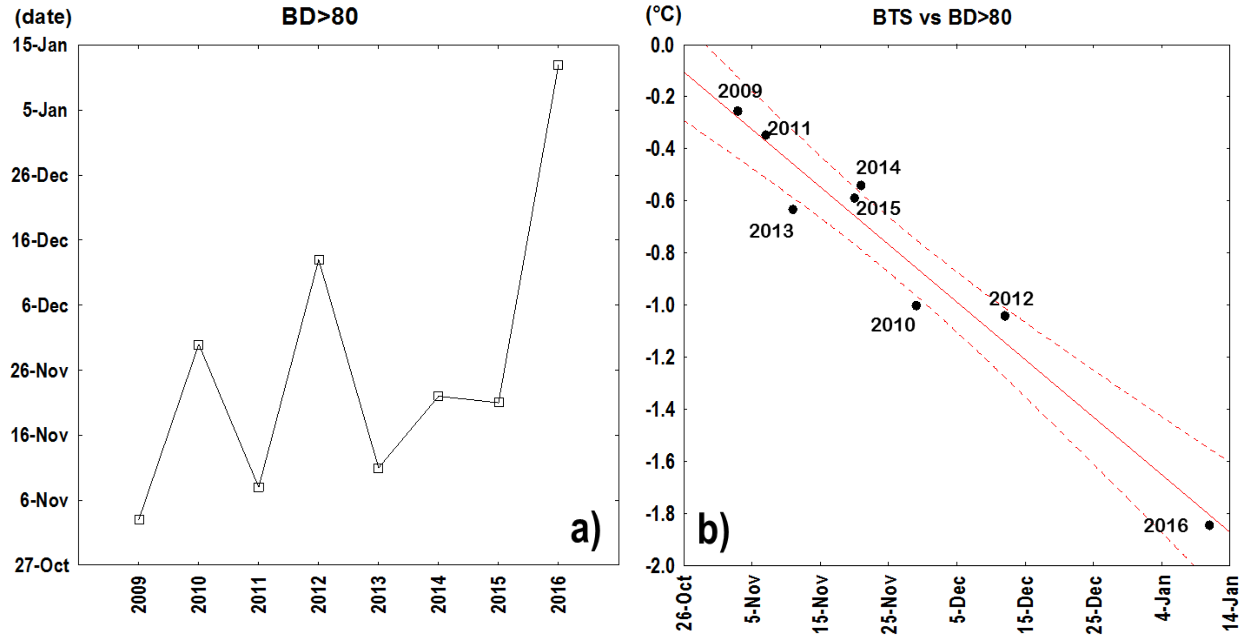

Figure III.5.C.b.2. Trend of the beginning of snow cover deeper than 80 cm (BD>80) recorded at La Foppa AWS over the study period (2009-2016) (a) and its relation with the mean BTS of the Foscagno valley as tested by linear regression (β=-0.02, R^2=0.95, $p<0.01$) (b).

Intra-surface types level

According to the observed inter-annual and intra-annual evolution of BTS for each surface type, we could divide the patterns of BTS in some subgroups.

The extreme coldest BTS of 2016 was recorded among all our plots, even if the entity of the temperature drop in 2016 was different according to the surface types.

For example some vegetated soils (i.e. *V.uliginosum*, *K.procumbens*, *R.ferrugineum* and *C.curvula*) during the “normal” years period (2009-2015) never exhibited values of BTS lower than -1.7 °C, thus indicating absence of permafrost (Fig. III.5.C.b.3).
C.curvula was also the only one vegetated soil where the BTS never dropped below -1.7°C, even in 2016 (Fig. III.5.C.b.3).

According to the mean values of BTS in 2016 a possible permafrost occurrence was found in coincidence of *V.uliginosum* (-2.0°C). Moreover, considering the minimum value of BTS in 2016, a possible permafrost occurrence was observed also in coincidence of *K.procumbens* (-1.8°C) and *R.ferrugineum* (-2.1°C) (Fig. III.5.C.b.3).

On the contrary, other vegetated soils (*C.uniflorum* and *S.herbacea*) displayed over the course of the study period (2009-2016) lowest BTS values not only in 2016, but also in other years (Fig. III.5.C.b.4).

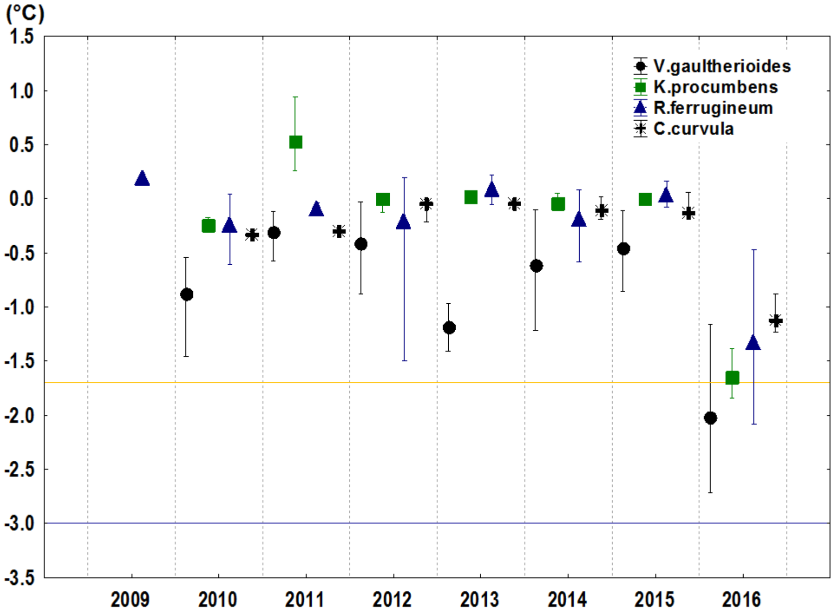

Figure III.5.C.b.3. BTS (mean, minimum and maximum) of *Vaccinium uliginosum*, *Kalmia procumbens*, *Rhododendron ferrugineum* and *Carex curvula* from 2009 to 2016. The orange and blue line represents respectively the possible and probable permafrost occurrence (according to Guglielmin & Tellini, 1994).

According to the mean values of BTS, *C.uniflorum* was the only one vegetated soils that clearly provided evidences of permafrost (Fig. III.5.C.b.4). For this species we observed possible permafrost occurrence in 2010, 2012 (respectively -1.8 and -2.5 °C), and probable permafrost occurrence in 2016 (-3.0°C). In the latter case, the mean values of *S.herbacea* showed absence of permafrost.

However, considering the minimum values of the BTS we found higher probability of permafrost occurrence for these two plant species (Fig. III.5.C.b.4). Indeed, for *C.uniflorum* a possible permafrost occurrence was identifiable in 2010 and 2013 (respectively -2.8 and -2.1 °C), and probable permafrost occurrence in 2012 and 2016 (respectively -4.1 and -4.4 °C). At the same time *S.herbacea* showed probable permafrost in 2012 (-3.1 °C) and possible permafrost occurrence in 2016 (-2.3 °C).

The bare ground soils showed larger variability. When considering the mean values of BTS they showed possible permafrost occurrence only in 2010 and 2016 (in both cases -1.8°C) (Fig. III.5.C.b.4). However, considering the minimum values of BTS they showed possible permafrost occurrence in 2013, 2014 and 2015 (respectively -2.3, -2.0 and -2.7 °C) and probable permafrost occurrence in 2010, 2012 and 2016 (respectively -3.1, -3.7 and -4.7 °C).

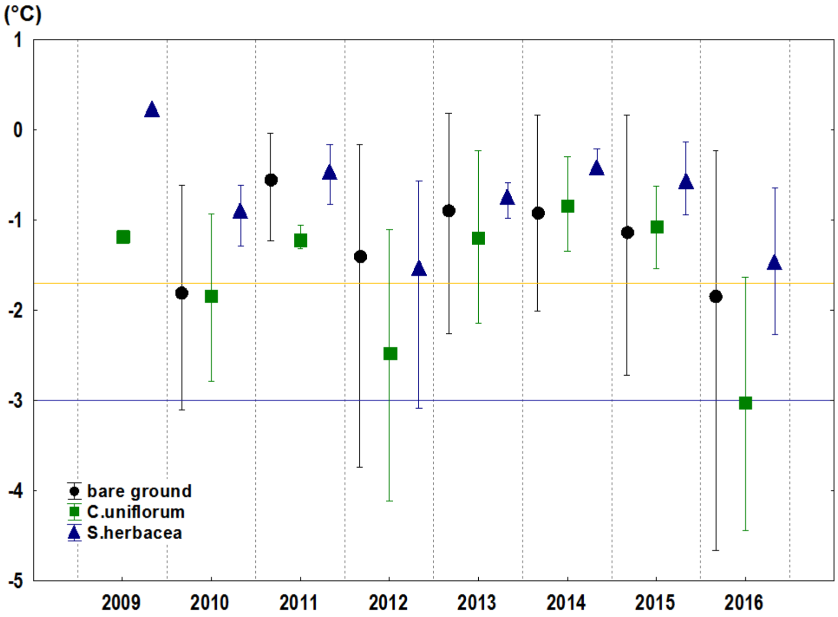

Figure III.5.C.b.4. BTS (mean, minimum and maximum) of bare ground, *Cerastium uniflorum* and *Salix herbacea* from 2009 to 2016. The orange and blue line represents respectively the possible and probable permafrost occurrence (according to Guglielmin & Tellini, 1994).

S.herbacea and bare grounds were the only two surface types that did not exhibit a statistically significant drop of BTS in 2016, as tested by t-test ($p>0.05$). Indeed all the other surface types showed a statistically significant BTS drop in 2016, as tested by t-test ($p<0.05$).

However, as tested by linear regression between BTS (both mean and minimum) and years, we did not find any statistically significant trends with time for all the surface types ($p>0.05$).

Comparison of trends among surface types

We observed different responses according to different surface types, which a large inter-annual variability of BTS (Fig. III.5.C.b.5).

Considering all the study period (2009-2016) the BTS were warmer for evergreen shrubs (*K.procumbens* and *R.ferrugineum*) and for *C.curvula*. Indeed, their BTS was respectively -0.2, -0.2 and -0.3 °C. Unexpectedly, the lowest mean value of BTS was recorded for *C.uniflorum* (-1.7 °C) (Fig. III.5.C.b.5).

When comparing the minimum values of BTS, we observed many cases of possible permafrost occurrence (i.e. *V.uliginosum*, *K.procumbens* and *R.ferrugineum*), while probable permafrost occurrence was identified for *S.herbacea*, *C.uniflorum* and bare ground sites (Fig. III.5.C.b.5).

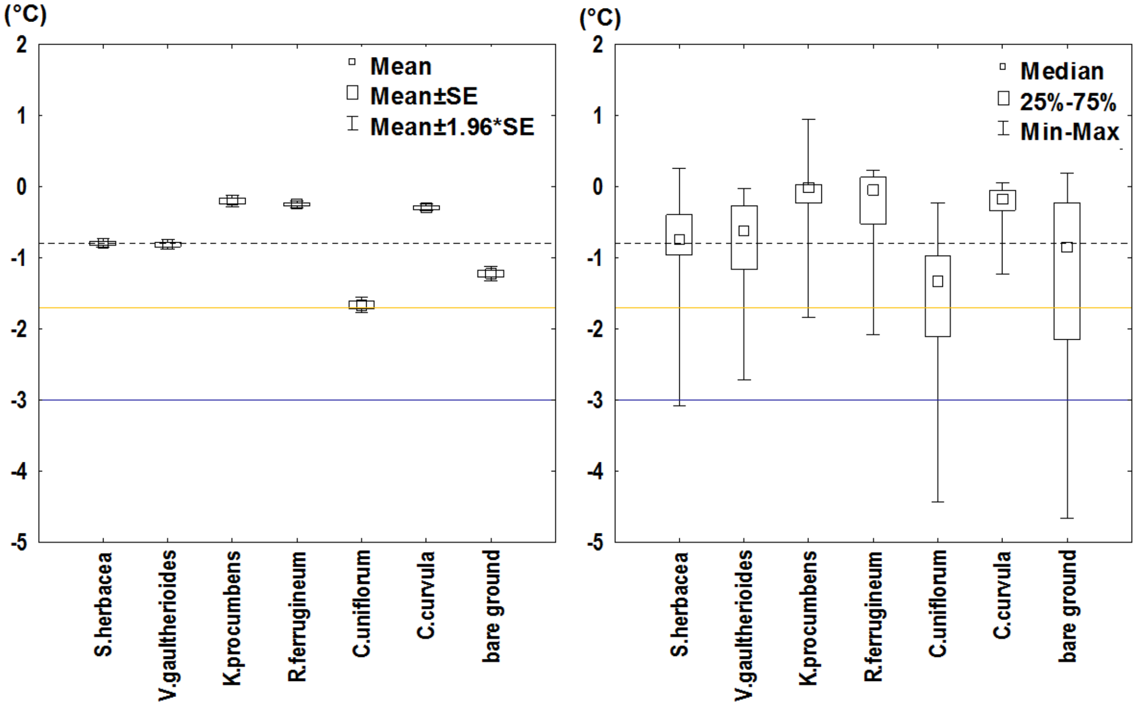

Figure III.5.C.b.5. BTS (mean, minimum and maximum) of the selected surface types over the study period (2009-2016). The orange and blue line represents respectively the possible and probable permafrost occurrence (according to Guglielmin & Tellini, 1994).

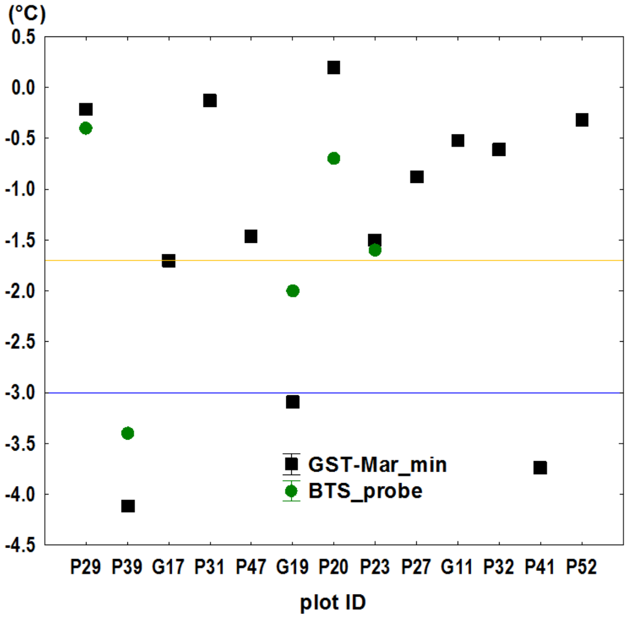

Figure III.5.C.b.6. Example of the comparison of BTS obtained by a field measure in 2012 (BTS probe) and the minimum GST recorded by data loggers. The orange and blue line represents respectively the possible and probable permafrost occurrence (according to Guglielmin & Tellini, 1994).

It was also interesting the comparison of the variability of mean and minimum values of BTS (GST in March) at each site. Indeed, we found large differences when comparing these two parameters, thus stressing the high variability of the GST in March, when the soils are supposed to be insulated by the snow cover.

From a methodological point of view, this could lead in different interpretation of permafrost distribution, when using the normally field BTS method (from probing). Measurement of the bottom temperature of winter snow (BTS) by field probing, have been used as a well-established method during the past years for mapping of mountain permafrost distribution in the Alps (e.g. Haeberli, 1973; Hoelzle, 1992; Guglielmin & Tellini, 1994; Isaksen et al., 2002). Usually, the BTS probing is executed one time per year when the snow cover is higher than 80 cm (normally in mid-March).

Thus, the BTS probing could be correct only if carried out during the period of minimum GST in March, such as plot G19 (Fig. III.5.C.b.6).

III.5.C.c. *Spatial distribution and temporal evolution of TDD*

Our analyses have been carried out following two steps: I) inter-site and II) intra-surface types level.

Inter-site level

Overall the study period (2009-2016), the TDD showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=3, p=0.01) (Fig. III.5.C.c.1).

According to the mean value, over the whole period the TDD coincided with 1027 °CDay (Table III.5.C.c.1).

Table III.5.C.c.1. Non-parametric statistics of thawing degree days (TDD) computed for each single year, as well as for the entire monitoring period (2009-2016), at the inter-sites level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	St.Dev.
2009	3	1024	880	880	907	1284	1284	225.4
2010	11	921	543	648	996	1124	1165	230.2
2011	11	1167	682	870	1348	1405	1426	292.3
2012	13	1139	807	1079	1138	1253	1418	196.2
2013	12	911	471	702	925	1151	1230	272.2
2014	13	869	421	715	840	1061	1240	273.0
2015	13	1150	721	1004	1152	1358	1483	230.5
2016	13	1026	470	907	1082	1165	1371	228.7
2009-2016	89	1027	421	860	1061	1217	1483	263.4

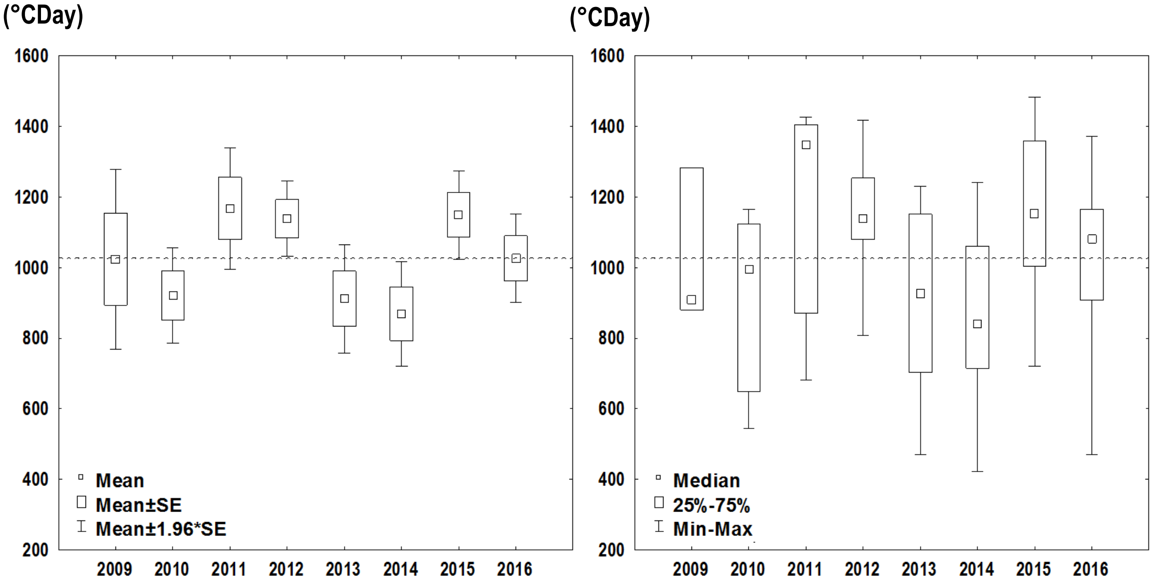

Figure III.5.C.c.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of thawing degree days (TDD) from 2009 to 2016, at inter-sites level. The dotted black line represents the mean value for the whole period.

The minimum TDD ranged from 421 °CDay (in 2014) to 880 °CDay (in 2009), while the maximum TDD spanned from 1165 °CDay (in 2010) to 1483 °CDay (in 2015) (Table III.5.C.c.1).

Considering the anomalies respect the mean of all the study period, the highest TDD was recorded in 2011 (+140 °CDay) while the lowest occurred in 2014 (-158 °CDay) (Fig. III.5.C.c.1). As tested by t-test at the inter-sites level we did not observe any years with statistically significant differences ($p>0.05$).

Analyzing thus all the dataset (2009-2016), we did not identify any statistically significant trend with time, as tested by linear regression ($p>0.05$).

As could be expected, the TDD displayed a statistically significant relation with the length of the snow free (SF; $\beta=8.7$, $R^2=0.68$, $p<0.01$) and with the timing of snow melt (SM; $\beta=-13.0$, $R^2=0.80$, $p<0.01$) (Fig. III.5.C.c.2a)

However the TDD were not related to the beginning date of snow cover (BD), as showed by the low proportion of variance explained when tested by linear regression ($\beta=11.7$, $R^2=0.22$, $p<0.01$) (Fig. III.5.C.c.2b), thus highlighting the most important role of SM.

Moreover, the TDD of the soils at 2 cm showed a statistically significant relation with the TDD of the air (computed for each plot x species x year combination), as tested by linear regression ($\beta=1.4$, $R^2=0.74$, $p<0.01$), even if we found deep differences when testing this relation at the intra-surface types level (see below).

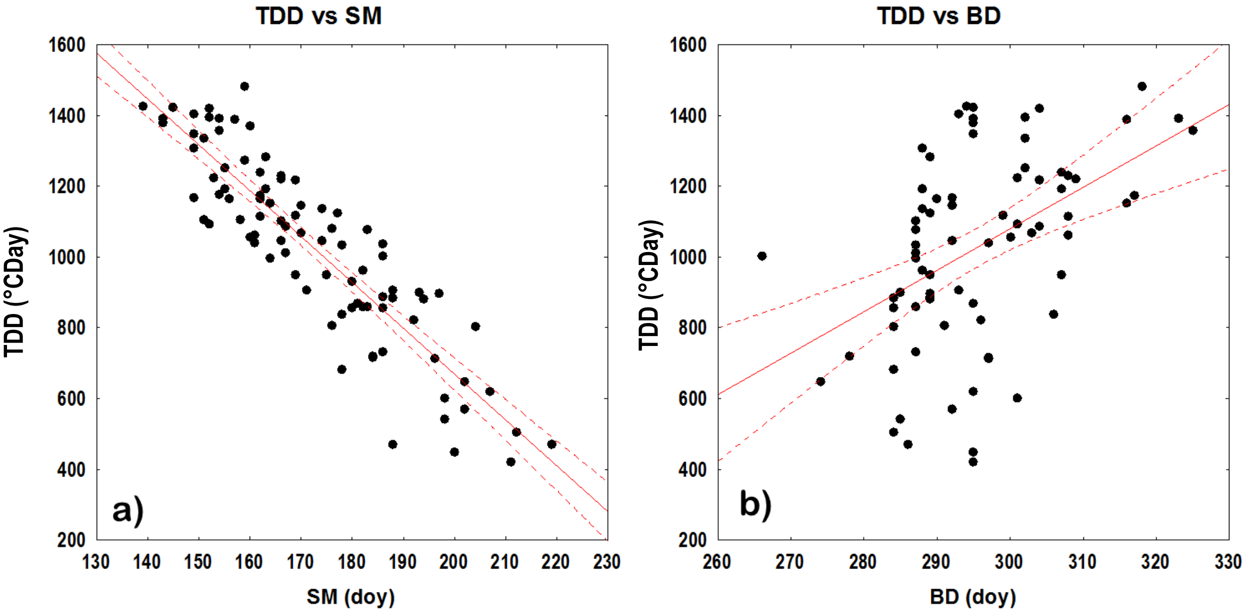

Figure III.5.C.c.2. Relation between a) TDD and SM ($\beta=-13.0$, $R^2=0.80$, $p<0.01$) and b) TDD and BD ($\beta=11.7$, $R^2=0.22$, $p<0.01$) as tested by linear regression at the inter-sites level.

Intra-surface types level

All the surface types exhibited statistically significant inter-annual variability (p<0.01) (Fig. III.5.C.c.3).

As tested by t-test, only the *K.procumbens* displayed a statistically significant and “extreme” warming in 2011 (p=0.01) (Fig. III.5.C.c.3).

Tested by linear regression on all the dataset (apart from *K.procumbens* where we removed the “extreme” 2011) we did not observe any TDD trend with time for all the surface types (p>0.05).

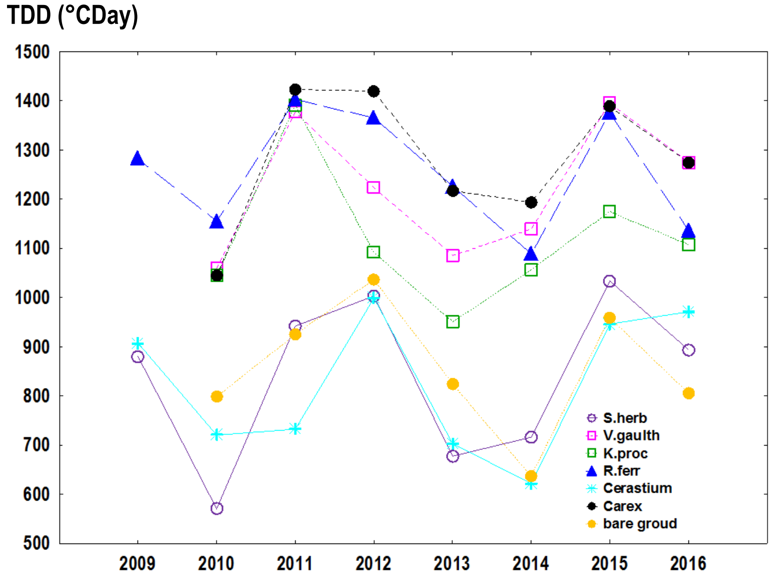

Figure III.5.C.c.3. TDD (mean values) of the selected surface types over the study period (2009-2016).

Comparison of trends among soil-coverage types

As tested by one-way ANOVA, we observed statistically significant differences of TDD among the selected surface types (F=17, p<0.01) (Fig. III.5.C.c.4).

According to the observed inter-annual and intra-annual variability of TDD for each surface type, we could divide the surface types classes in two groups: surface types with TDD always lower than c.1000 °CDay (bare ground, *C.uniflorum and S.herbacea*) or higher than c.1000 °CDay (all the other groups) (Fig. III.5.C.c.4 and Fig. III.5.C.c.5).

Considering all the dataset (2009-2016) the TDD was warmer for *V.uliginosum*, *R.ferrugineum* and *C.curvula* (respectively 1233, 1252 and 1280 °CDay) and *K.procumbens* even if with some less degree-days (1117 °CDay) (Fig. III.5.C.c.4). On the contrary, the colder TDD was found for *C.uniflorum* (826 °CDay), and for *S.herbacea* and bare grounds (respectively 856 and 854 °CDay).

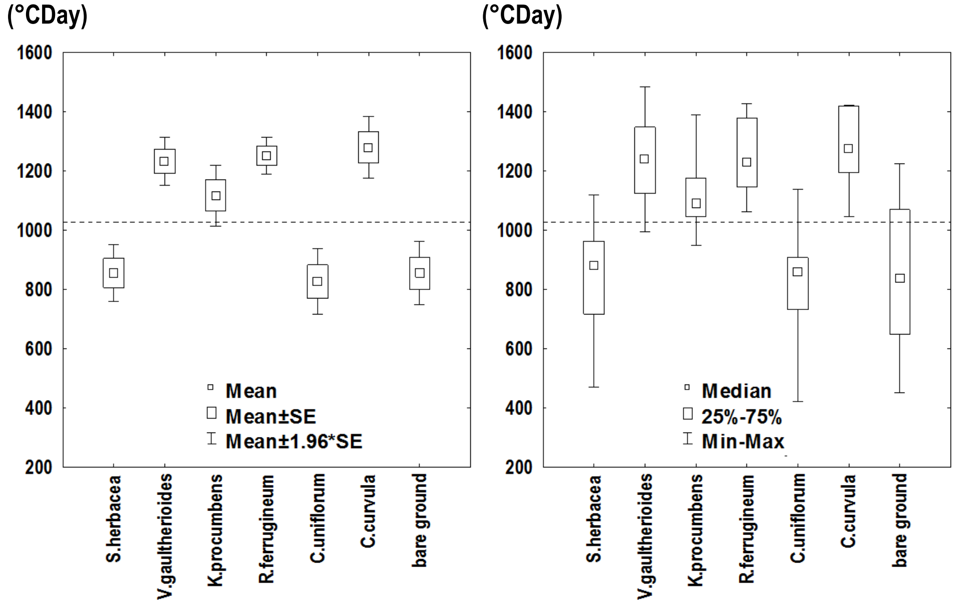

Figure III.5.C.c.4. Non-parametric statistics of thawing degree days (TDD) computed for each single growth form on the entire monitoring period (2009-2016). The dotted black line represent the mean value for all the period.

Considering the whole range exhibited by TDD for the different surface types (Fig. III.5.C.c.4) the largest variability was observed for bare ground sites that ranged from 449 to 1224 °CDay, and for *C.uniflorum* that spanned from 421 to 1138 °CDay. The lowest variability of TDD was observed instead for *R.ferrugineum*, which ranged from 1061 to 1230 °CDay.

The warmer TDD was also largely related to the ecology of the selected species rather than the growth form types. Indeed, shrublands species (*R.ferrugineum* and *V.uliginosum*), dwarf shrublands (*K.procumbens*) and grasslands (*C.curvula*) showed the highest TDD, while snowbed (*S.herbacea*) and pioneers (*C.uniflorum*) showed temperature more similar to bare ground (Fig. III.5.C.c.4).

It was relevant that the “extreme” high TDD was recorded only for *K.procumbens* in 2011, which was most likely caused by an “extreme” SM recorded by *K.procumbens* in that year (-15 days respect the mean of all the period), as tested by t-test ($p<0.01$).

The analysis of each single surface type, confirmed that the SM was the best explanatory variable related to the snow free season parameters, but not for all the surface types. As tested by linear regression TDD and SM showed a statistically significant relation for *S.herbacea* (β=-11.9, R^2=0.85, $p<0.01$), *K.procumbens* (β=-13.5, R^2=0.73, p=0.01), *C.uniflorum* (β=-15.4, R^2=0.76, $p<0.01$), *C.curvula* (β=-13.1, R^2=0.86, $p<0.01$), and bare ground (β=-11, R^2=0.57, $p<0.01$). Low regressions were found for *V.uliginosum* (β=-10, R^2=0.30, $p<0.05$) and *R.ferrugineum* (β=-8.9, R^2=0.40, $p=0.01$).

The TDD were not related to the beginning date of snow cover (BD), as tested by the linear regression for all the selected growth forms ($p>0.05$), thus highlighting the most important role of SM on regulating the TDD, as already observed at the inter-surface types level.

We found large differences among surface types when testing the relation between the TDD of the soils and that of the air. Indeed, as tested by linear regression we found a statistically significant relation for *S.herbacea* (β=1.1, R^2=0.94, $p<0.01$), *R.ferrugineum* (β=1.0, R^2=0.86, $p<0.01$), *C.uniflorum* (β=1.2, R^2=0.65, $p<0.01$), *C.curvula* (β=1.0, R^2=0.78, $p<0.01$) and bare ground (β=1.0, R^2=0.55, $p<0.01$). On the contrary lower proportion of variances of soil TDD were explained by air TDD for *V.uliginosum* (β=0.9, R^2=0.39, $p=0.02$) while we even found no statistically significant relation for *K.procumbens* ($p>0.05$).

The pattern of TDD among growth forms was almost similar to the observed pattern of MAGST (see chap. III.5.C.a and Fig. III.5.C.a.5). Indeed, we observed higher values of TDD in the same surface types where we observed higher MAGST (i.e. *V.uliginosum, K.procumbens, R.ferrugineum* and *C.curvula*), thus underlying the importance of the thawing season temperatures in determining the MAGST.

As tested by linear regression we found a statistically significant relation between the TDD and MAGST at the inter-surface types level (R^2=0.65, $p<0.01$). Similarly, a statistically significant relation between TDD and MAGST was observed also for *V.uliginosum* (R^2=0.65, $p<0.01$), *K.procumbens* (R^2=0.63, $p=0.03$), *R.ferrugineum* (R^2=0.62, $p<0.01$) and *C.curvula* (R^2=0.54, $p=0.05$). On the contrary, the surface types with lower TDD (Fig. V.1.c.5) showed lower regressions as for *S.herbacea* (R^2=0.46, $p<0.01$) and bare ground (R^2=0.27, $p=0.02$) whereas, no statistically significant regression for *C.uniflorum* ($p>0.05$).

III.5.C.d. *Spatial distribution and temporal evolution of N-factor TDD*

Our analyses have been carried out following two steps: I) inter-site and II) intra-surface types level.

Inter-site level

Overall the study period (2009-2016), the N-factor TDD did not show any statistically significant inter-annual variability, as tested by one-way ANOVA at the inter-site level ($p>0.05$) (Fig. III.5.C.d.1) and the mean value, over the whole period was 1.37 (Table III.5.C.d.1).

Table III.5.C.d.1. Non-parametric statistics of N-factor TDD computed for each single year, as well as for the entire monitoring period (2009-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	St.Dev.
2009	3	1.32	1.26	1.26	1.26	1.44	1.44	0.10
2010	11	1.44	1.14	1.29	1.41	1.56	1.80	0.19
2011	11	1.29	0.89	1.16	1.42	1.44	1.49	0.21
2012	13	1.28	1.02	1.22	1.28	1.39	1.49	0.13
2013	12	1.38	1.01	1.28	1.41	1.50	1.59	0.17
2014	13	1.47	0.97	1.43	1.51	1.59	1.82	0.24
2015	13	1.35	1.05	1.30	1.36	1.41	1.59	0.15
2016	13	1.36	0.75	1.31	1.35	1.49	1.69	0.23
2009-2016	89	1.37	0.75	1.27	1.39	1.49	1.82	0.19

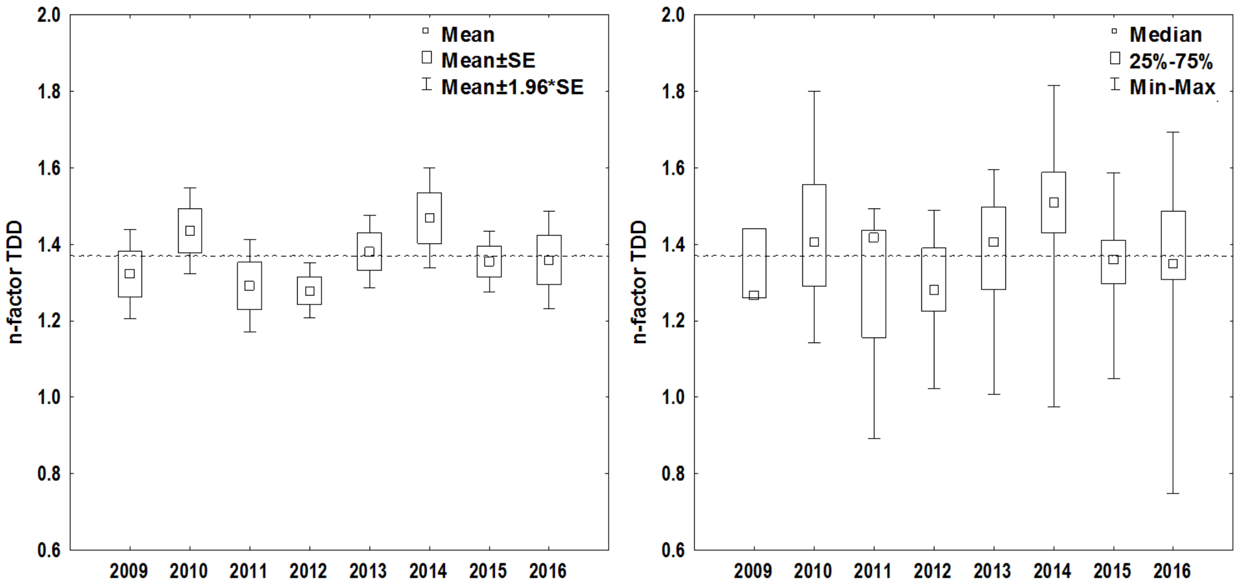

Figure III.5.C.d.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of N-factor TDD from 2009 to 2016, at inter-site level. The dotted black line represents the mean value for the whole period.

The lowest N-factor TDD ranged from 0.75 (in 2016) to 1.26 (in 2009), while the highest spanned from 1.44 (in 2009) to 1.82 (in 2014) (Table III.5.C.d.1).

According to the mean values, the highest N-factor TDD was recorded in 2014 (1.47) and the lower in 2011 and 2012 (respectively 1.29 and 1.28) (Table III.5.C.d.1). As tested by t-test at the inter-site level we did not observe any year with statistically significant differences ($p>0.05$).

Analyzing thus all the dataset (2009-2016), we did not identify any statistically significant trend of N-factor TDD with time, as tested by linear regression ($p>0.05$).

Intra-surface types level

As tested by one-way ANOVA among years for each surface types, only *Rhododendron ferrugineum* exhibited statistically significant inter-annual variability of the N-factor TDD (F=6, $p<0.01$) (Fig. III.5.C.d.2).

The N-factor TDD followed different patterns during the study period according to the surface types, which could be divided in two groups (Fig. III.5.C.d.2 and Fig III.5.C.d.3): group A (*Vaccinium uliginosum, Kalmia procumbens, Rhododendron ferrugineum and Carex curvula*) and group B (*Salix herbacea, Cerastium uniflorum and bare ground*).

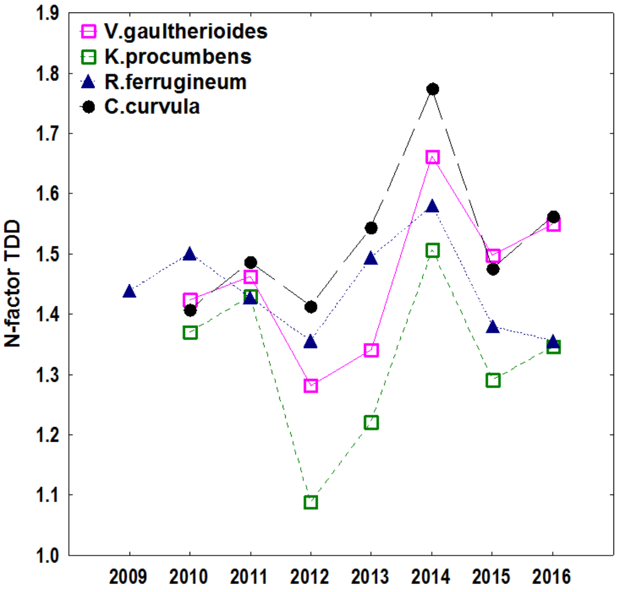

Figure III.5.C.d.2. N-factor TDD (mean values) of *Vaccinium uliginosum, Kalmia procumbens, Rhododendron ferrugineum* and *Carex curvula* over the study period (2009-2016).

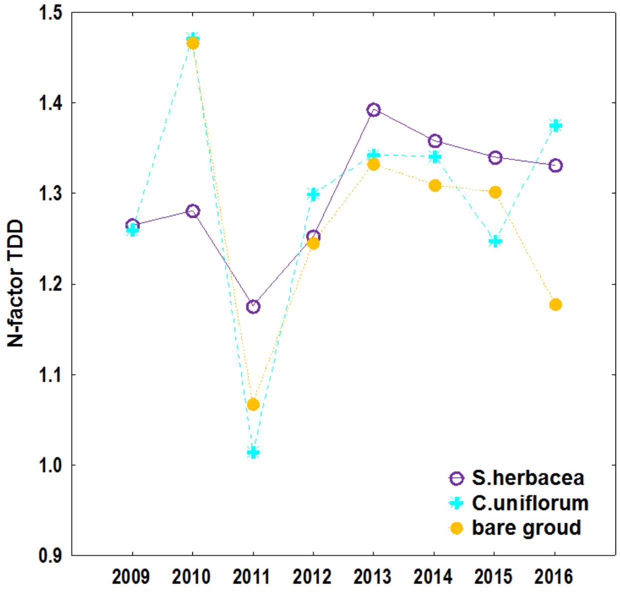

Figure III.5.C.d.3. N-factor TDD (mean values) of *Salix herbacea*, *Cerastium uniflorum* and bare ground over the study period (2009-2016).

In the group A we observed a reduction of the N-factor TDD in 2012, and a marked increase in 2014 (Fig. III.5.C.d.2), while in the group B (Fig. III.5.C.d.3) we observed a less identifiable pattern, with lower values of N-factor TDD in 2011 (and in 2016, but only for the bare ground) and an increase in 2010 (not observed for *S.herbacea* that showed a lower inter-annual variability).

As tested by t-test, *C.uniflorum* was the only one surface type that displayed a statistically significant and “extreme” decrease of the N-factor TDD in 2011 ($p<0.01$) (Fig. III.5.C.d.2).

Tested by linear regression on all the dataset (apart for *C.uniflorum* where we removed the “extreme” 2011) we did not observe any trend of N-factor TDD with time for all the surface types ($p>0.05$).

Comparison of trends among surface types

As tested by one-way ANOVA, we observed statistically significant differences of N-factor TDD among the selected surface types ($F=4$, $p<0.01$) (Fig. III.5.C.d.4).

Considering the mean values over all the dataset (2009-2016), the N-factor TDD was higher for *V.uliginosum*, *R.ferrugineum* and *C.curvula* (respectively 1.47, 1.44 and 1.52), while all the other surface types showed lower and comparable values (Fig. III.5.C.d.4).

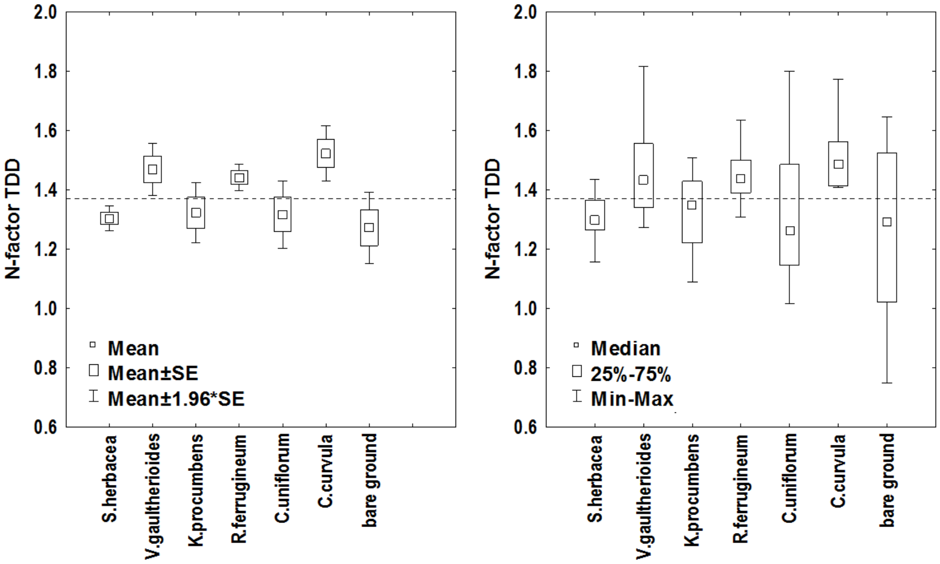

Figure III.5.C.d.4. Non-parametric statistics of thawing N-factor TDD computed for each single growth form on the entire monitoring period (2009-2016). The dotted black line represent the mean value for all the period.

Considering the lowest N-factor TDD, only bare ground exhibited values lower than unity (0.75) (Fig. III.5.C.d.4), while among the vegetated sites *C.uniflorum* showed the lowest value of N-factor (1.01). The highest N-factors was observed instead for *V.uliginosum*, *C.uniflorum* and *C.curvula* (respectively 1.82, 1.80 and 1.77).

The range exhibited by N-factor TDD showed also large differences (Fig. III.5.C.d.4) The largest variability was observed for bare ground sites that ranged from 0.65 to 1.75, and for *C.uniflorum* (1.01-1.80). The lowest variability of N-factor TDD was observed instead for *S.herbacea* (1.16 – 1.43) and *R.ferrugineum* (1.31-1.63).

III.5.C.e. *Spatial distribution and temporal evolution of FDD*

Our analyses have been carried out following two steps: I) inter-site and II) intra-surface types level.

Inter-site level

Overall the study period (2009-2016), the FDD showed a statistically significant inter-annual variability, as tested by one-way ANOVA (F=7, p=0.01) (Fig. III.5.C.e.1) and the mean FDD value for the whole period was -179 °CDay (Table III.5.C.e.1).

Table III.5.C.e.1. Non-parametric statistics of freezing degree days (FDD) computed for each single year, as well as for the entire monitoring period (2009-2016), at the inter-site level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	St.Dev.
2009	3	-175	-175	-175	-175	-175	-175	
2010	11	-184	-649	-206	-114	-47	-30	201
2011	12	-71	-242	-109	-51	-17	-1	70
2012	13	-225	-703	-243	-148	-78	-15	217
2013	12	-87	-310	-134	-56	-2	0	107
2014	13	-107	-362	-114	-69	-47	-5	101
2015	12	-101	-386	-140	-77	-9	-2	119
2016	13	-445	-886	-480	-427	-341	-45	225
2009-2016	89	-179	-886	-243	-105	-45	0	199

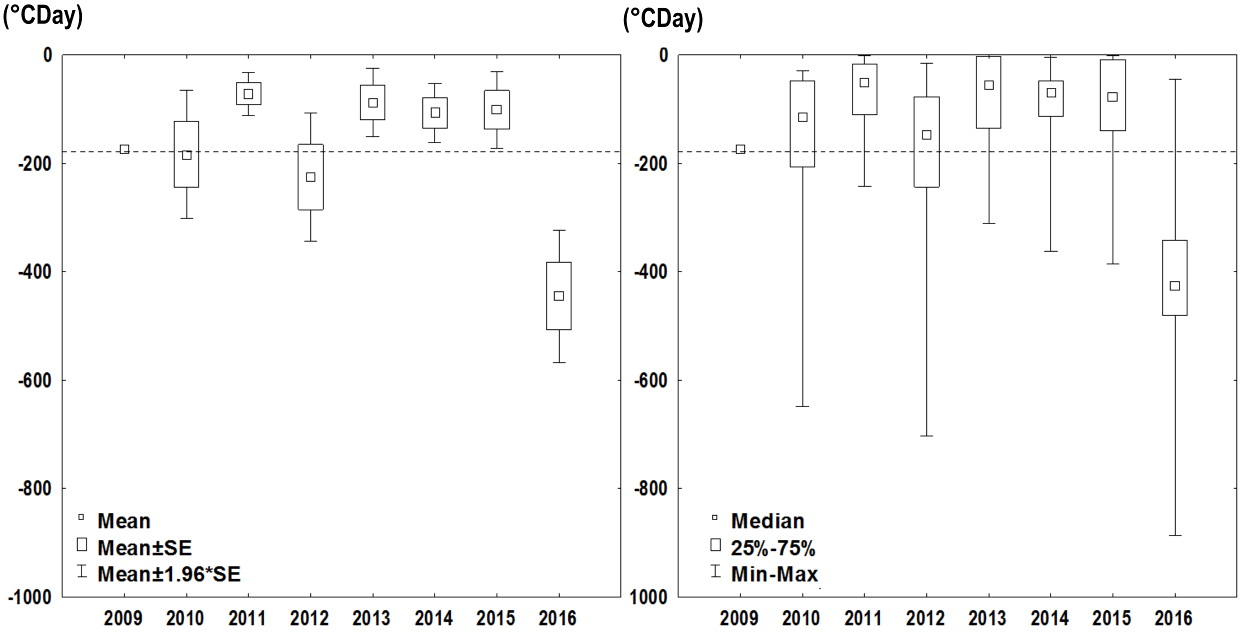

Figure III.5.C.e.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of freezing degree days (FDD) from 2009 to 2016, at inter-sites level. The dotted black line represents the mean value for the whole period.

The minimum FDD ranged from -175 °CDay (in 2009) to -886 °CDay (in 2016), while the maximum FDD spanned from 0°CDay (in 2013) to -175 °CDay (in 2019) (Table III.5.C.e.1).

Considering the anomalies respect the mean of all the study period, the highest FDD was recorded in 2011 (+108 °CDay) while the lowest occurred in 2016 (-266 °CDay) (Fig. III.5.C.e.1). As tested by t-test at the inter-soil coverage level the FDD in 2016 were identified as statistically significant different ($p<0.01$).

Analyzing thus only the “normal” period (2009-2015), we did not identify any statistically significant trend with time, as tested by linear regression ($p>0.05$).

As tested by linear regression at the inter-site level, the FDD displayed statistically significant relations with the snow cover duration although it explained a very low amount of variance (SCD; $\beta=-2.0$, $R^2=0.06$, $p=0.02$), as well as the timing of snow melt (SM; $\beta=-2.5$, $R^2=0.05$, $p=0.04$), while the beginning date of snow cover did not show any statistically significant relation (BD; $p>0.05$).

The effect of the snow cover depth on the buffering effect was evident at our sites (see also next chapter III.5.C.f). Indeed, as tested by linear regression at the inter-site level, the relation between air FDD and soil FDD was statistically significant, but the air FDD explained a very low amount of the variance of soil FDD ($\beta=-0.3$, $R^2=0.05$, $p<0.04$).

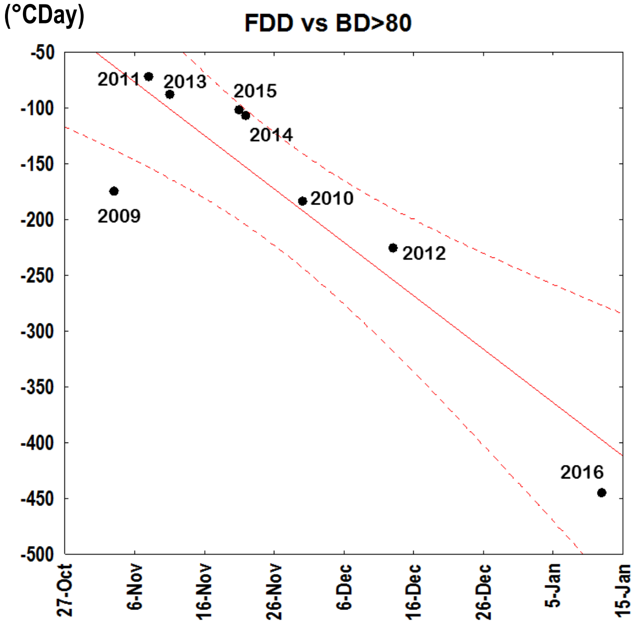

Figure III.5.C.e.2. Relation between the FDD of the soils and the beginning date of snow cover deeper than 80 cm (BD>80; $\beta=-4.7$, $R^2=0.80$, $p<0.01$) measured at La Foppa AWS, as tested by linear regression at the inter-soil coverage and inter-annual level.

Similarly to what observed for the BTS, also the FDD were statistically significant related with the beginning date of snow cover deeper than 80 cm recorded at La Foppa AWS (BD>80; β=-4.7, $R^2=0.80$, $p<0.01$) (Fig. III.5.C.e.2).

Intra-surface types level

As tested by one-way ANOVA on the entire dataset, we observed statistically significant inter-annual variability of the FDD only for *Rhododendron ferrugineum* (F=17, $p<0.01$) and *Vaccinium uliginosum* (F=9, $p<0.01$) (Fig. III.5.C.e.3). However, such differences were mainly attributable to the "extreme" 2016, while in all the other years the FDD were almost constant. Perhaps, considering only the normal years, we observed a larger inter-annual variability (even if not statistically significant, as tested by one-way ANOVA) for *Cerastium uniflorum* and bare ground sites (compared to the other soil coverage types) (Fig. III.5.C.e.3).

The bare ground was the less sensitive soil coverage type respect the "extreme" snow cover of 2016. It was the only soil coverage type that did not show any statistically significant difference in 2016 FDD ($p>0.05$) (Fig. III.5.C.e.3). However for bare ground the FDD were always lower, comparable only to *C.uniflorum*, indicating a freezing state of the soils present in almost all the years and not only due to extreme conditions (as that occurred in 2016).

Tested by linear regression on the "normal" years period (apart for bare ground where we analyzed all the dataset) we did not observe any FDD trend with time for all the soil coverage types ($p>0.05$).

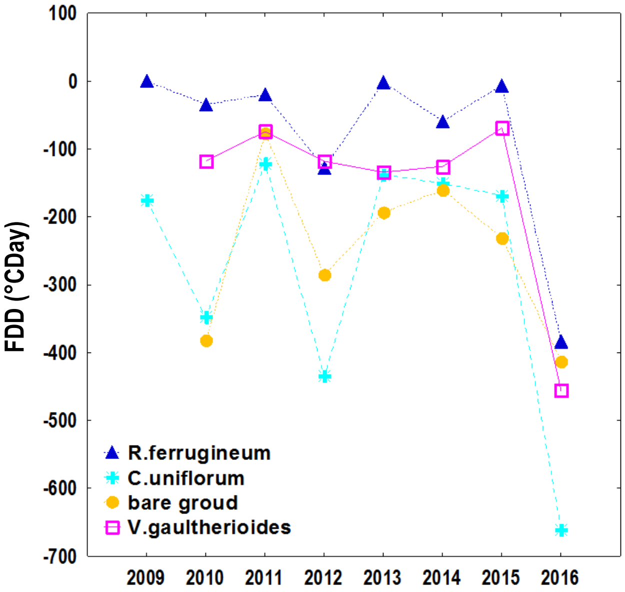

Figure III.5.C.e.3. FDD (mean values) of the most representative soil coverage types over the study period (2009-2016).

Comparison of trends among surface types

As tested by one-way ANOVA, we did not observe statistically significant differences of FDD among the selected surface types ($p>0.05$) (Fig. III.5.C.e.4).

Considering the entire dataset (2009-2016) the FDD was low only for *C.uniflorum* and bare ground (Fig. III.5.C.e.4), respectively -281 and -255 °CDay, according to the mean values. On the contrary, *K.procumbens*, *R.ferrugineum* and *C.curvula* showed higher mean values of FDD (respectively -78, -97 and -95).

The same pattern was observable for the lowest FDD, with *C.uniflorum* and bare ground reaching values of -886 °CDay. Therefore *C.uniflorum* and bare ground sites showed a variability almost double respect all the other soil coverage types.

S.herbacea, *K.procumbens* and *R.ferrugineum* showed a maximum value of zero, thus meaning that in some years they did not experienced any freezing state. In particular, this phenomenon occurred for *S.herbacea* in 2009, *R.ferrugineum* in 2009 and 2013, while for *K.procumbens* in 2013.

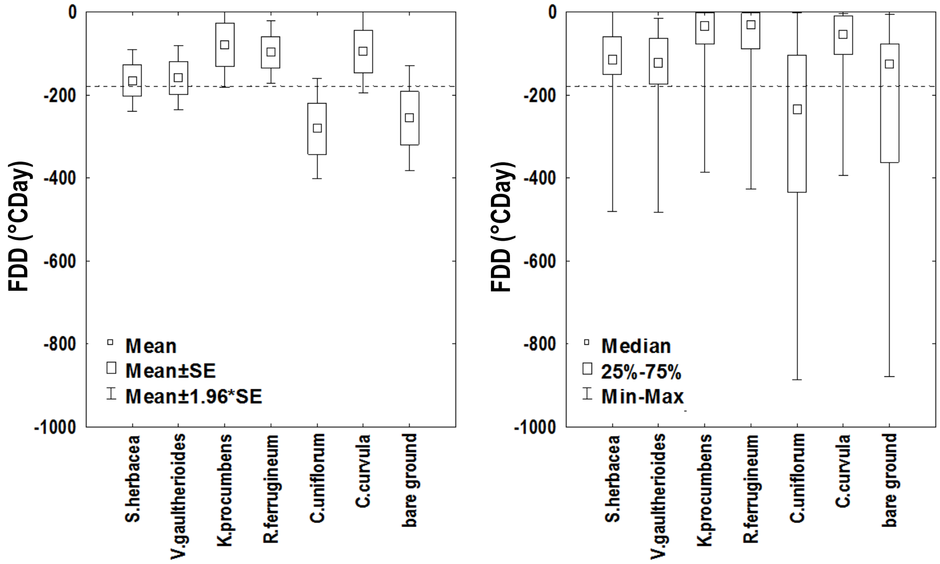

Figure III.5.C.e.4. Non-parametric statistics of freezing degree days (FDD) computed for each single surface type on the entire monitoring period (2009-2016). The dotted black line represent the mean value for all the period.

The analysis of each surface type, confirmed that the BD>80 was the best explanatory variable related to the FDD, for all the surface types: *S.herbacea* ($\beta=-5.2$, $R^2=0.92$, $p<0.01$), *V.uliginosum* ($\beta=-5.2$, $R^2=0.75$, $p=0.01$), *K.procumbens* ($\beta=-5.8$, $R^2=0.88$, $p<0.01$), *R.ferrugineum* ($\beta=-5.4$,

$R^2=0.88$, $p<0.01$), *C.uniflorum* ($\beta=-8.0$, $R^2=0.91$, $p<0.01$), *C.curvula* ($\beta=-5.6$, $R^2=0.85$, $p<0.01$), and bare ground ($\beta=-4.4$, $R^2=0.67$, $p=0.02$).

Moreover, all the selected soil coverage types did not exhibited any relations between FDD of the soils and that of the air, as tested by linear regression ($p>0.05$), thus confirming the same pattern observed at the inter-soil coverage type levels.

III.5.C.f. *Spatial distribution and temporal evolution of N-factor FDD*

Our analyses have been carried out following two steps: I) inter-site and II) intra-surface types level.

Inter-site level

Overall the study period (2009-2016), the N-factor FDD showed statistically significant inter-annual variability, as tested by one-way ANOVA (F=11, p<0.01) (Fig. III.5.C.f.1) and the mean value, over the whole period was 0.18 (Table III.5.C.f.1).

Table III.5.C.f.1. Non-parametric statistics of N-factor FDD computed for each single year, as well as for the entire monitoring period (2009-2016) at the inter-site level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	St.Dev.
2009	3	0.05	0.00	0.00	0.00	0.15	0.15	0.09
2010	11	0.15	0.02	0.04	0.09	0.16	0.53	0.17
2011	11	0.07	0.00	0.03	0.05	0.11	0.23	0.07
2012	13	0.22	0.01	0.08	0.15	0.24	0.68	0.21
2013	12	0.06	0.00	0.00	0.03	0.09	0.24	0.08
2014	13	0.12	0.01	0.05	0.08	0.13	0.41	0.11
2015	13	0.09	0.00	0.01	0.02	0.13	0.39	0.12
2016	13	0.52	0.05	0.41	0.50	0.55	1.02	0.25
2009-2016	89	0.18	0.00	0.03	0.09	0.24	1.02	0.21

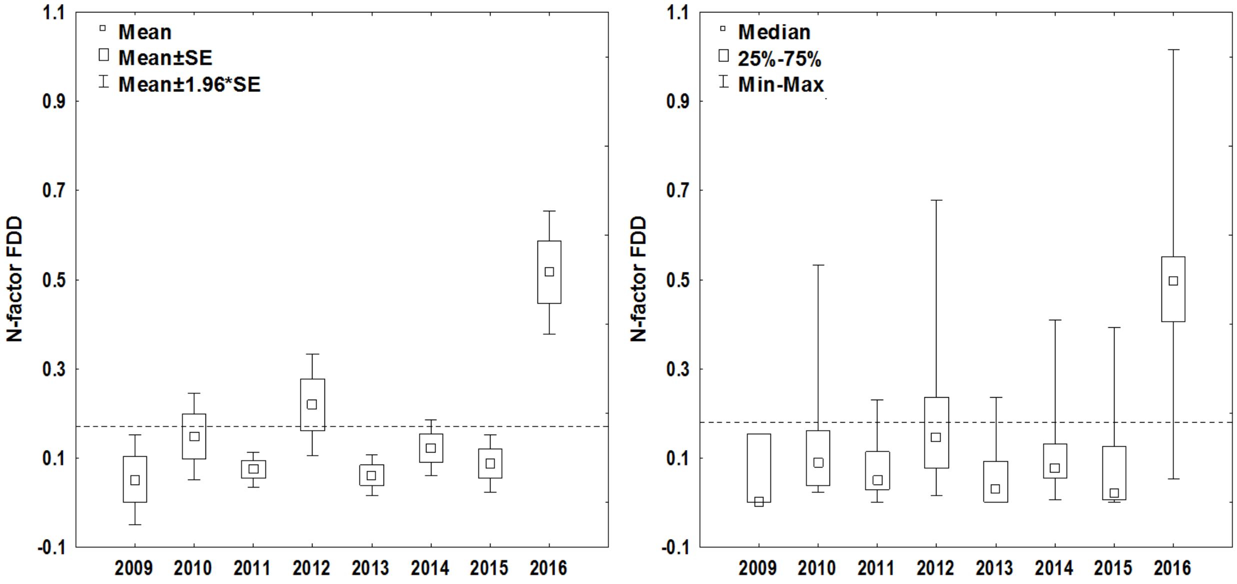

Figure III.5.C.f.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of N-factor FDD from 2009 to 2016, at inter-sites level. The dotted black line represents the mean value for the whole period.

The minimum N-factor FDD ranged from 0 to only 0.05 (in 2016), while the maximum spanned from 0.15 (in 2009) to 1.02 (in 2016) (Table III.5.C.f.1).

According to the mean values, the highest N-factor FDD was recorded in 2016 (0.34) and the lowest in 2009 (0.05) (Table III.5.C.f.1). As tested by t-test at the inter-soil coverage level we observed a statistically significant increase of the N-factor in 2016 (p<0.01).

Analyzing thus all the dataset (2009-2016), we did not identify any statistically significant trend of N-factor FDD with time, as tested by linear regression (p>0.05).

Intra-surface types level

As tested by one-way ANOVA among years for each surface types, only *Rhododendron ferrugineum* (F=20, p<0.01) and *Vaccinium uliginosum* (F=12, p<0.01) exhibited statistically significant inter-annual variability of the N-factor FDD (F=6, p<0.01) (Fig. III.5.C.f.2).

Similarly to the N-factor TDD, also the N-factor FDD followed different patterns during the study period, which could be divided in two groups (Fig. III.5.C.f.2 and Fig III.5.C.f.3): group A (*Vaccinium uliginosum, Kalmia procumbens, Rhododendron ferrugineum* and *Carex curvula*) and group B (*Salix herbacea, Cerastium uniflorum* and bare ground).

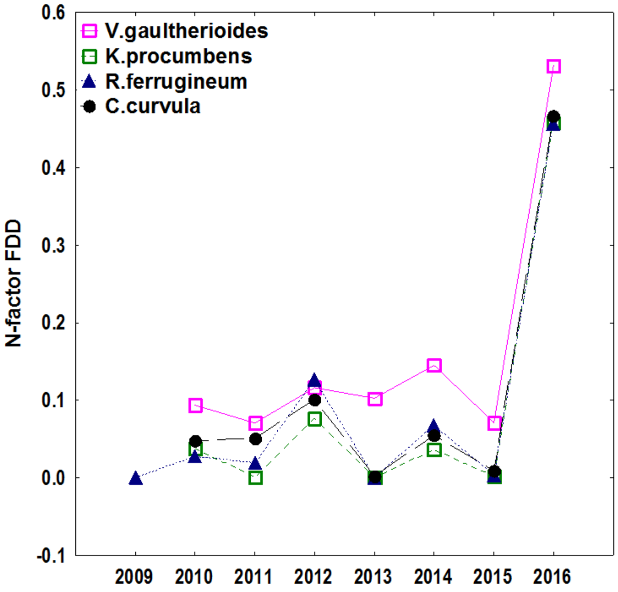

Figure III.5.C.f.2. N-factor FDD (mean values) of *Vaccinium uliginosum, Kalmia procumbens, Rhododendron ferrugineum* and *Carex curvula* over the study period (2009-2016).

In the group A we observed low inter-annual variability of the N-factor over the “normal” years period (2009-2015) with values always close to zero (Fig. III.5.C.f.2), while in the group B (Fig. III.5.C.f.3) we observed a larger inter-annual variability on the same period (Fig. III.5.C.f.3).

In 2016 we observed for all the soil coverage types a statistically significant increase of the N-factor FDD, as tested by t-test ($p<0.05$) (Fig. III.5.C.f.2 and Fig III.5.C.f.3), thus stressing the importance of the extreme snow cover depth in 2016 (see chap III.5.C.b).

However, as tested by linear regression on “normal” years period for each soil coverage types, we did not observe any trend of N-factor FDD with time ($p>0.05$).

It was remarkable that the N-factor FDD of *Cerastium uniflorum* was almost similar to that of bare ground, or even higher in some years

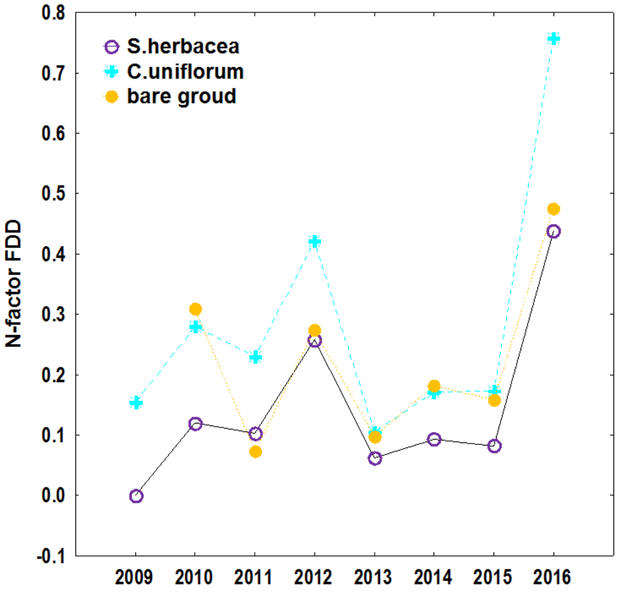

Figure III.5.C.f.3. N-factor FDD (mean values) of *Salix herbacea, Cerastium uniflorum* and bare ground over the study period (2009-2016).

Comparison of trends among surface types

As tested by one-way ANOVA over the entire dataset, the N-factor FDD did not show statistically significant differences among the selected surface types ($p>0.05$) (Fig. III.5.C.f.4).

Considering the mean values over all the dataset (2009-2016), the N-factor FDD was higher for *C.uniflorum* and bare ground (respectively 0.30 and 0.23), while all the other surface types showed low and comparable values (Fig. III.5.C.f.4).

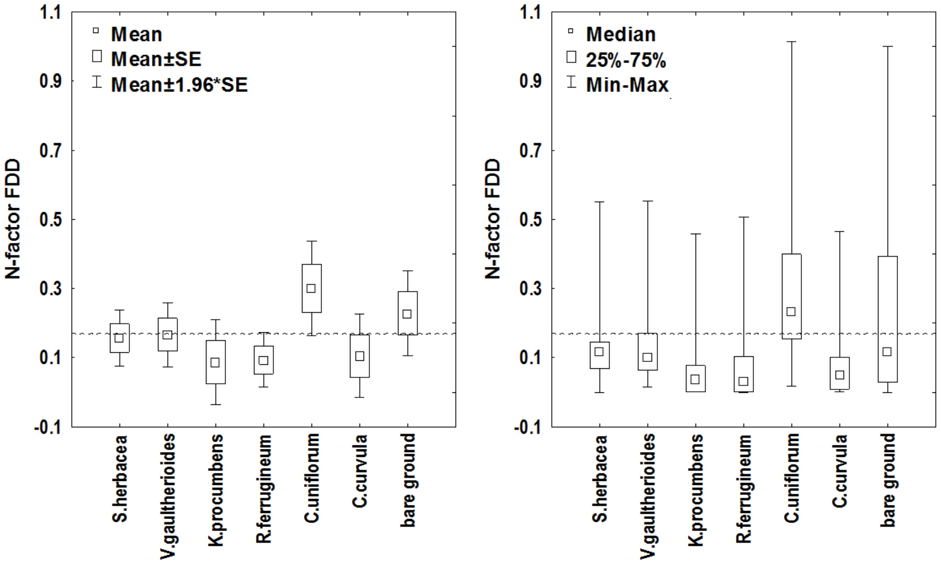

Figure III.5.C.f.4. Non-parametric statistics of N-factor FDD computed for each single surface type on the entire monitoring period (2009-2016). The dotted black line represent the mean value for all the period.

Considering the highest N-factor FDD, only bare ground and *C.uniflorum* showed values close to unity (indicating that soil temperatures were colder than the air), while all the other soil coverage types exhibited values close to 0.5 (Fig. III.5.C.f.4)

The largest variability of N-factor FDD was observed for bare ground sites (0.00-1.00) and for *C.uniflorum* (0.02-1.02) (Fig. III.5.C.f.4). The lowest variability of N-factor FDD was observed instead for *K.procumbens* (0.0-0.46) and *C.curvula* (0.0-0.47).

III.5.D. Manipulation experiments (ME)

III.5.D.a. *Effects of ME on first shoots length (FS_beg_n)*

Concerning the manipulation experiments (ME), the analysis have been carried out following two steps: I) inter-specific level; II) intra-community level. Here we will present the results only for 2016 because the effect of the ME on this specific parameter (FS_beg_n) could be assessed only one year after the beginning of the experiment (see methods).

Inter-specific level

To assess the effectiveness and the impacts of each ME, we assessed the differences of FS_beg_n with reference to the control plot. At the beginning of the season 2016, the FS_beg_n of the cc ranged between 1 and 18 mm, with a median and 75% quartile of respectively 6 and 10 mm (Table III.5.D.a.1).

Table III.5.D.a.1. Non-parametric statistics of first shoots length (FS_beg_n), computed for each single treatment, at the inter-specific level, for the year 2016.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	51	7	1	3	6	10	18	4.9
FL	51	8	1	3	6	10	25	5.5
xN	50	7	1	3	7	10	18	4.4
xNPK	51	9	1	4	8	12	35	6.2
xU	51	8	1	4	7	10	22	4.6
xW	51	8	1	3	8	12	18	4.8
x2W	50	8	1	3	6	10	25	5.4

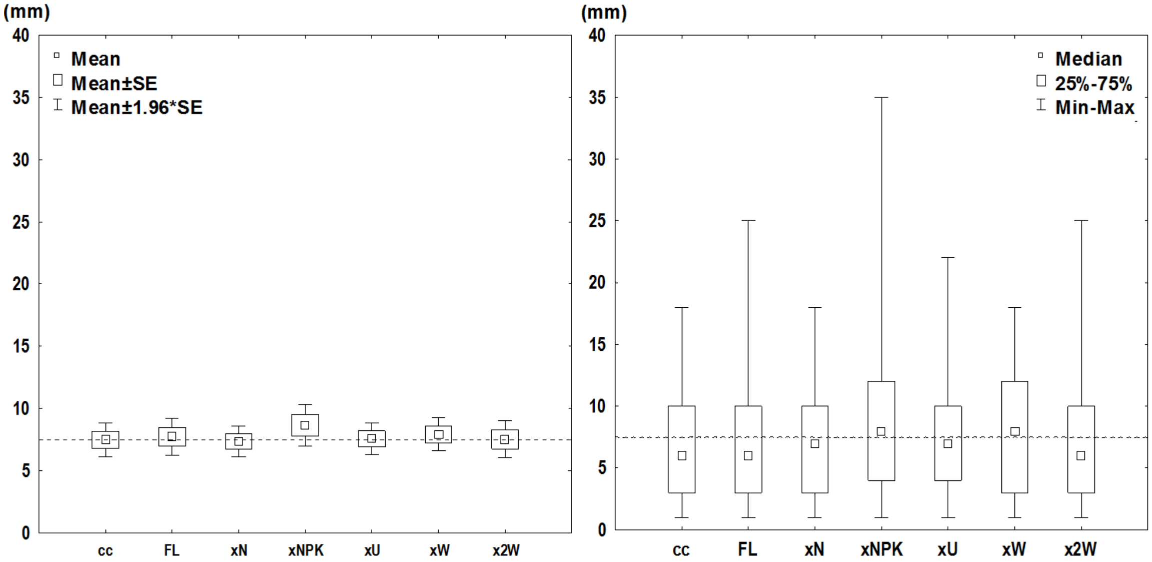

Figure III.5.D.a.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of first shoots length (FS_beg_n) among treatments at the inter-specific level for the year 2016. The dotted black line represents the mean value of the control plots (cc).

Analyzing the effect of the different treatments on the maximum values of FS_beg_n, the addition of ammonium and phosphate (xNPK) produced the largest size (+17 mm) while, the ammonium nitrate addition (xN) and one weekly addition of water (xW) produced no effect, showing the same value of the cc (Table. III.5.D.a.1).

Considering all the non-parametric statistics, according to the 75% quartiles, only xNPK and xW involved longer FS_beg_n (+2 mm). The median values followed a similar pattern with xNPK and xW exerting the largest positive effect (+2 mm). At this stage (soon after snow melt), we did not record negative effects of any treatment (Table III.5.D.f.1).

As tested by Wilcoxon test, the effect on FS_beg_n was statistically significant only for the xNPK treatment (p=0.04) respect to the control plot.

As tested by t-test among the nutrient additions (xN, xNPK, xU), as well as among the two water additions (xW and x2W), the differences between treatments were not statistically significant (p>0.05).

Intra-community level

Grassland

In the grassland community, the FS_beg_n of the cc ranged from 1 to 18 mm, with median and 75% quartile respectively of 10 and 15 mm (Table III.5.D.a.2). Analyzing the maximum values of FS_beg_n, xN and xW showed no effect on shoots length, while all the other treatments exerted positive effects, reaching its maximum in xNPK (+17 mm, almost the double respect cc) (Table III.5.D.e.2).

Table III.5.D.a.2. Non-parametric statistics of grassland first shoots length (FS_beg_n), computed for each single treatment for the year 2016.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	30	10	1	6	10	15	18	5.0
FL	30	9	1	4	8	15	25	6.3
xN	29	9	1	5	10	12	18	4.7
xNPK	30	11	1	6	10	12	35	7.0
xU	30	9	1	5	10	12	22	5.0
xW	30	9	1	5	10	13	18	4.7
x2W	29	9	1	5	10	15	25	6.1

Considering the 75% quartiles, all treatments exerted negative effects on FS_beg_n with the exception of FL and x2W (no effect for both). Indeed, we observed a reduced shoot length with xN, xNPK and xU (all cases -3 mm). Similarly, all treatments did not exert any effect on the median values, excluding only FL treatment that showed a negative impact (-2 mm) (Table III.5.D.a.2).

As tested by Wilcoxon test none of the treatments exerted statistically significant effects compared to cc (p>0.05) (Fig. III.5.D.a.2).

Similarly, we did not find any statistically significant difference, among the nutrient treatments (xN, xNPK, xU), or among the two water treatments (xW vs x2W), as tested by t-test (p>0.05).

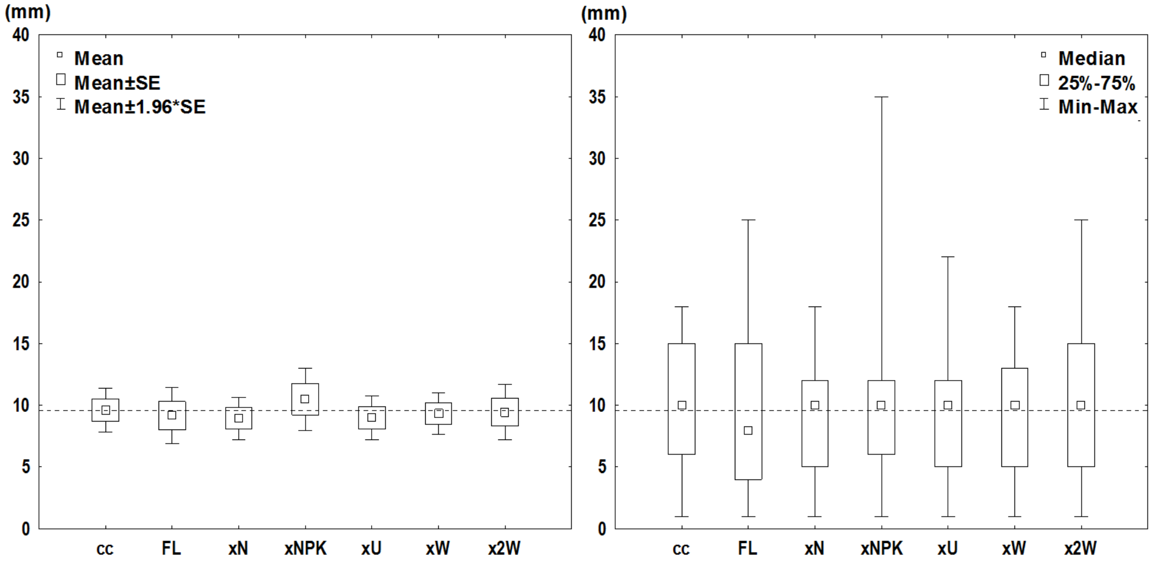

Figure III.5.D.a.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of grassland first shoots length (FS_beg_n), among different treatments. The dotted black line represents the mean value of the control plots (cc).

Snowbed

In the snowbed community, the FS_beg_n of the cc ranged from 2 to 10 mm, with median and 75% quartile respectively of 4 and 6 mm (Table III.5.D.a.3).

Analyzing the maximum values of FS_beg_n, we observed a positive response among all the treatments, with the longest shoots length recorded for xW and xNPK treatments (+8 and +5 mm, respectively) (Table III.5.D.a.3).

Considering the 75% quartiles, only x2W showed same value of cc, while all other treatments showed enhanced shoot length. The median values indicated similar responses, with FL and xU exerting the highest effect (both cases + 2mm) (Table III.5.D.a.3).

As tested by Wilcoxon test, only the enhanced FS_beg_n for FL and xNPK treatments were identified as statistically significant, compared to cc (in both cases p=0.04) (Fig. III.5.D.a.3). On the contrary, the comparison among nutrients addition (xN, xNPK, xU), or among water additions (xW and x2W) did not display statistically significant differences, as tested by t-test (p>0.05).

Table III.5.D.a.3. Non-parametric statistics of snowbed first shoots length (FS_beg_n) computed for each single treatment for the year 2016.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	21	4	2	2	4	6	10	2.7
FL	21	6	2	3	6	8	12	3.2
xN	21	5	2	3	4	7	12	3.0
xNPK	21	6	2	4	5	8	15	3.4
xU	21	5	2	2	6	8	12	3.0
xW	21	6	2	2	5	8	18	4.3
x2W	21	5	2	3	5	6	12	2.6

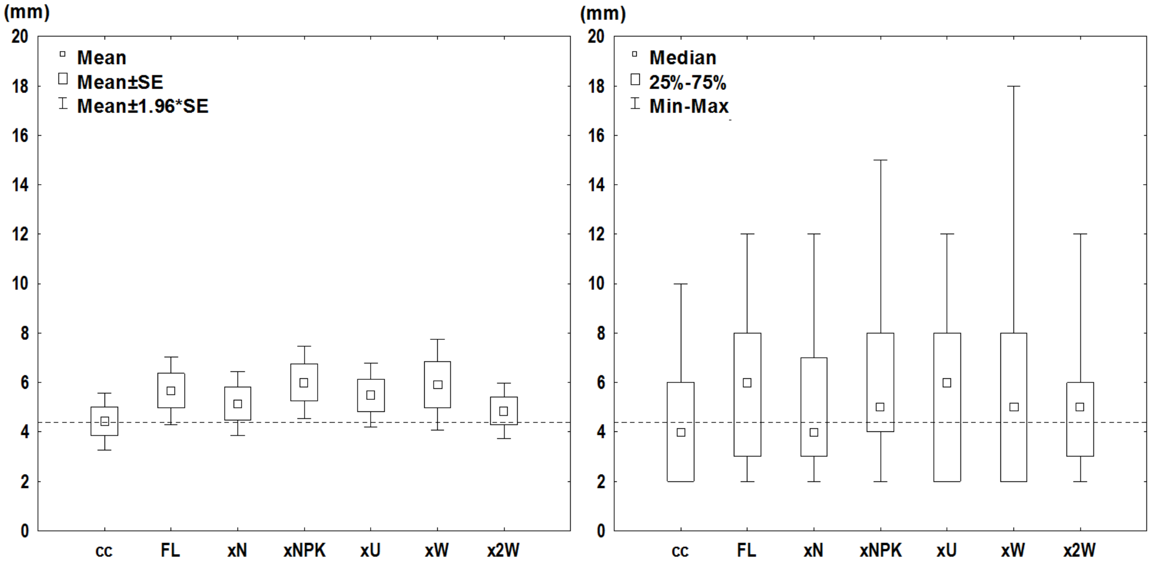

Figure III.5.D.a.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snowbed first shoots length (FS_beg_n) among different treatments. The dotted black line represents the mean value of the control plots (cc).

Comparison of treatments effects among communities

Our findings highlighted that shoots length at the beginning of the season was positively influenced by treatments (longer shoots) for snowbeds, even if we found statistically significant differences only for xNPK and FL.

Grassland species did not show any statistically significant effects of our treatments; however, the addition of ammonium and phosphate (xNPK) involved the highest value of FS_beg_n (almost double respect the cc).

The largest response of snowbed species was in correspondence of the addition of xNPK and FL, thus highlighting that:
a) In their natural condition, they are strongly nutrient limited (in particular P-limited, since they responded to nitrogen input only when combined with phosphorous);
b) They were able to enhance their growth with flower removal treatment (FL), indicating higher capability respect grassland species to move nutrients among different plant organs;
c) They demonstrated carry-over effects from the previous year; indeed the measure of first shoots length was executed soon after SM and before the beginning of treatments, and was thus the response to the previous year manipulations.

According to our data, snowbeds are thus the most sensitive communities in relation to changing of environmental parameters, compared to grasslands.

Snowbed communities are among the most threatened by current climate change, indeed they show high sensitivity to changing of environmental parameters, especially of snow cover. However, their positive response to altered nutrient availability, allow to hypothesize that non-linear changes could be expected under future anthropogenic related climate change scenario.

III.5.D.b. *Effects of ME on the main flowering day (MF)*

Concerning the manipulation experiments, the analysis have been carried out following two steps: I) inter-specific (both inter-annual and intra-annual) level; II) intra-communities level.

Inter-specific and inter-annual level

During the first two years of ME (2015, 2016), the MF of the cc ranged between mid-June and late August (164-236 DOY), with a median and 75% quartile respectively occurring at mid-July (198 DOY) and late July (294 DOY) (Table III.5.D.b.1).

Table III.5.D.b.1. Non-parametric statistics of main flowering day (MF) computed for each single treatment during the entire monitoring period (2015-2016), at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	78	198	164	190	198	204	236	13
xN	74	198	168	188	198	204	232	14
xNPK	70	200	168	188	198	210	267	17
xU	69	199	168	188	198	204	236	15
xW	58	199	168	188	198	204	236	15
x2W	64	199	164	189	198	210	236	14

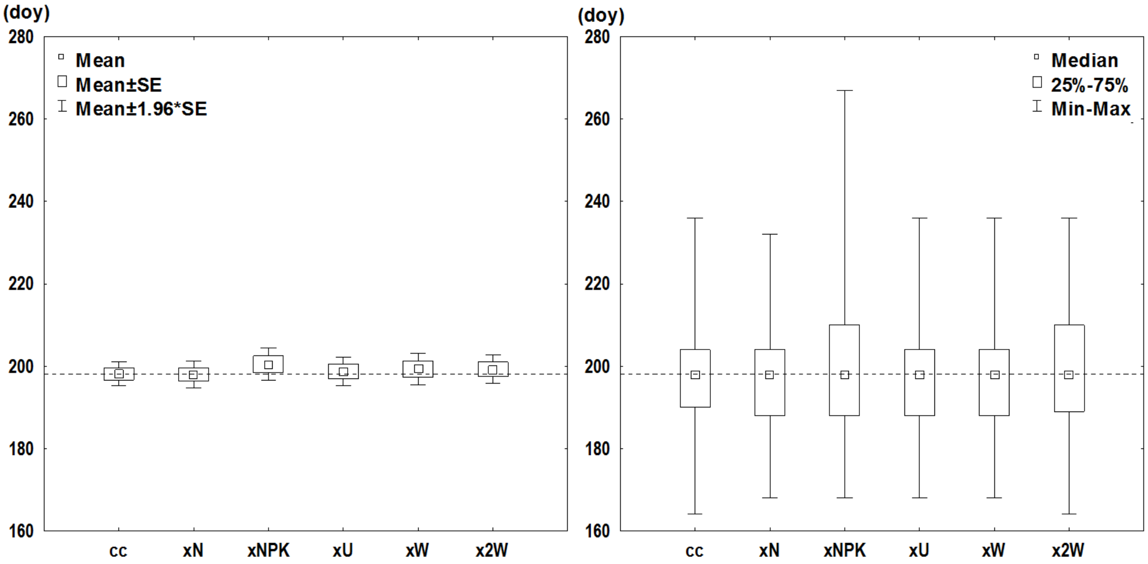

Figure III.5.D.b.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) between different treatments at the inter-annual and inter-specific level. The dotted black line represents the mean value of the control plots (cc).

Analyzing the effect of the different treatments on the onset of MF, we observed a delay for all the treatments compared to the cc (+4 days), except for x2W which showed the same value of the cc.

Considering the median values, we did not observe any influence of the treatments (same value of the cc), while according to the 75% quartile xNPK and x2W exerted a delay of +6 days (Table III.5.D.c.1).

The MF completion occurred earlier for xN treatment (-4 days) and later for xNPK (+31 days), while all the other treatments did not show differences from the cc (Table III.5.D.c.1).

The xNPK thus exerted a strong influence on the MF duration (99 days) compared to the cc (only 72 days), but also respect all the other treatments ,which total duration ranged from 64 days (xN) to 72 days (x2W) (Fig. III.5.D.c.1).

However, as tested by Wilcoxon test, none of the treatments exerted statistically significant influences on the MF compared to the cc (p>0.05). Also the comparison between similar treatments (among nutrients additions or among water additions) confirmed that treatments were not statistically significant different, as tested by t-test (p>0.05) (Fig III.5.D.c.1).

Inter-specific and intra-annual level

2015

In 2015, the MF of the cc ranged from early July to early August (188-216 DOY), with median and 75% quartile occurring at mid-July (respectively 194 and 198 DOY) (Table III.5.D.c.2).

Table III.5.D.c.2. Non-parametric statistics of main flowering day (MF) computed for each single treatment in 2015, at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	35	196	188	190	194	198	216	7.6
xN	30	193	184	188	190	198	204	6.0
xNPK	27	194	184	188	198	198	216	7.2
xU	31	195	184	188	194	198	216	8.1
xW	27	195	188	188	190	198	216	7.9
x2W	29	195	188	188	190	198	212	7.7

Analyzing the effect of the different treatments on the onset of MF, in 2015, we observed an advance of -4 days for the xN, xNPK and xU treatments, while the water additions showed same value of the cc. The MF completion occurred earlier for xN (-12 days) and x2W (-4 days), while no effects were identifiable for the other treatments compared to the cc (Table III.5.D.c.2).

Considering the median values, we observed an advance of MF for xN and xW (-4 days), and a delay for xNPK (+4 days), while according to the 75% quartile we did not observe any difference (Table III.5.D.c.2).

In 2015 the MF duration was thus not influenced by the xNPK addition, while we observed a reduction of the MF duration for xN (20 days) compared to the cc (28 days)

As tested by Wilcoxon test, the xN was the only treatment that exerted statistically significant influences on the MF (p=0.04) compared to the cc; while the comparison between similar treatments (among nutrients additions or among water additions) did not identify any statistically significant difference, as tested by t-test (p>0.05) (Fig III.5.D.c.2).

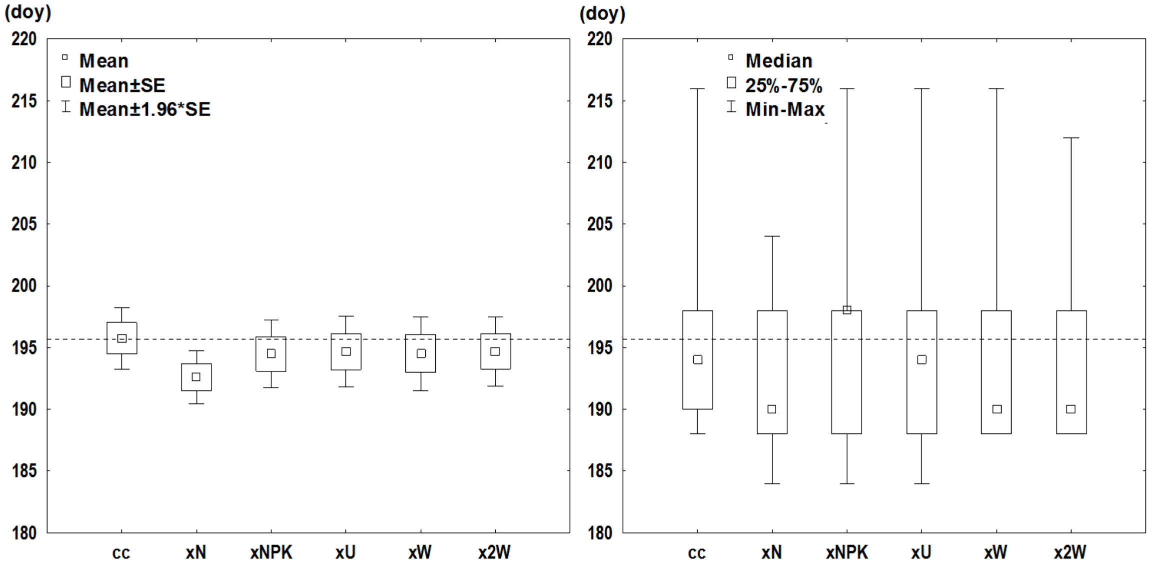

Figure III.5.D.c.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) among different treatments at the inter-specific level for the year 2015. The dotted black line represents the mean value of the control plots (cc).

2016

In 2016, the MF of the cc ranged from early July to early August (188-216 DOY), with median and 75% quartile occurring both at mid-July (respectively 194 and 198 DOY) (Table III.5.D.c.3).

Analyzing the effect of the different treatments on the onset of MF compared to the cc, in 2016, we observed an advance of -4 days only for the x2W treatment, while all the other treatments did not exert any influence. The MF completion occurred earlier for xN (-4 days) and later only for xNPK (+31 days) (Table III.5.D.c.3).

Table III.5.D.c.3. Non-parametric statistics of main flowering day (MF) computed for each single treatment in 2016, at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	43	200	164	189	201	210	236	16.2
xN	44	202	168	194	201	214	232	16.7
xNPK	43	204	168	189	203	221	267	20.0
xU	38	202	168	194	201	210	236	17.9
xW	31	203	168	198	201	221	236	17.8
x2W	35	203	164	194	203	214	236	17.1

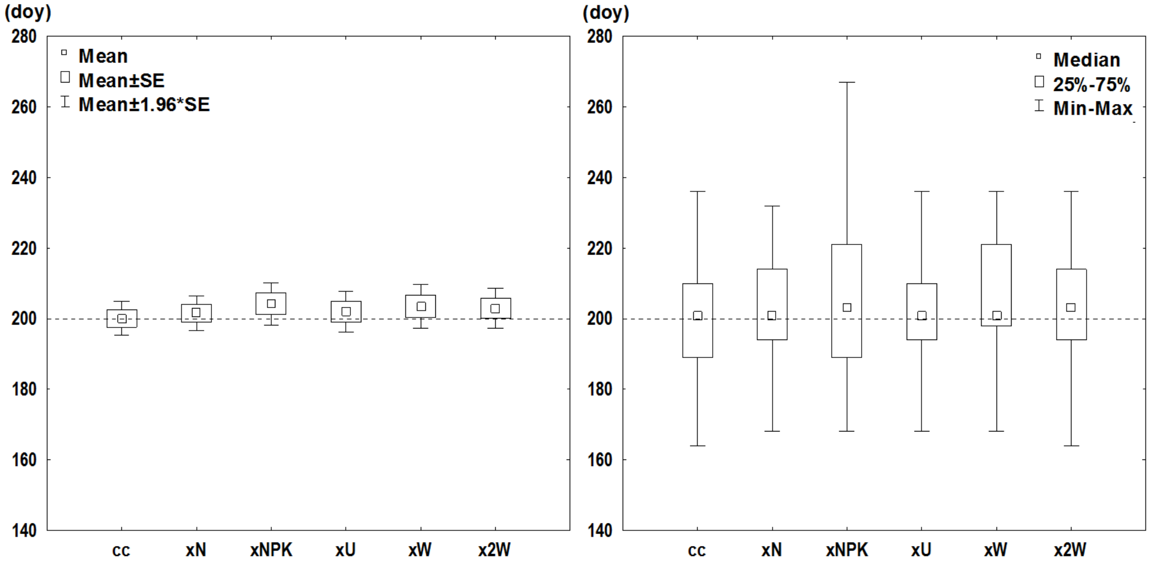

Figure III.5.D.c.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of main flowering day (MF) among different treatments at the inter-specific level for the year 2016. The dotted black line represents the mean value of the control plots (cc).

Considering the median values, we observed a delay of +2 days for xNPK and x2W, and no effects for the other treatments, while according to the 75% quartile, xU showed the same value of the cc, and all the other treatments exerted a delay, up to 11 days for xNPK and x2W (Table III.5.D.c.3).

In 2016 the MF duration was longer for the xNPK treatment (99 days), almost the double of the cc (72 days), while with xN we observed the shorter MF duration (64 days).

As tested by Wilcoxon test, the xNPK was the only one treatment that exerted statistically significant influences on the MF (p=0.04) compared to the cc; while the comparison between similar treatments (among nutrients additions or among water additions) did not identify any statistically significant difference, as tested by t-test (p>0.05) (Fig III.5.D.c.3).

Intra-communities level

Grassland

In the grassland community, the MF of the cc ranged from mid-June to late August (164-236 DOY), with median and 75% quartile occurring both at mid-July (respectively 194 and 201 DOY) (Table III.5.D.c.4).

Analyzing the effect of the different treatments on the onset of MF compared to the cc, we observed an advance of -4 days only for the x2W treatment, while all the other treatments did not exert any influence. The MF completion occurred earlier for xN (-8 days) xNPK (-4 days), while all the other treatments did not exert any influence (Table III.5.D.c.4).

Table III.5.D.c.4. Non-parametric statistics of grassland main flowering day (MF), computed for each single treatment, as well as for the entire monitoring period (2016-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	46	195	164	190	194	201	236	12.1
xN	40	194	168	188	194	200	228	12.6
xNPK	38	195	168	188	194	201	232	13.9
xU	37	196	168	188	194	201	236	15.4
xW	33	196	168	188	198	201	236	13.6
x2W	34	196	164	189	194	201	236	14.1

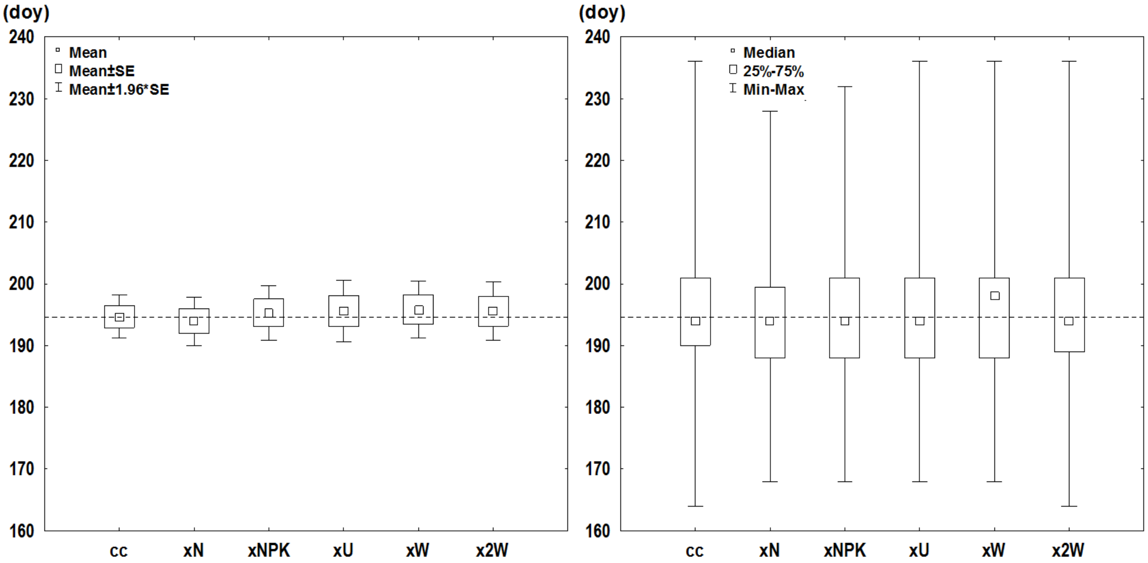

Figure III.5.D.c.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of grassland main flowering day (MF), among different treatments. The dotted black line represents the mean value of the control plots (cc).

Considering the median values, we observed a delay of +4 days only for xW, and no effects were identified for all the other treatments, while according to the 75% quartile, the only one effect was a little advance of -1 days for xN (Table III.5.D.c.4).

The xN addition exerted thus a negative impact on the MF duration (60 days) compared to the cc (72 days), while all the other treatments showed limited differences with the cc, spanning from 64 days (xNPK) to 72 days (x2W) (Fig. III.5.D.c.4).

As tested by Wilcoxon test, we did not find any statistically significant effect between each single treatment and the cc (p>0.05). Moreover, also the comparison between similar treatments (among nutrients additions or among water additions) did not identify any statistically significant difference, as tested by t-test (p>0.05) (Fig III.5.D.c.4).

Snowbed

In the snowbed community, the MF of the cc ranged from early July to mid-August (183-236 DOY), with median and 75% quartile occurring in late July (respectively 204 and 211 DOY) (Table III.5.D.c.5).

Table III.5.D.c.5. Non-parametric statistics of snowbed main flowering day (MF) computed for each single treatment, as well as for the entire monitoring period (2016-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	32	203	183	190	204	211	236	13.2
xN	34	203	183	194	201	214	232	14.4
xNPK	32	207	177	198	204	215	267	18.3
xU	32	202	183	192	201	210	232	13.3
xW	25	204	183	194	201	212	232	15.0
x2W	30	203	183	190	203	214	232	13.3

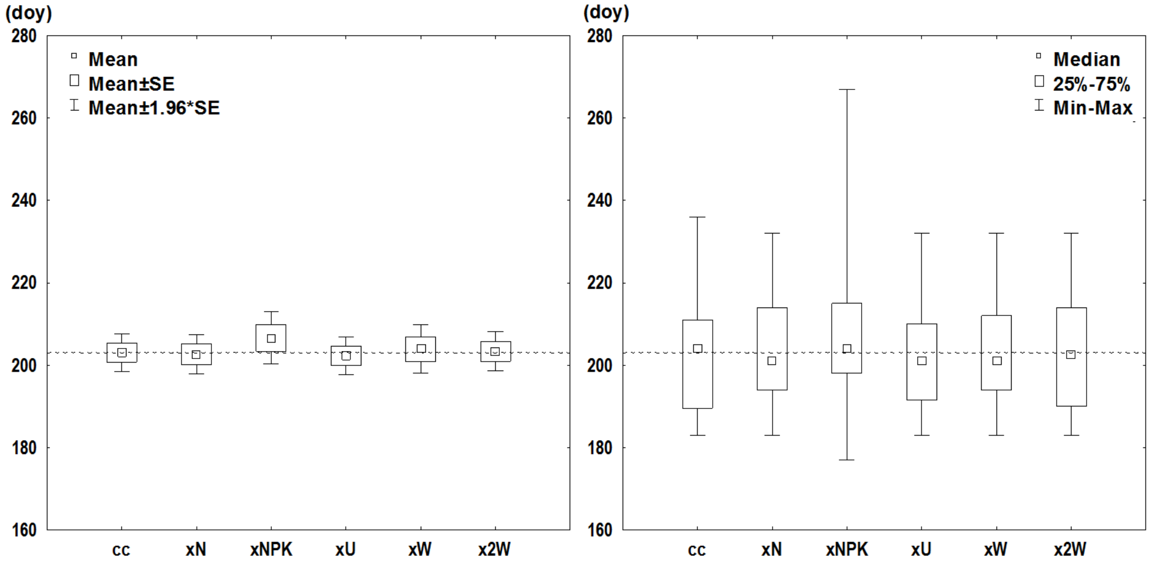

Figure III.5.D.c.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snowbed main flowering day (MF) among different treatments. The dotted black line represents the mean value of the control plots (cc).

Analyzing the effect of the different treatments on the onset of MF compared to the cc, we observed an advance of -6 days only for the xNPK treatment, while all the other treatments did not exerted any influence. The MF completion occurred earlier for xN (-4 days) and only the xNPK showed a delay of LS (+31 days) (Table III.5.D.c.5).

Considering the median values, we observed an advance for xN, xU and xW (all -3 days) and for x2W (-1 days), while xNPK did not involve any effect. According to the 75% quartile, xU showed an advance of only -1 days, and all the other treatments exerted a delay, up to 4 days for xNPK (Table III.5.D.c.5).

The xNPK thus exerted for the snowbed community a strong impact concerning the MF duration (90 days) compared to the cc (only 53 days), while all the other treatments exerted only negligible influence.

As tested by Wilcoxon test, we did not find any statistically significant effect between each single treatment and the cc ($p>0.05$). Moreover, also the comparison between similar treatments (among nutrients additions or among water additions) did not identify any statistically significant difference, as tested by t-test ($p>0.05$) (Fig III.5.D.c.5).

Comparison of treatments effects among communities

Comparing the onset of the MF, both the snowbed and grassland communities did not show any statistically significant effect of treatments compared to the control plots, thus confirming our findings from the long-term monitoring of a strong photoperiodic control on the start of the main flowering day (see chap. V.1.g and V.1.k).

Interestingly we observed instead longer duration of MF with xNPK addition, only for the snowbed community (+37 days compared to the cc). The main contribute of this longer duration was exerted by the MF completion. The photoperiod plays thus an important role on the onset of MF, but its effect was overwhelmed by the xNPK addition.

Snowbeds were thus more able to exploit new resources (in particular ammonium and phosphate) in order to enforce their reproductive phenology, lengthening MF duration, with thus large potentially a) positive feedbacks on the reproductive success, and b) advantages under future Fall warming scenario.

This is in agreement with findings from the other studied plant traits at the manipulation experiments, highlighting high sensitivity of snowbed vegetation communities.

Considering grassland community, we observed instead a higher sensitivity to the xN addition that exerted a reduction of the MF duration (-12 days). Also in this case the effect was mainly driven by an earliest MF completion, confirming again the strong photoperiodic control on the onset of MF, as well as highlighting the higher sensitivity of grassland to nitrate addition.

For grasslands thus we could hypothesize that a larger nitrate supply could exert negative impact on the flowering duration and thus on the reproductive success.

III.5.D.c. *Effects of ME on plant height (Hmax)*

Concerning the manipulation experiments, the analyses have been carried out following two steps: I) inter-specific (both inter-annual and intra-annual) level; II) intra-communities level.

Inter-specific and inter-annual level

During the first two years of ME (2015, 2016), the Hmax of the cc ranged between 7 and 240 mm, with a median and 75% quartile of respectively 55 and 100 mm (Table III.5.D.c.1).

Table III.5.D.c.1. Non-parametric statistics of plant height (Hmax) computed for each single treatment during the entire monitoring period (2015-2016), at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	102	70	7	25	55	100	240	54.7
FL	102	60	5	20	50	85	220	46.7
xN	102	66	8	25	60	90	220	49.1
xNPK	102	74	9	25	63	105	260	54.8
xU	102	66	10	25	55	80	300	52.4
xW	102	59	5	25	45	90	190	43.4
x2W	100	65	10	25	50	90	220	51.0

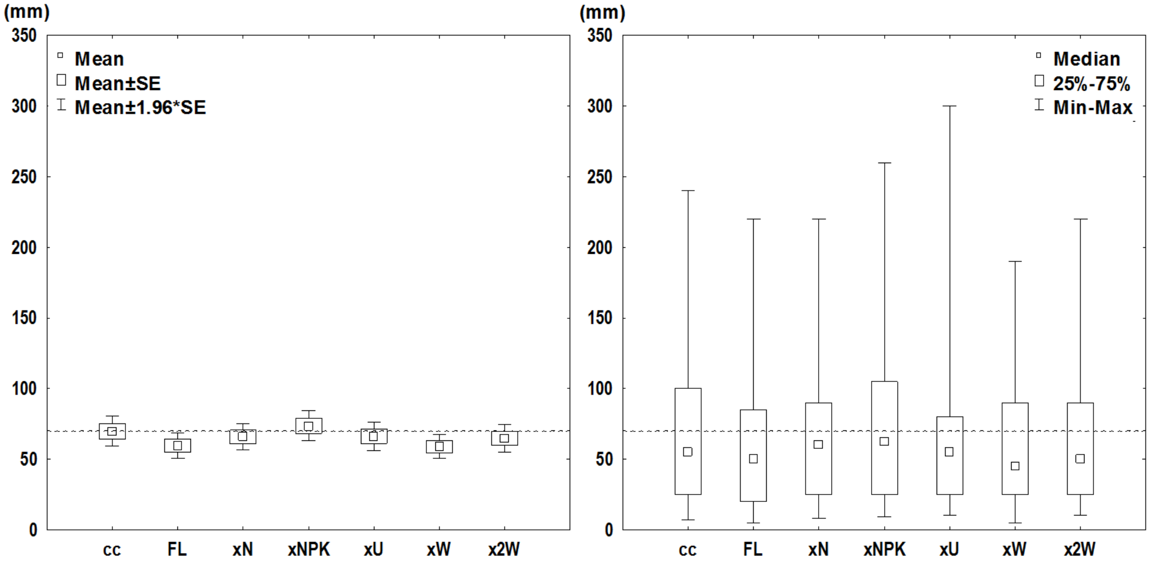

Figure III.5.D.c.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) between different treatments at the inter-annual and inter-specific level. The dotted black line represents the mean value of the control plots (cc) for the whole period.

Analyzing the effect of the different treatments on the maximum values of Hmax, the addition of urea (xU) produced the largest size (+60 mm), coupled with xNPK (but only +20 mm), while, surprisingly, the water addition performed once a week (xW) produced a negative effect implying the smallest Hmax of the whole dataset (-50 mm) (Table III.5.D.c.1).

Considering all the non-parametric statistics, according to the 75% quartiles, only xNPK involved an increase of Hmax (+5 mm), while all the other treatments showed negative effects, reaching the maximum with xU (-20 mm) (Table III.5.D.c.1). Similarly, also analyzing the median, we observed the largest positive effect of Hmax with xNPK (+8 mm), coupled with a positive effect of xN (+5 mm), while all the other treatments exerted negative (xW, x2W, xFL) or no effect respect to the control plots. The xW addition exerted the largest negative impact on Hmax (-10 mm).

As tested by Wilcoxon test the effect on Hmax was statistically significant for the xNPK increase (p=0.04), and for the FL (p=0.03) and xW (p=0.04) reduction respect to the control plot. The comparison among nutrient additions (xN, xNPK, xU), and among water additions (xW and x2W) did not show statistically significant differences between similar treatments, as tested by t-test (p>0.05).

Inter-specific and intra-annual level

2015

In 2015, the Hmax of the cc ranged from 25 to 210 mm, with median and 75% quartile respectively of 60 and 110 mm (Table III.5.D.c.2).

Concerning the maximum value of Hmax, all treatments, with the exception of xU, exerted negative impacts, exhibiting lower values than the cc. In particular, it is remarkable that this negative effect was highest with xNPK. A similar trend is apparent analyzing the 75% quartiles, with all treatments exerting negative effects compared to cc, while, according to the median, both xW and xN succeeded in producing positive effects on Hmax (+5 mm) than the cc, and all the other treatments exerted negative effects.

Table III.5.D.c.2. Non-parametric statistics of plant height (Hmax) computed for each single treatment in 2015, at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	51	74	10	25	60	110	210	54
FL	51	61	8	25	50	90	185	44
xN	51	69	12	25	65	100	200	49
xNPK	51	64	9	25	55	90	170	45
xU	51	68	10	25	50	90	210	53
xW	51	63	12	25	65	100	190	43
x2W	50	67	10	25	53	90	200	50

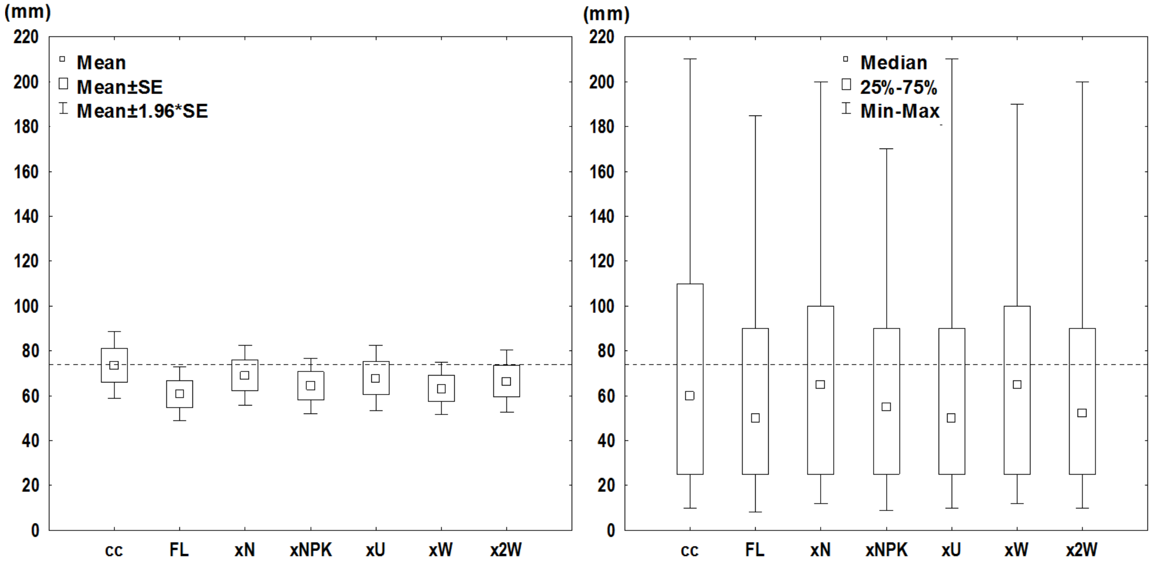

Figure III.5.D.c.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) among different treatments at the inter-specific level for the year 2015. The dotted black line represents the mean value of the control plots (cc).

As tested by Wilcoxon test the Hmax reduction of the FL and xNPK were identified as statistically significant respect to the control plot (in both cases p=0.04). Comparing the effects among nutrient additions and those among the water additions (xW and x2W), we did not find statistically significant differences, as tested by t-test (p>0.05).

2016

In 2016, the Hmax of the cc ranged from 7 to 240 mm, with median and 75% quartile respectively of 50 and 90 mm (Table III.5.D.c.3). Analyzing the maximum values of Hmax, both xU and xNPK exerted positive effects (+60 and +20 mm, respectively), while all the other treatments induced negative effects, in particular the water addition once a week (xW, -65 mm) (Table III.5.D.c.3).

Considering the 75% quartiles, the xNPK was the only one treatment that exerted a positive effect on Hmax (+30 mm) with all the other treatments exhibiting negative responses (-10 mm). According to the median values, xNPK, xN and xU showed positive effects (+20, +10, +5 mm, respectively) (Table III.5.D.c.3), while water additions (xW and x2W) exerted negative effects (-8 and -1 mm, respectively).

In 2016, the xNPK treatment followed the opposite pattern respect to 2015. The increase of Hmax with xNPK was identified as statistically significant respect to the control plot, as tested by Wilcoxon test (p=0.03), as well as the negative effect of FL (p=0.04) and xW (p=0.03) (Fig. III.5.D.c.3). Comparing the effects among nutrient additions and those among water additions we did not find statistically significant differences between similar treatments, as tested by t-test (p>0.05).

Table III.5.D.c.3. Non-parametric statistics of plant height (Hmax) computed for each single treatment in 2016, at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	51	66	7	23	50	90	240	55
FL	51	59	5	18	50	80	220	50
xN	51	62	8	25	60	80	220	50
xNPK	51	83	10	25	70	120	260	62
xU	51	65	10	22	55	80	300	52
xW	51	55	5	18	42	80	175	44
x2W	50	63	10	25	49	80	220	53

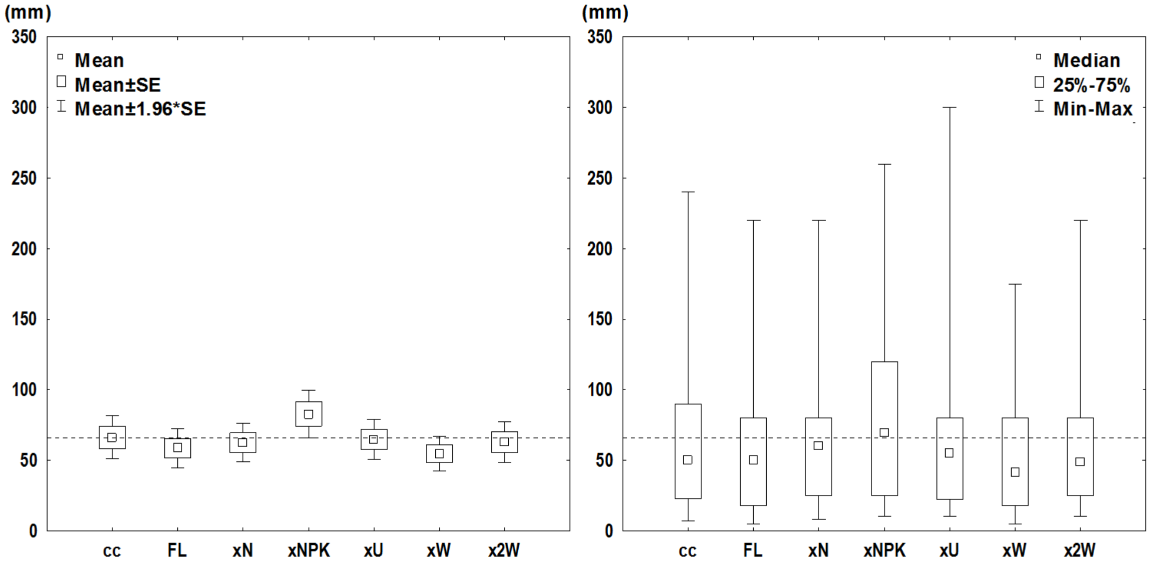

Figure III.5.D.c.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of plant height (Hmax) among different treatments at the inter-specific level for the year 2016. The dotted black line represents the mean value of the control plots (cc).

Intra-communities level

Grassland

In the grassland community, the Hmax of the cc ranged from 12 to 240 mm, with median and 75% quartile respectively of 68 and 115 mm (Table III.5.D.c.3). Analyzing the maximum values of Hmax, both xU and xNPK exerted positive effects (+60 and +20 mm, respectively), while all the other treatments induced negative effects, in particular the two water additions xW and x2W (-50 and -45 mm, respectively) (Table III.5.D.c.3).

Considering the 75% quartiles, the xNPK and x2W treatments, exerted a positive effect on Hmax (+15 and + 5 mm, respectively). According to the median values, xNPK (+12 mm), xN, xW and x2W (all +2 mm) showed positive effects (Table III.5.D.c.3), while urea addition (xU) did not exert any effect (no change respect to cc), and FL treatment exerted negative effect (-13 mm).

The negative influence of FL on Hmax was the only one case identified as statistically significant respect to the control plot, as tested by Wilcoxon test (p=0.03) (Fig. III.5.D.c.3). The comparison among similar treatments (among the nutrient additions as well as among the water additions, did not display any statistically significant difference, as tested by t-test (p>0.05).

Table III.5.D.c.4. Non-parametric statistics of grassland plant height (Hmax), computed for each single treatment, as well as for the entire monitoring period (2016-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	60	85	12	45	68	115	240	56.2
FL	60	72	8	38	55	103	220	51.2
xN	60	81	10	35	70	110	220	52.1
xNPK	60	92	10	45	80	130	260	57.8
xU	60	82	12	40	68	110	300	56.3
xW	60	70	10	35	70	100	190	42.1
x2W	58	79	10	40	70	120	195	51.0

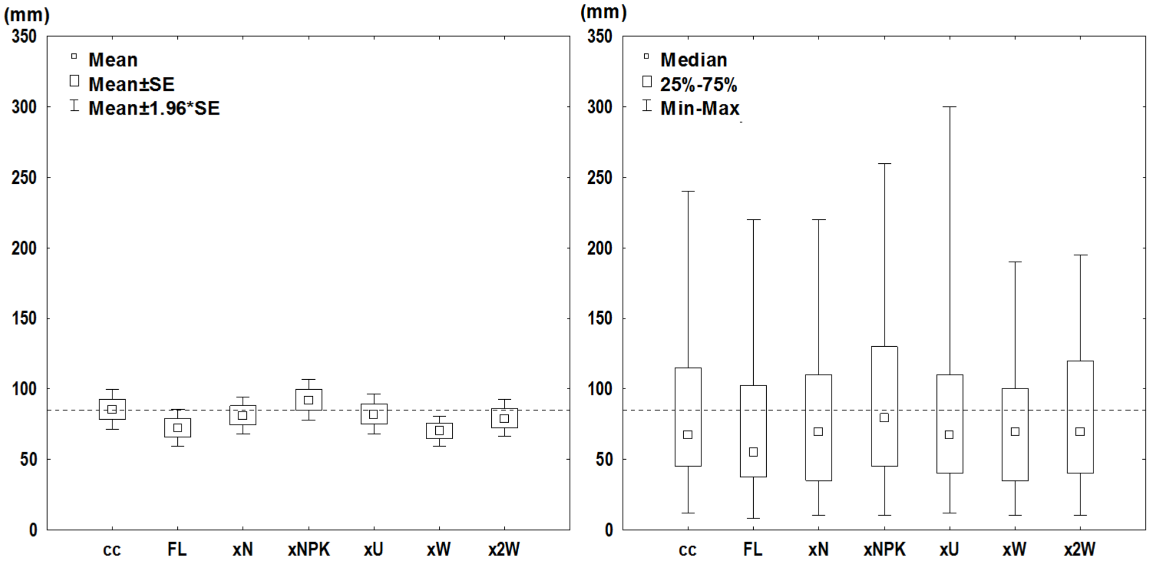

Figure III.5.D.c.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of grassland plant height (Hmax), among different treatments. The dotted black line represents the mean value of the control plots (cc).

Snowbed

In the snowbed community, the Hmax of the cc ranged from 7 to 200 mm, with median and 75% quartile respectively of 25 and 60 mm (Table III.5.D.c.5).

Analyzing the maximum values of Hmax, only x2W exerted a positive effect (+20 mm), while all the other treatments induced negative effects, in particular the flower removal (FL, -80 mm) (Table III.5.D.c.5).

Table III.5.D.c.5. Non-parametric statistics of snowbed plant height (Hmax) computed for each single treatment, as well as for the entire monitoring period (2016-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	42	48	7	20	25	60	200	44.3
FL	42	41	5	15	29	65	120	31.8
xN	42	44	8	18	28	60	160	34.4
xNPK	42	47	9	20	30	70	170	36.8
xU	42	44	10	20	25	60	200	36.1
xW	42	43	5	18	25	65	190	40.6
x2W	42	45	10	20	29	50	220	44.3

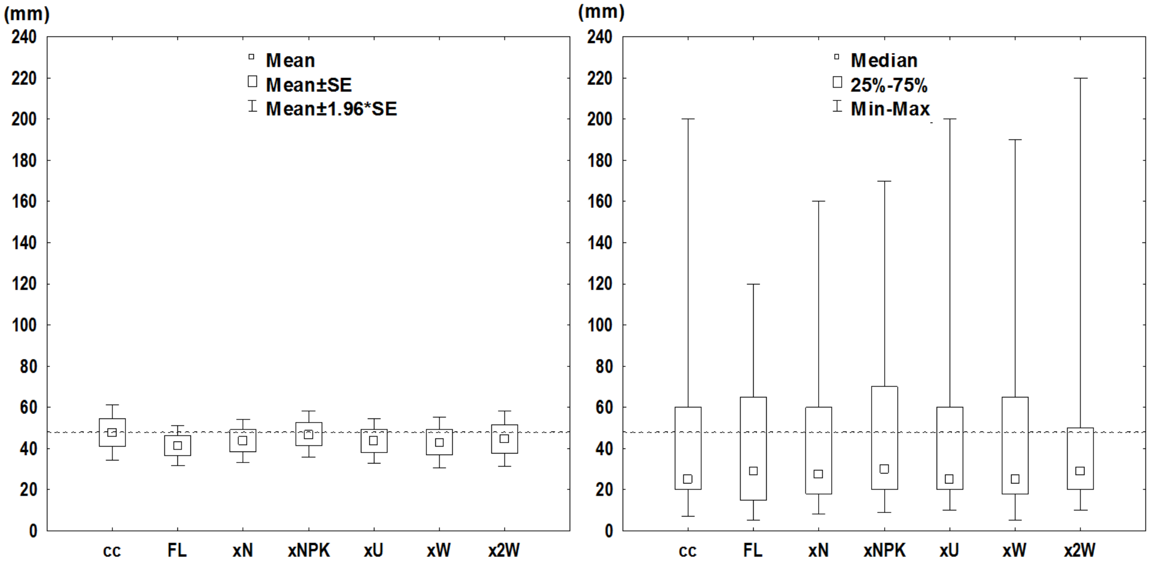

Figure III.5.D.c.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snowbed plant height (Hmax) among different treatments. The dotted black line represents the mean value of the control plots (cc).

Considering the 75% quartiles, the largest size effect was exerted by the xNPK treatment (+10 mm), but also FL and xW displayed positive effects (+5 mm). According to median values, positive effects were observed for xNPK (+ 5 mm), FL and x 2W (+4 mm) and xN (+3 mm), while the other treatments did not show any effect (Table III.5.D.c.5).

As tested by Wilcoxon test, none of each single treatment exerted statistically significant effects on Hmax respect to the control plot (Fig. III.5.D.c.5). Also in this case, comparing only the nutrient additions between each other, as well as water additions between each other, we did not find any statistically significant difference between similar treatments (p>0.05).

Comparison of treatments effects among communities

Interestingly, the comparison between the two selected vegetation communities highlighted different responses of Hmax to the FL treatment. Grassland showed a statistically significant reduction of Hmax, when flowers were removed (FL) analyzing all the population data (min, 25% and 75%, mean and median, max), while the same treatment did not exert any statistically significant effect in the snowbed community and affected differently the different components of the population data (in particular median and 75% vs all the others).

The response to the flowering treatment (FL) thus indicates that the grassland community was less able to continue its growth after the removal of flowers, like if reproduction was the main aim of these plants and, lost this option, they decided not to allocate more nutrients into the vegetative development.

Unexpectedly, the once per week water addition (xW) induced a reduction of Hmax. The intra-annual analysis revealed that such negative effect occurred in 2016, but not in 2015. In 2015 we had an extreme drought period in summer (see Cannone & Dalle Fratte, 2016 submitted), that most likely influenced such responses. Even if without statistically significance, the comparison of the maximum value stressed that such negative effect in 2016 could be driven mainly by grassland more than snowbed.

The xNPK exerted always the largest and positive response (both in grassland and snowbed) even if not statistically significant when tested against the control plot (cc). However, at the inter-specific level we observed a positive and statistically significant response to xNPK treatment, thus indicating that most likely the low statistically significance found at the intra-community level, could be just the result of both the short duration of the experiments and the large inter-annual variability of the two years of the experiment.

In any case, our results emphasize that the growth of alpine plant is strongly limited by the nitrogen, but only when combined with phosphorous (highlighting a strong P-limitation).

III.5.D.d. *Effects of ME on maximum leaf length (LLmax)*

Concerning the manipulation experiments, the analysis have been carried out following two steps: I) inter-specific (both inter-annual and intra-annual) level; II) intra-communities level.

Inter-specific and inter-annual level

During the first two years of ME (2015, 2016), the LLmax of the cc ranged between 3 and 202 mm, with a median and 75% quartile of respectively 26 and 45 mm (Table III.5.D.d.1).

Table III.5.D.d.1. Non-parametric statistics of leaf length (LLmax) computed for each single treatment during the entire monitoring period (2015-2016), at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	102	39	3	12	26	45	202	39.5
FL	102	37	4	12	26	47	169	36.0
xN	102	36	4	12	25	45	155	34.2
xNPK	102	44	6	15	28	51	219	45.6
xU	102	40	4	13	25	45	200	40.9
xW	101	37	3	11	23	45	187	36.4
x2W	100	36	4	12	23	44	185	34.5

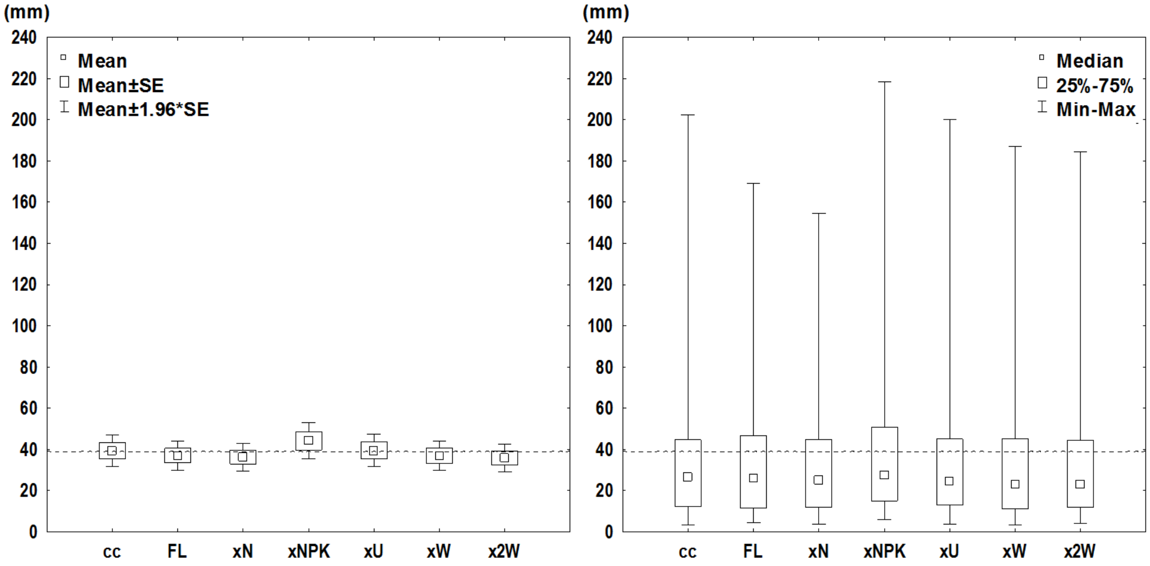

Figure III.5.D.d.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf length (LLmax) among different treatments at the inter-annual and inter-specific level. The dotted black line represents the mean value of the control plots (cc) for the whole period.

Analyzing the effect of the different treatments on the maximum values of LLmax, only the addition of ammonium and phosphate (xNPK) produced positive effect than the cc (+17 mm), while the ammonium nitrate addition (xN) produced the strongest negative effect of the whole dataset (-47 mm) (Fig. III.5.D.d.1).

Considering all the non-parametric statistics, according to the 75% quartiles, only xNPK involved an increase of LLmax (+6 mm). The median values followed a similar pattern with only xNPK exerting a positive effect (+2 mm), while surprisingly the two water additions (xW and x2W) exerted negative effects (in both cases -3 mm) (Table III.5.D.d.1).

As tested by Wilcoxon test, only the increase of LLmax exerted by xNPK was statistically significant (p=0.03) respect to the control plot. The comparison among similar treatments (both among nutrients additions as well as among water additions) did not show statistically significant differences, as tested by t-test (p>0.05).

Inter-specific and intra-annual level

2015

In 2015, the LLmax of the cc ranged from 7 to 202 mm, with median and 75% quartile respectively of 28 and 45 mm (Table III.5.D.d.2).

Concerning the maximum value of LLmax, all treatments, with the exception of xNPK, exerted negative effects, with lower values than the control plots, and reaching their maximum with xN (-47 mm). Analyzing the 75% quartiles no one of the treatments displayed a positive effect compared to cc; also according to the median (Table III.5.D.d.2), the treatments implied no or negative effects, in particular for all the nutrients additions (-3 mm).

As tested by Wilcoxon test the LLmax reduction of the xN treatments was identified as statistically significant (p=0.05) respect to the cc. Comparing the nutrient additions among each other, as well as the two water additions among each other, we did not identify any statistically significant difference, as tested by t-test (p>0.05) (Fig. III.5.D.d.2).

Table III.5.D.d.2. Non-parametric statistics of leaf length (LLmax) computed for each single treatment in 2015, at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	51	41	7	12	28	45	202	41.9
FL	51	39	4	12	28	41	169	39.5
xN	51	39	5	12	25	45	155	37.8
xNPK	51	42	6	14	25	45	213	43.2
xU	51	40	7	13	25	41	200	42.4
xW	50	38	7	11	28	43	187	37.6
x2W	50	37	6	11	27	42	185	35.7

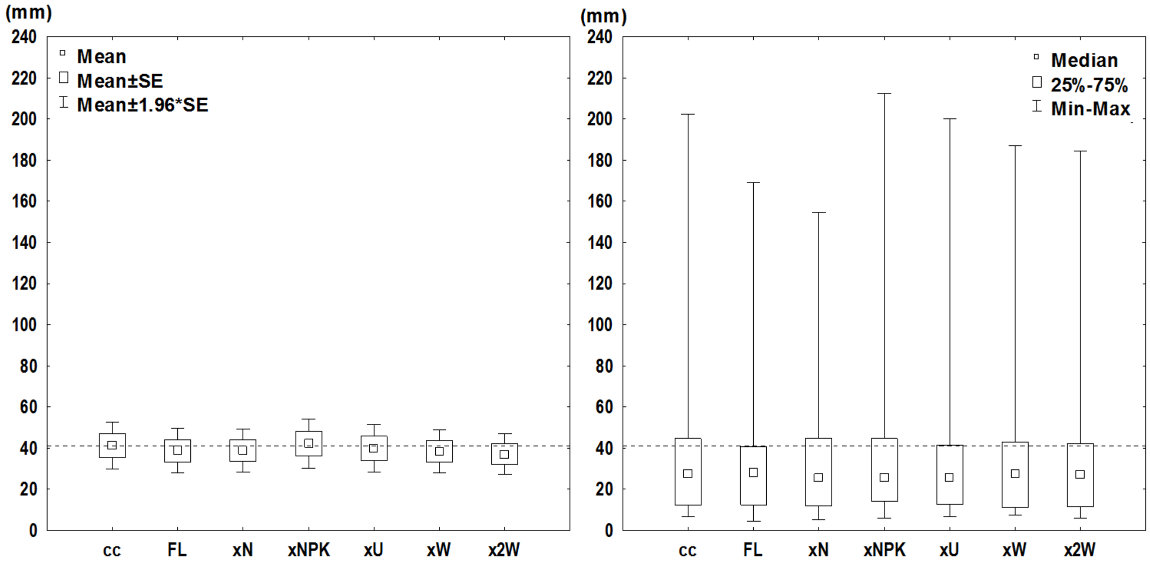

Figure III.5.D.d.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf length (LLmax) among different treatments at the inter-specific level for the year 2015. The dotted black line represents the mean value of the control plots (cc).

2016

In 2016, the LLmax of the cc ranged from 3 to 162 mm, with median and 75% quartile respectively of 26 and 46 mm (Table III.5.D.d.3). Analyzing the maximum values of LLmax, xNPK, xU and x2W exerted positive effects (+57, +8 and +2mm, respectively), while all the other treatments induced negative effects, in particular for FL and xN treatments (-31 and -25 mm, respectively) (Table III.5.D.d.3).

Considering the 75% quartiles, the xN was the only one treatment that exerted a negative effect on LLmax (-1 mm), while, the most positive effect was that of xNPK (+14 mm). According to the median values only xNPK showed positive effects (+6 mm) (Table III.5.D.d.3), while water additions (xW and x2W) and flower removal (FL) exerted the largest size negative effects (-5, -3 and -4 mm, respectively).

Table III.5.D.d.3. Non-parametric statistics of leaf length (LLmax) computed for each single treatment in 2016, at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	51	38	3	12	26	46	162	37.4
FL	51	35	6	11	22	48	131	32.4
xN	51	34	4	11	24	45	137	30.3
xNPK	51	46	6	15	33	60	219	48.1
xU	51	39	4	13	24	54	170	39.8
xW	51	35	3	11	21	51	148	35.5
x2W	50	35	4	12	23	51	164	33.6

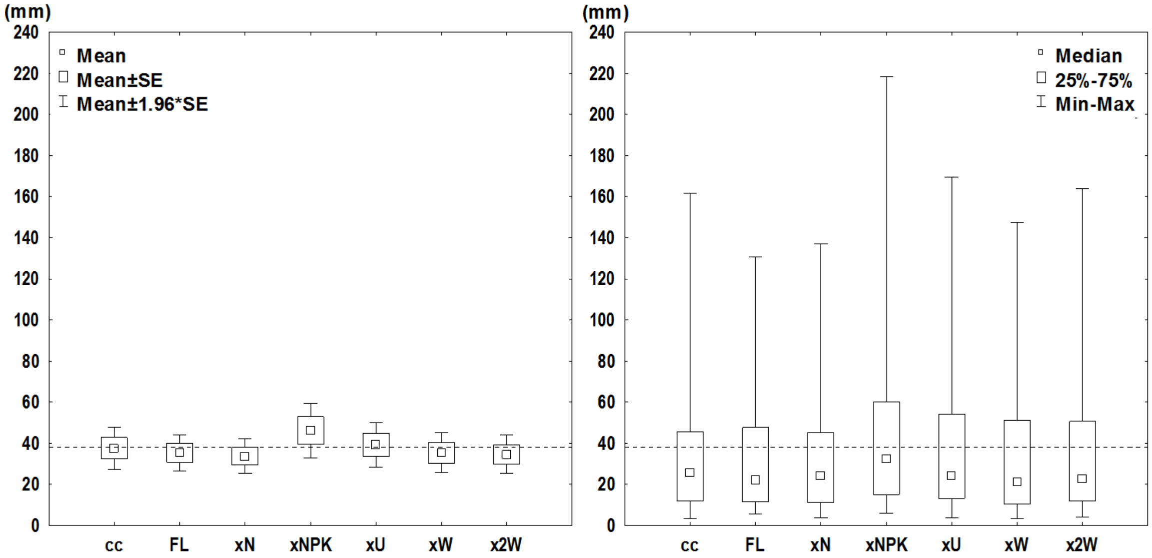

Figure III.5.D.d.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf length (LLmax) among different treatments at the inter-specific level for the year 2016. The dotted black line represents the mean value of the control plots (cc).

The positive effect of xNPK on LLmax was the only one identified as statistically significant respect to the control plots, as tested by Wilcoxon test (p=0.03) (Fig. III.5.D.d.3). Comparing only the nutrient additions between each other, as well the water additions between each other, they did not show any statistically significant difference, as tested by t-test (p>0.05).

Intra-community level

Grassland

In the grassland community, the LLmax of the cc ranged from 7 to 202 mm, with median and 75% quartile respectively of 38 and 81 mm (Table III.5.D.d.3). Analyzing the maximum values of LLmax, the xNPK treatment was the only one that exerted positive effects (+17 mm), while all the other treatments induced negative responses reaching their maximum with xN (-47 mm, respectively) (Table III.5.D.d.3).

Considering the 75% quartiles, only the xNPK treatment exerted a positive effect on LLmax (+2 mm); also according to the median values, xNPK (+3 mm) and, to a lesser extent, xU (+1 mm) showed positive effects (Table III.5.D.d.3). The most negative effect according to the median values was recorded for xW and x2W (-2 and -3 mm, respectively).

The negative effect of FL, xN, xW and x2W on LLmax were all identified as statistically significant compared to cc, as tested by Wilcoxon test (in all cases p=0.03) (Fig. III.5.D.d.3). Comparing similar treatments between each other (only nutrients additions or only water additions) we did not find any statistically significant difference, as tested by t-test (p>0.05).

Table III.5.D.d.4. Non-parametric statistics of grassland leaf length (LLmax), computed for each single treatment, as well as for the entire monitoring period (2016-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	60	54	7	23	38	81	202	45.6
FL	60	50	6	16	38	70	169	41.8
xN	60	49	6	22	37	63	155	38.8
xNPK	60	60	7	22	41	83	219	53.1
xU	60	55	8	19	39	70	200	47.3
xW	60	50	5	21	36	79	187	41.6
x2W	58	49	4	20	35	72	185	39.8

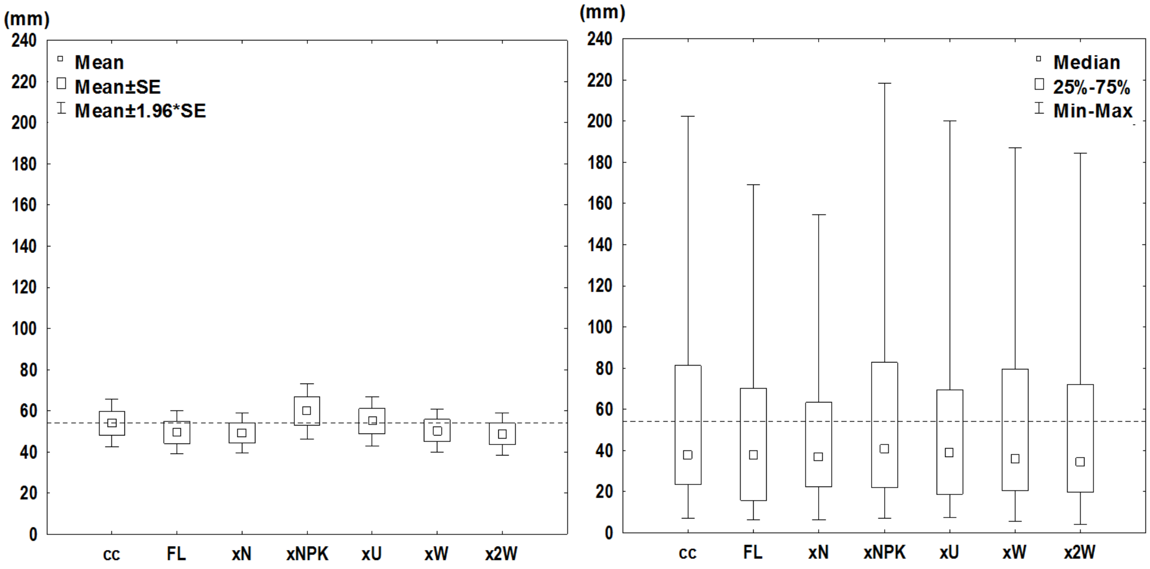

Figure III.5.D.d.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of grassland leaf length (LLmax), among different treatments. The dotted black line represents the mean value of the control plots (cc).

Snowbed

In the snowbed community, the LLmax of the cc ranged from 3 to 40 mm, with median and 75% quartile respectively of 15 and 28 mm (Table III.5.D.d.5).

Table III.5.D.d.5. Non-parametric statistics of snowbed leaf length (LLmax) computed for each single treatment, as well as for the entire monitoring period (2016-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	42	19	3	10	15	28	40	10.0
FL	42	19	4	11	17	28	42	10.5
xN	42	18	4	10	16	25	45	10.5
xNPK	42	22	6	13	18	29	75	13.4
xU	42	18	4	11	17	23	33	8.4
xW	41	17	3	10	16	22	37	9.7
x2W	42	18	5	10	16	23	44	10.7

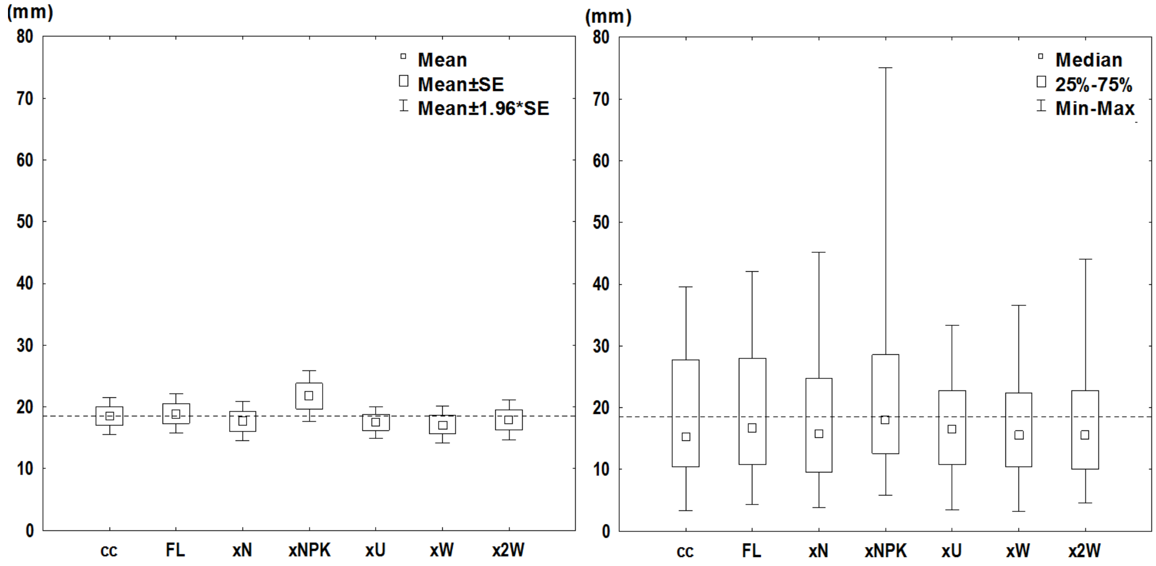

Figure III.5.D.d.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snowbed leaf length (LLmax) among different treatments. The dotted black line represents the mean value of the control plots (cc).

Analyzing the maximum values of LLmax, we found positive effects with the following treatments: FL (+2 mm), xN (+5 mm), xNPK (+35 mm) and x2W (+4 mm), while only xW and xU induced negative effects, reaching their maximum with the urea addition (xU, -7 mm) (Table III.5.D.d.5).

Considering the 75% quartiles, only xNPK involved an increment of LLmax (only +1 mm) compared to cc, while FL did not exert any effect and all the other treatments involved negative effects, up to -6 mm (in xW). According to median values, positive effects were observed for all the treatments, with xNPK exerting the largest size effect (+3 mm) (Table III.5.D.d.5).

As tested by Wilcoxon test, the positive effects of xNPK was identified as statistically significant ($p=0.03$) respect to the cc. Comparing similar treatments between each other (only the nutrient additions or only water additions), we did not find any statistically significant difference, as tested by t-test ($p>0.05$).

Comparison of treatments effects among communities

The xNPK exerted always the largest and most positive response (in both grassland and snowbed) even if for grasslands we did not get a statistically significant difference with the control plots.

Also in this case, as already observed for the Hmax (see chap. III.5.D.c), we could hypothesize that alpine ecosystems are strongly P-limited concerning their leaves development and thus carbon acquisition.

The water addition (x W and x2W) exerted negative influence only on grassland species, while we did not identify any statistically significant influence on snowbed species.

The flower removal involved a negative impact on grassland leaves development, that showed a reduction compared to cc (similarly to what observed for Hmax, see chap. III.5.D.c). Probably, as hypothesized for Hmax, grassland communities are less able to continue their vegetative development when reproductive organs have been removed.

In general, grassland was the community type that showed the largest negative and thus unexpected responses to treatments, indicating their higher sensitivity to the experiments.

III.5.D.e. *Effects of ME on leaf senescence (LS)*

Concerning the manipulation experiments, the analyses have been carried out following two steps: I) inter-specific level; II) intra-community level. In this chapter we will present the results only for 2015 because the collection of the LS data in 2016 was completed only in October and therefore, due to time constraints, it could not be possible to include them in the data elaboration (see methods).

Inter-specific level

At the end of the season 2015, the LS of the cc ranged from early July to mid-September (188-256 DOY), with a median and 75% quartile occurring respectively at the end of July (212 DOY) and in mid-August (223 DOY) (Table III.5.D.e.1).

Table III.5.D.e.1. Non-parametric statistics of leaf senescence (LS), computed for each single treatment, at the inter-specific level, for the year 2016.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	50	214	188	201	212	223	256	17.7
FL	51	215	190	201	216	223	263	16.1
xN	51	212	188	204	208	216	256	14.1
xNPK	50	217	188	204	214	229	256	18.5
xU	50	213	188	201	216	220	256	14.9
xW	47	217	188	204	220	226	256	17.4
x2W	48	212	188	203	210	220	256	14.1

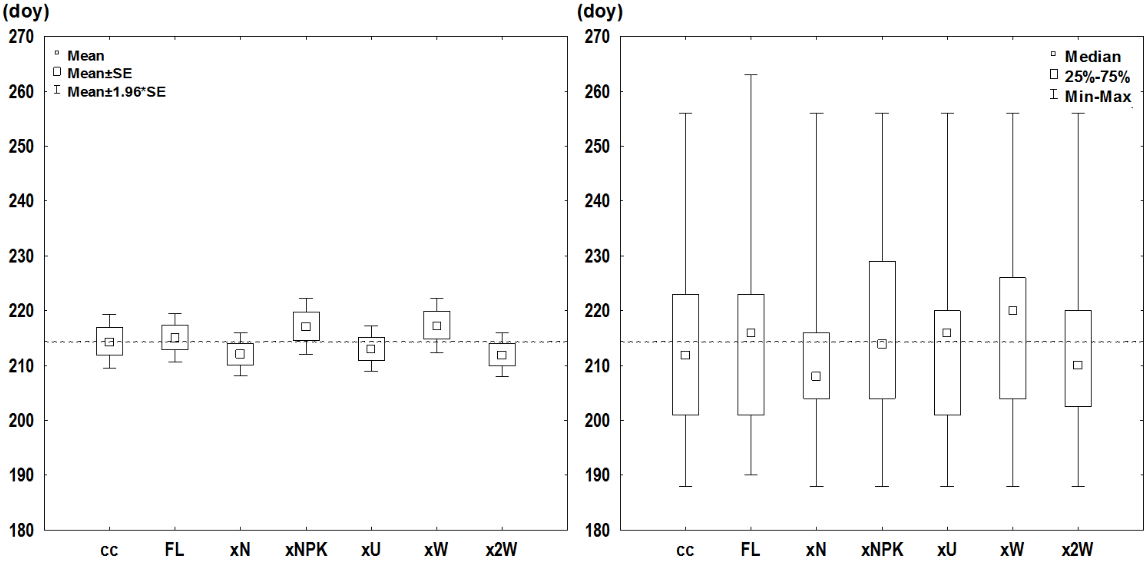

Figure III.5.D.e.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of leaf senescence (LS) among treatments at the inter-specific level for the year 2015. The dotted black line represents the mean value of the control plots (cc).

Analyzing the effect of the different treatments on the onset of LS, we did not observe large differences: only FL exerted a small delay (+2 days compared to cc), while all the other treatments started LS the same day of cc (Table III.5.D.e.1). Similarly, the LS completion showed no effect among the different treatments, apart for FL that showed a delay of one week (+7 days).

Considering all the non-parametric statistics, according to the 75% quartiles, only xNPK and xW involved latest LS (+6 and +3 days, respectively). On the contrary, the largest advance of LS resulted from xN addition. According to the median values, LS was delayed for FL (+4 days), xNPK (+2 days), xU (+4 days) and the latest delay was obtained with one weekly addition of water (xW, +8 days), while xN exerted the largest negative impact (advance of LS of -4 days) (Table III.5.D.f.1).

As tested by Wilcoxon test, we did not find any statistically significant difference, comparing each single treatment to the cc ($p>0.05$). Similarly, also similar treatments showed no statistically significant differences between each others, as tested by t-test among nutrients additions (xN, xNPK, xU) as well as among water additions (xW and x2W) ($p>0.05$).

Intra-community level

Grassland

In the grassland community, the LS of the cc ranged from early July to mid-September (88-256 DOY), while the median and 75% quartile respectively occurred at the end of July (212 DOY) and in early August (220 DOY) (Table III.5.D.e.2).

Analyzing the onset of LS, it followed the inter-specific pattern, thus without any effect exerted from all treatments, apart for a small delay of 2 days with FL (Table III.5.D.e.3). The LS completion was not affected by most of the treatments: only FL and xW exerted an advance of LS (-6 days).

Considering the 75% quartiles, the xNPK treatment exerted the strongest delay of LS (+24 days), while all the other treatments showed the same value of cc, or a delay of few days, as for xN (+3 days) or xU and xW (in both cases +6 days) (Table III.5.D.e.2).
Concerning the median values, only x2W involved an advance of LS (-4 days), while all the other treatments, exerted a delay, the largest of which with xW treatment (+8 days) (Table III.5.D.e.2).

However, as tested by Wilcoxon test, none of the treatments exerted statistically significant effects on LS compared to cc ($p>0.05$) (Fig. III.5.D.e.2). Similarly, we did not find any statistically significant difference of LS also among the nutrients addition (xN, xNPK, xU), or among the water addition (xW, x2W), as tested by t-test ($p>0.05$).

Table III.5.D.e.2. Non-parametric statistics of grassland leaf senescence (LS), computed for each single treatment, for the year 2015.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	29	214	188	201	212	220	256	19.4
FL	30	215	190	201	214	220	250	15.6
xN	30	216	188	204	214	223	256	17.1
xNPK	30	219	188	201	214	244	256	22.2
xU	29	215	188	204	216	226	256	16.2
xW	28	217	188	204	220	226	250	17.4
x2W	27	211	188	201	208	220	256	14.7

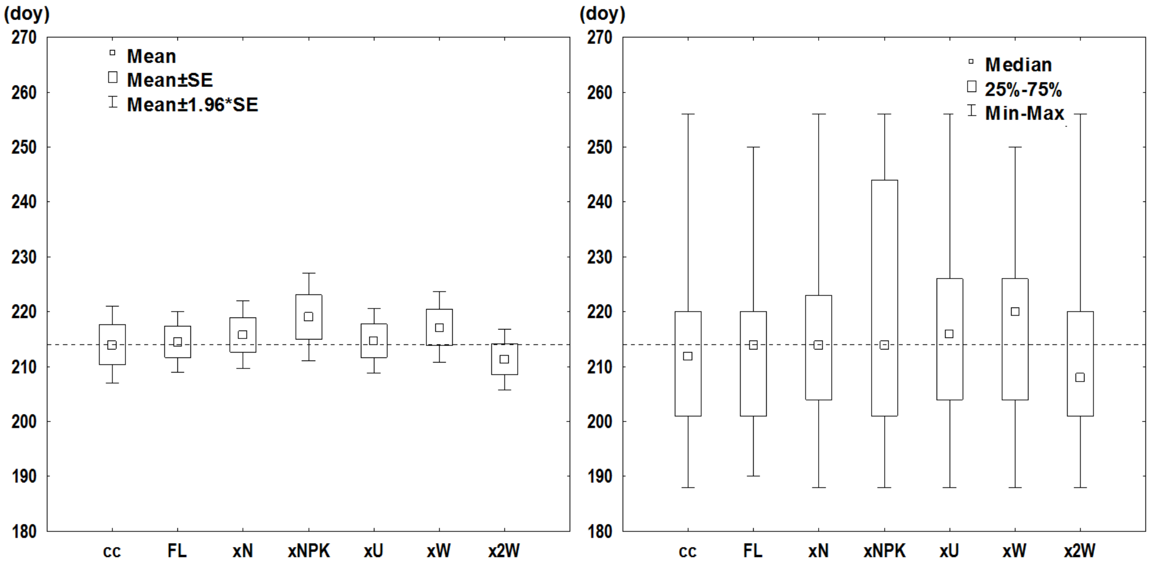

Figure III.5.D.e.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of grassland leaf senescence (LS), among different treatments. The dotted black line represents the mean value of the control plots (cc).

Snowbed

In the snowbed community, the LS of the cc ranged from mid-July to early September (194-244 DOY), with the median and 75% quartile respectively occurring at end of July (212 DOY) and mid-August (223 DOY) (Table III.5.D.e.3).

Analyzing the earliest onset of LS, only xU and xW treatments exerted an advance of 4 days compared to cc. Here, the LS completion showed a larger variability among treatments. The latest LS completion occurred for FL (+19 days) and xW (+12 days), and the earliest for xN (-32 days) (Table III.5.D.e.3).

Considering the 75% quartiles, only xW showed a delay of LS (+3 days), while all the other treatments exerted an advance, reaching the maximum with xN (-15 days). The median values indicated little change respect the cc: FL delayed LS of +4 days, while xN advanced of -4 days (Table III.5.D.e.3).

Table III.5.D.e.3. Non-parametric statistics of snowbed leaf senescence (LS) computed for each single treatment, for the year 2015.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	21	215	194	201	212	223	244	15.7
FL	21	216	194	208	216	223	263	17.3
xN	21	207	194	204	208	208	212	4.7
xNPK	20	214	194	206	214	223	229	11.0
xU	21	211	190	201	212	216	236	12.8
xW	19	218	190	204	212	226	256	17.8
x2W	21	213	194	204	212	216	244	13.7

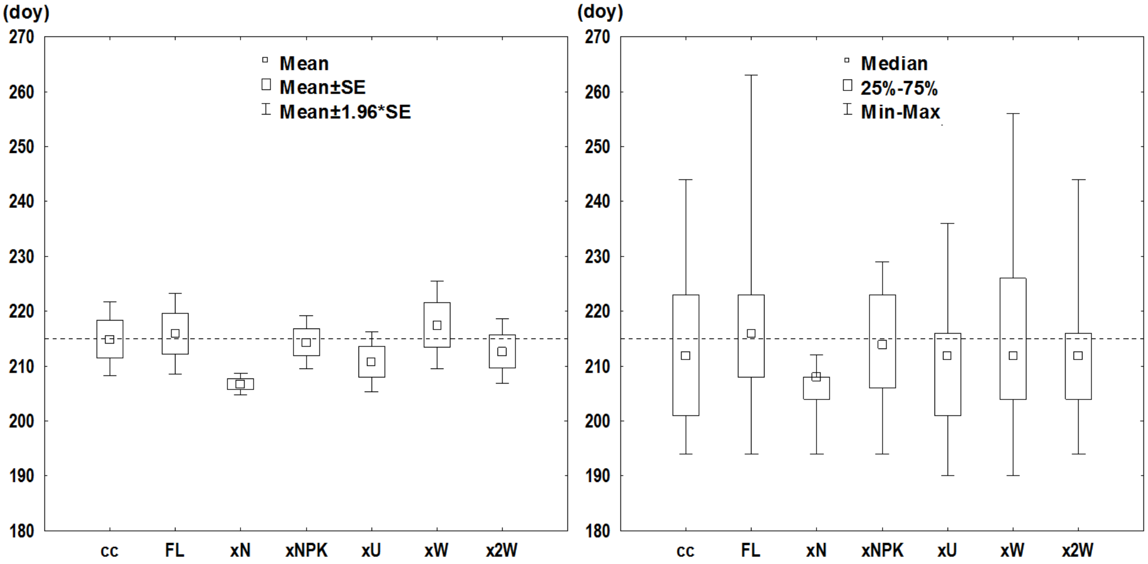

Figure III.5.D.e.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snowbed leaf senescence (LS) among different treatments. The dotted black line represents the mean value of the control plots (cc).

As tested by Wilcoxon test, we did not identify statistically significant treatments effect compared to cc (Fig. III.5.D.e.3). Similarly we did not find statistically significant differences among similar treatments, as tested by t-test between nutrients additions and between water additions ($p>0.05$).

Comparison of treatments effects among communities

Our data showed low evidences of statistically significant treatments effects on LS. This is not surprising, given the high photoperiodic limitation of this phenophase (see chap III.5.B.j and III.5.B.k.).

However, we found differences between the two vegetation communities. In particular, we found snowbed to be highly sensitive to the ammonium sulfate (xN), which exerted a negative input on LS (i.e. advance of LS).

It could be supposed that this advance of LS, could be related to a process of acidification due to the addition of ammonium sulfate. If this was true, we could expect a similar response to occur also in grassland community. This was not the case, leaving space for other hypothesis, such as species-specific metabolism, or differences of the background soil pH, or also a conservative strategy peculiar of snowbed communities: once received nitrogen supply enough to recharge their nutrient storage for the next year, the metabolism could become like a surplus, only driving plants to higher exposure to risks (such as early frosts and potentially loss of nutrients).

We also found remarkable evidences that water addition, in particular once a week (xW) exerted a positive impact on LS. In summer 2015, an extreme drought period occurred (see Cannone & Dalle Fratte, 2016 submitted), and thus the response to water could be also biased on such extreme event. However, with our data, we could say that LS was delayed when water was available, but only in “normal” proportion (xW), since the twice addition of water (x2W) exerted the opposite pattern (small advance of LS).

FL exerted the largest effect on the snowbed communities, confirming results from the other studied plant traits that snowbed species were more reactive to flower removal compared to grassland species.

It is also remarkable to note the strong delay of LS exerted by xNPK in the grassland community, even if without statistically significant differences respect to cc. Snowbeds did not show any effect from xNPK, highlighting that grassland species could benefit from nitrogen addition in combination to phosphorous, protracting their growing season later in Fall.

Moreover, we found evidences of a strong influence of FL treatment, in particular for the snowbed community, where LS was strongly delayed after flower removals. These findings are extremely important in terms of energetic balance and efficiency of soil resources exploitation of alpine snowbeds compared to grasslands. No-flowering years could thus affect vegetation communities in different ways, with snowbed species exhibiting higher efficiency concerning the balance of energetic resources between vegetative and reproductive organs.

III.5.D.f. *Effects of ME on above ground biomass (ABG) at the peak of the growing season*

Concerning the manipulation experiments, the analysis have been carried out following two steps: I) inter-specific (both inter-annual and intra-annual) level; II) intra-communities level.

Inter-specific and inter-annual level

During the first two years of ME (2015, 2016), the ABG at the peak of the season (H2) of the cc ranged between 5.7 and 25.2 g, with the median and 75% quartile of respectively 13.6 and 20.1 g (Table III.5.D.f.1).

Table III.5.D.f.1. Non-parametric statistics of above ground biomass (ABG) computed for each single treatment during the entire monitoring period (2015-2016), at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	12	14.4	5.7	8.4	13.6	20.1	25.2	6.9
FL	12	15.9	4.6	9.6	12.4	22.0	35.5	9.4
xN	12	13.6	4.4	8.2	11.3	18.9	30.2	7.8
xNPK	12	25.9	8.9	15.3	21.4	36.1	47.8	13.1
xU	12	19.1	3.5	12.8	18.1	28.1	31.1	8.8
xW	12	18.2	5.6	11.1	17.1	23.2	34.8	8.9
x2W	12	20.2	10.5	12.8	16.9	25.9	36.7	9.4

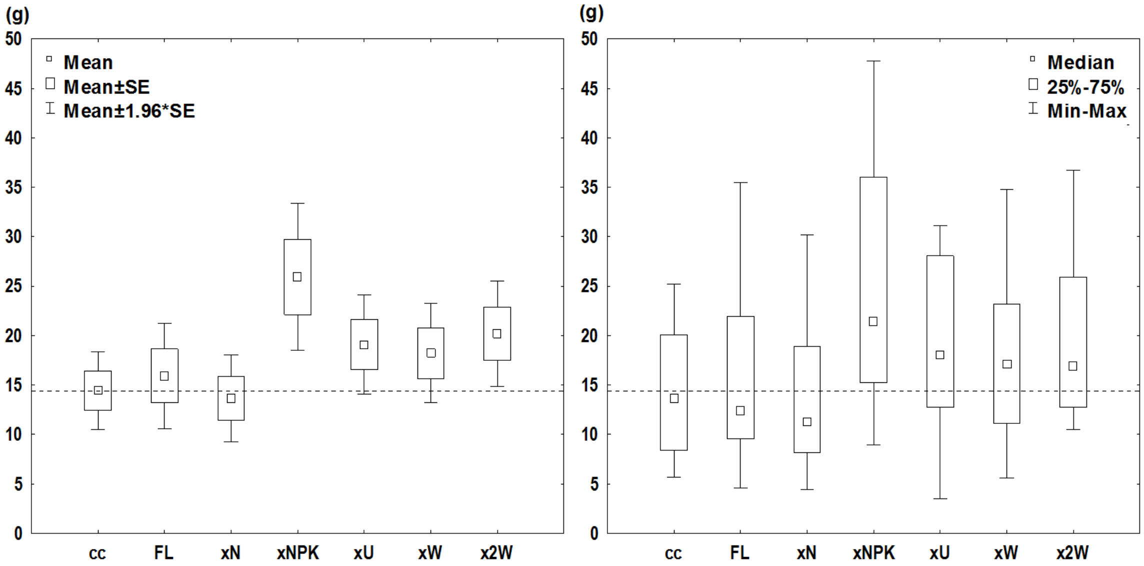

Figure III.5.D.f.1. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of above ground biomass (ABG) among different treatments at the inter-annual and inter-specific level. The dotted black line represents the mean value of the control plots (cc) for the whole period.

Analyzing the effect of the different treatments on the maximum values of ABG, all the treatments exerted positive influence, reaching its maximum with addition of xNPK (+22.6 g) (Table III.5.D.f.1).

Considering all the non-parametric statistics, according to the 75% quartiles, only xN involved a negative effect on the ABG (-1.9 g), while all the other treatments increased the ABG, up to maximum +16 g, with xNPK (Table III.5.D.f.1). According to the median, also FL exerted negative impact on ABG (-1.2 g) coupled with xN (-2.3 g), while all the other treatments increased the ABG, with the maximum positive effect recorded, again, with xNPK (+7.8 g).

As tested by Wilcoxon test, the positive effects on ABG exerted by xNPK (p=0.03), xU (p=0.05), xW (p=0.05) and x2W (p=0.03) were identified as statistically significant respect to the control plots (Fig. III.5.D.f.1).

The comparison among nutrients additions (xN, xNPK, xU), as well as among water additions (xW and x2W) did not show statistically significant differences, as tested by t-test (p>0.05) (Fig. III.5.D.f.1).

Inter-specific and intra-annual level

2015

In 2015, the ABG of the cc ranged from 5.7 to 25.2 g, with median and 75% quartile respectively of 11.4 and 25 mm (Table III.5.D.f.2).

Concerning the maximum value of ABG, negative impacts were exerted by FL and xN (-4.4 and -5.6 g, respectively), while all the other treatments exerted positive effects compared to the cc, reaching the maximum with xNPK (+22.6) (Table III.5.D.f.2).

Analyzing the 75% quartiles, all treatments, except for xNPK (+7.5 g), exerted negative effects compared to the cc, with the most negative effect achieved by FL (-7.5 g). According to the median, only xN involved lower ABG of that of the cc (-0.7 g), while all the other treatments exerted positive effect, reaching its maximum with xNPK (+5.7 g). (Table III.5.D.f.2).

Table III.5.D.f.2. Non-parametric statistics of above ground biomass (ABG) computed for each single treatment in 2015, at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	6	14.4	5.7	7.7	11.4	25.0	25.2	8.9
FL	6	12.2	4.6	6.0	12.1	17.5	20.8	6.3
xN	6	11.0	4.4	5.5	11.2	14.2	19.6	5.7
xNPK	6	22.6	8.9	12.0	17.1	32.5	47.8	14.9
xU	6	14.7	3.5	10.7	12.8	21.5	27.0	8.4
xW	6	16.3	5.6	8.4	15.2	18.4	34.8	10.3
x2W	6	18.9	10.8	11.5	16.0	22.5	36.7	9.7

As tested by Wilcoxon test, the negative effects on ABG exerted by FL (p=0.05) and xN (p=0.03), as well as the positive effects of xNPK (p=0.03) and x2W (p=0.05), were identified as statistically significant respect to the control plots (Fig. III.5.D.f.2).

The comparison among similar treatments (only nutrients additions as well as only water additions) did not show statistically significant differences, as tested by t-test (p>0.05) (Fig. III.5.D.f.2).

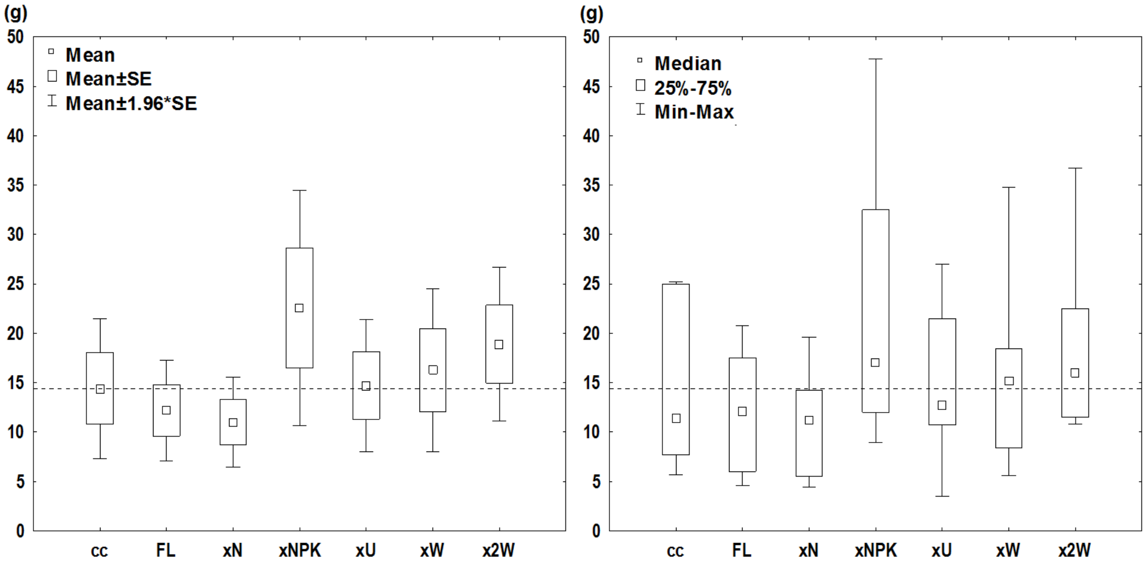

Figure III.5.D.f.2. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of above ground biomass (ABG) among different treatments at the inter-specific level for the year 2015. The dotted black line represents the mean value of the control plots (cc).

2016

In 2016, the ABG of the cc ranged from 9 to 22.2 g, with median and 75% quartile respectively of 14 and 17.9 g (Table III.5.D.f.3).

Table III.5.D.f.3. Non-parametric statistics of above ground biomass (ABG) computed for each single treatment in 2016, at the inter-specific level.

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	6	14.4	9.0	9.5	14.0	17.9	22.2	5.2
FL	6	19.6	9.4	9.7	17.3	28.6	35.5	11.1
xN	6	16.3	6.7	9.7	14.1	23.0	30.2	9.1
xNPK	6	29.3	16.0	19.4	28.9	37.5	45.0	11.4
xU	6	23.5	14.3	17.2	24.0	30.2	31.1	7.5
xW	6	20.2	10.8	11.4	22.6	23.3	30.7	7.7
x2W	6	21.5	10.5	14.0	19.2	29.3	36.6	9.9

Analyzing the maximum values of ABG, all the treatments exerted positive effect, reaching its maximum in xNPK (+22.8 g, more than double respect the cc) (Table III.5.D.f.3). The same pattern was observed also considering the 75% quartiles or the median, with xNPK exerting always the largest size effect (respectively +19.6 and +14.9 g; in both cases more than double respect the cc).

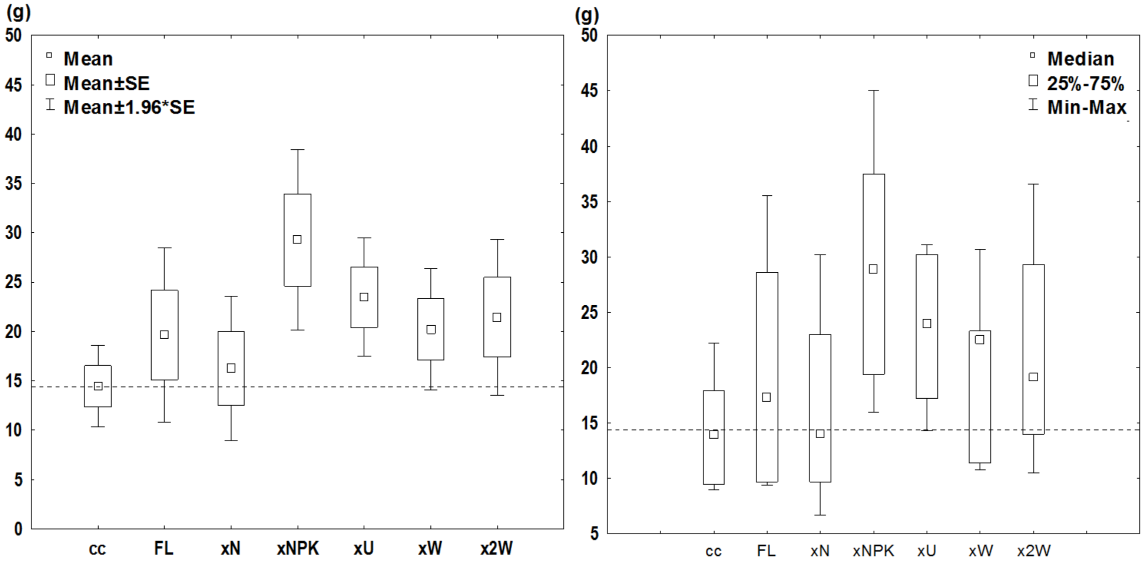

Figure III.5.D.f.3. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of above ground biomass (ABG) among different treatments at the inter-specific level for the year 2016. The dotted black line represents the mean value of the control plots (cc).

As tested by Wilcoxon test, all treatments, except for xN, exerted statistically significant increase of the biomass (in all cases p=0.03) (Fig. III.5.D.f.3). Comparing the effects among similar treatments (i.e. among only nutrients additions, or only water additions), the xNPK displayed a statistically significant increase of the ABG when compared to the xN (p=0.05) (Fig. III.5.D.f.3).

Intra-communities level

Grassland

In the grassland community, the ABG of the cc ranged from 15 to 25.2 g, with median and 75% quartile respectively of 20.1 and 25 g (Table III.5.D.f.3).

Analyzing the maximum values of ABG, all treatments exerted positive effect, reaching the maximum with xNPK (+22.6 g) (Table III.5.D.f.3).

Considering the 75% quartile, only xN exerted negative influence (but only -2 g compared to the cc), while all the other treatments involved a positive response, up to +20 g (in xNPK). The same pattern was observed also for the median values, with xN exerting negative response (-1.2 g), and all the other treatments displaying positive effects, up to +16 g (in xNPK) (Table III.5.D.f.4).

However, as tested by Wilcoxon test, only the enhanced ABG of xNPK ($p=0.03$), xU ($p=0.05$) and x2W ($p=0.03$) were identified as statistically significant. The xNPK exerted a statistically significant increase of the ABG compared with both xN ($p<0.01$) and xU ($p=0.05$), as tested by t-test. The comparison of the two water treatments instead did not reveal any statistically significant difference, as tested by t-test ($p>0.05$) (Fig. III.5.D.f.4).

Table III.5.D.f.4. Non-parametric statistics of grassland above ground biomass (ABG), computed for each single treatment, as well as for the entire monitoring period (2016-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	6	20.2	15.0	15.8	20.1	25.0	25.2	4.6
FL	6	23.1	13.3	17.5	22.0	28.6	35.5	8.0
xN	6	19.6	12.6	14.2	18.9	23.0	30.2	6.4
xNPK	6	36.2	19.6	32.5	36.1	45.0	47.8	10.1
xU	6	25.5	14.0	21.5	28.1	30.2	31.1	6.6
xW	6	23.7	14.5	15.8	23.2	30.7	34.8	8.0
x2W	6	27.2	16.7	21.2	25.9	36.6	36.7	8.4

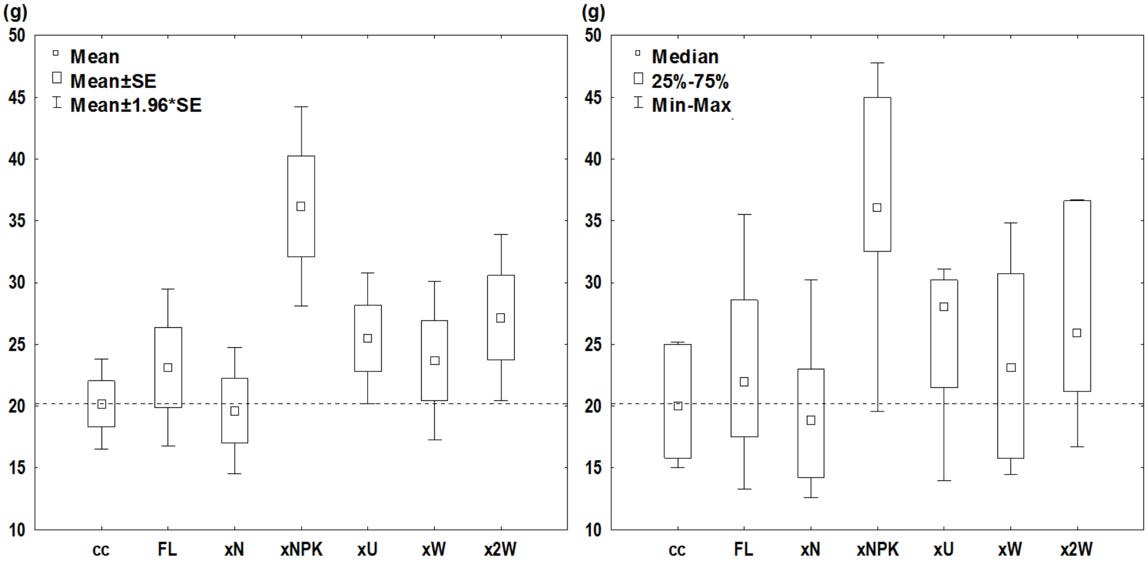

Figure III.5.D.f.4. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of grassland above ground biomass (ABG), among different treatments. The dotted black line represents the mean value of the control plots (cc).

Snowbed

In the snowbed community, the ABG of the cc ranged from 5.7 to 12.2 g, with median and 75% quartile respectively of 8.4 and 9.5 g (Table III.5.D.f.5).

Table III.5.D.f.5. Non-parametric statistics of snowbed above ground biomass (ABG) computed for each single treatment, as well as for the entire monitoring period (2016-2016).

	Valid N	Mean	Minimum	25%	Median	75%	Maximum	Std.Dev.
cc	6	8.7	5.7	7.7	8.4	9.5	12.2	2.2
FL	6	8.7	4.6	6.0	9.6	10.9	11.5	2.8
xN	6	7.7	4.4	5.5	8.2	9.7	9.9	2.4
xNPK	6	15.7	8.9	12.0	15.3	19.4	23.2	5.1
xU	6	12.7	3.5	10.7	12.9	17.2	18.9	5.5
xW	6	12.8	5.6	8.4	11.1	18.4	22.1	6.2
x2W	6	13.2	10.5	10.8	12.8	15.2	17.1	2.7

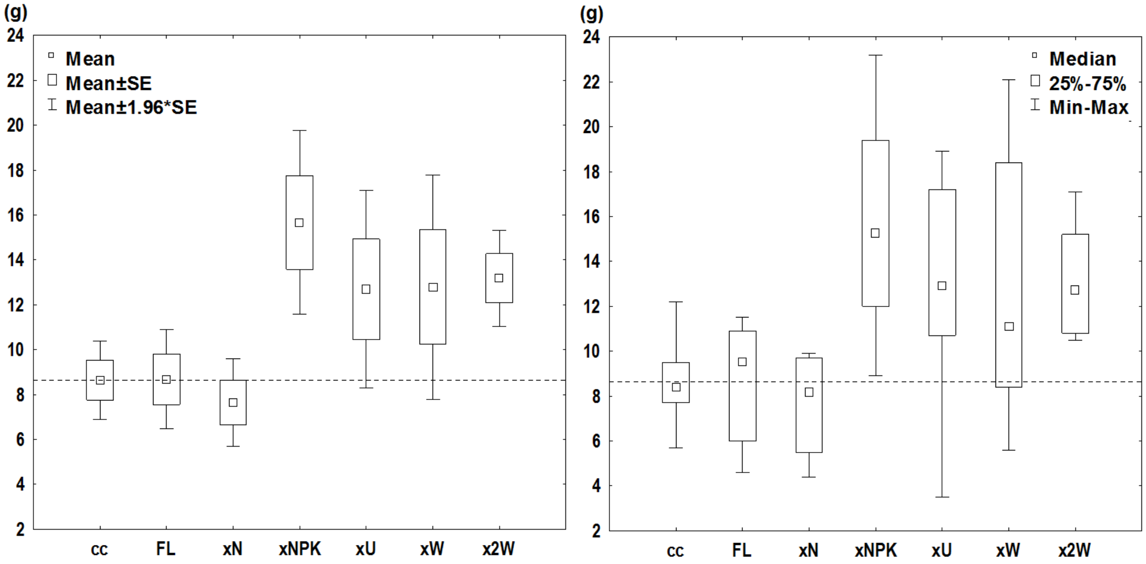

Figure III.5.D.f.5. Non-parametric statistics (left panel: means ± standard error; right panel: minimum, 25%, median, 75%, maximum) of snowbed above ground biomass (ABG) among different treatments. The dotted black line represents the mean value of the control plots (cc).

Analyzing the maximum values of ABG, the FL and xN treatment exerted negative effects (-0.7 and -2.3 g, respectively), while all the other treatments involved a positive response, reaching its maximum with xNPK (+11 g) (Table III.5.D.f.5).

However, considering the 75% quartiles, all the treatments exerted positive effects, from +0.2 g (in xN) to +9.9 g (in xNPK). The median values indicated a small negative effect for xN (-0.2 g) and the largest positive effect with xNPK (+6.9 g) (Table III.5.D.f.5).

As tested by Wilcoxon test for each treatments with cc, we observed statistically significant effects for all the treatments, except FL: xN induced a negative impact (p=0.05), while xNPK (p=0.03), xU (p=0.05), xW (p=0.05) and x2W (p=0.03) induced a positive effect (Fig. III.5.D.f.5).
The comparison between similar treatments revealed a statistically significant difference between xN and xNPK, as tested by t-test (p<0.01) (Fig. III.5.D.f.5).

Comparison of treatments effects among communities

Our results highlighted strong responses of ABG to treatments, with some common responses between snowbed and grassland, but also with some divergences.

In both the communities (grassland and snowbed), we observed a statistically significant increase of the ABG with the addition of ammonium and phosphate (xNPK), urea (xU), and with a twice-weekly addition of water (x2W). The xNPK treatment exerted the largest impact (on both grassland and snowbed), which was identified as statistically significant different respect the nitrate addition (xN).

Above all the plant traits investigated (where we already observed the strong response to xNPK), the ABG showed the largest and more evident effect, highlighting again the high sensitivity of the investigated communities to nitrogen, when combined with phosphate.

The FL treatment showed low effect in both the communities, even if the response was always positive.

Both the communities displayed negative response with xN, but snowbeds exhibited a statistically significant difference of ABG compared to cc, indicating again a higher sensitivity to this compounds (see also chap. III.5.D.c).

III.6. Discussion

III.6.A. Long-term alpine plant phenology

III.6.A.a. *Influence of elevation on the phenology of alpine plants*

According to our data, the influence of the elevation gradient was almost negligible on the phenological data both considering the inter-annual and inter-specific level as well as the inter-annual and intra-growth forms level.

Literature data clearly indicate a delay of phenology with elevation in the alpine region (e.g. Ziello et al., 2009; Cornelius et al., 2012), mostly associated to the temperature decrease due to the increase in geographical elevation (Ziello et al., 2009). Therefore, the low relation of our phenological data with elevation was likely due to the restricted elevation range (250 m), compared to the potential elevation range of the species (according to Ziello et al., 2009).

Moreover, high elevation environments are characterized by a mosaic of micro-habitats in relation to the high variability of morphology, and in few meters the soil temperature can change drastically together with the season length (Scherrer & Korner, 2011), thus overwhelming the air temperature elevation gradient and its influence on phenology.

According to our data, the SM (that was the best predictor of the earlier phenophases) was not influenced by the elevation gradient, indicating that micro-habitat variability (topography, roughness, slope, aspect) was the main driver of the snow melt spatial distribution, and thus of the start of the growing season.

III.6.A.b. *Inter-annual variability of snow melt (SM)*

The snow is a typical feature of polar and alpine habitats and constitutes a determinant factor for species distribution and community composition, physiology and plant growth, and is thus a key determinant of primary production (e.g. Walker et al., 2001).

Considering that the climate warming of the Alpine region could lead to higher frequency of early snow melt events (Foppa & Seiz, 2012), this study provides a good perspective for evaluating the impacts of climate warming and extreme SM events on Alpine plants.

The observed patterns of inter-annual variation of SM on our study period were representative of the entire Alpine region, demonstrating that our study area is representative at a regional scale and that the results of our work are exportable to the whole alpine context. The extreme SM observed in 2007 was indeed the earliest SM observed at least since the last two decades over all the European Alps.

Despite the large inter-annual variability of the SM, when considering only “normal” years (2008-2016) at the inter-specific level, we found a statistically significant trend with time, with an advance of the earliest SM and thus of the onset of growing season over the study period. This result is in agreement with previous observations over the last few decades for Arctic and alpine regions that showed a drastic advance of the snow melt (Gobiet et al., 2014; Chersich et al, 2015; Kunkel et al., 2016; Klein et al., 2016).

Satellite data clearly indicate an earlier onset of greening over all the Northern Hemisphere (e.g. Jeong et al., 2011; Garonna et al., 2016; Mao et al., 2016). Our field-scale observations confirm such results, even if our rates are not strictly comparable to the available literature data due to different spatial and temporal scales, and allow us to stress the importance of field resolution studies to detect differences among growth forms responses, that are not evident from a remote sensing approach.

Indeed, we found different sensitivity of the SM trend with time according to the growth form types. In particular, earlier SM was evident for graminoids, deciduous shrubs and evergreen dwarf shrubs, and affecting differently their population data.

The increase of grasslands and shrublands toward higher elevation documented in the last 50 years in the Italian Alps not so far from our study area (Cannone et al., 2007), could thus be explained by the higher sensitivity to SM for graminoids and evergreen shrubs.

III.6.A.c. *Influence of SM on the phenology of alpine plants*

Our results highlighted the importance of the SM in regulating the phenology of alpine plants; in particular of the onset of the greening development (with high confidence FS, but also NL for deciduous species). Thus, the onset of plant growth and the greening stages are strongly determined by the patterns of SM, confirming other evidences from Arctic and alpine regions (Arft et al., 1999; Steltzer et al., 2009; Wipf & Rixen, 2010; Julitta et al., 2014; Chen et al., 2015; Filippa et al., 2015; Livensperger et al., 2016; Vitasse et al., 2016)

Few long-term dataset are available from high altitude alpine ecosystems that allow relating how plant growth may respond to inter-annual variation in climate parameters (e.g. Vitasse et al., 2016). Thus, the role of extreme climate events or climate oscillation remains often unexplored, despite they can have large impacts on plants and ecosystem functioning (Smith et al. 2011).

The strong signal of SM on regulating the onset of the growing season was evident for most growth forms, thus stressing that changes of the snow melt can strongly influence the onset of growing season among the majority of alpine species.

Therefore, despite the observed trend of SM with time over our study period was not statistically significant for all the growth forms (according to Wipf & Rixen, 2010; Livensperger et al., 2016), potential future SM changes may affect significantly the vegetative development of alpine species, with either potential benefits (e.g. growing season lengthening) or risks (e.g. cold slash and frost event) depending on their capability to adapt to the observed abiotic changes (Inouye, 2000; 2008; Bjork & Molau, 2007; Wipf et al., 2009; Wheeler et al., 2014; 2016).

Changes in vegetative development could lead to dramatic impacts on ecosystem productivity and soil respiration (Arnold et al., 2014). Due to different responses of the vegetative development to environmental cues among growth forms, changes in synchrony between growth forms could be expected, with important consequences on such ecosystem processes (e.g. Calvagno et al., 2013).

The pre-unfolding period (NL-SM), constitute a potentially period of carbon source for these ecosystems (Wohlfhart et al., 2008), and a comprehension of its dynamics could help to explain if plants are able to enhance their carbon acquisition due to earlier SM.

At the inter-specific level, the “extreme” SM of 2007 coincided to a lengthening of NL-SM, highlighting that the earlier and extreme SM did not correspond to an anticipation of NL, indicating both potentially conservative strategies or influences of other climatic factors occurred in the period of leaves unfolding in this year.

According to the GRMs, the most important factor regulating the length of NL-SM was the air TDD of the period NL-SM. The date of SM was instead the best predictor of leaves unfolding (NL), but the air temperature after the snow melt thus modulate the rate to which leaves are unfolded (length of NL-SM). Similar results have been recently reported for grasslands communities from the close Swiss Alps, by the analyses of ultrasonic sensors data (Vitasse et al., 2016), but long-term field based observations of alpine plants vegetative phenology are today lacking (see Iler et al., 2013a; Bjorkman et al., 2015; Vitasse et al., 2016).

The importance of field observations is relevant to compare patterns among species. Indeed, we identified differences among growth forms in their response to the earlier and extreme SM of 2007. Deciduous shrubs and forbs showed a statistically significant different NL-SM in this year, resembling the pattern observed at the inter-specific level (according to Vitasse et al., 2016), while, deciduous dwarf shrubs and graminoids, did not exhibit a delay of NL in 2007, indicating their high potential of exploiting earlier onset of growing season.

This could help to explain the observed increase of graminoids compared to forbs, recently observed for alpine and Arctic tundra plants (e.g. Elmendorf et al., 2012b; Cannone & Pignatti, 2014).

As tested by GRMs we found that the SM was again the main predictor for the first two flowering stages (FB and FF), coupled with the air TDD since SM, which is in agreement with other findings from alpine and polar tundra (e.g. Hulber et al., 2010; Oberbauer et al., 2013; Bjorkman et al., 2015; Rosa et al., 2016). However, at the FF stage the photoperiod started to exert some influence, even if not comparable to SM and TDD since SM. The photoperiodic constrain becomes more evident analyzing the MF stage, but the influence on FF, even if small, underlines that the flower opening is a critical stage in terms of reproduction efficiency and, thus, that alpine plants adapted their flowering to occur at specific range of day length with a certain amount of variability given by the climate inter-annual oscillation.

Bjorkman et al. (2015) indicated by manipulation experiments over 21 years period that flowering could occur earlier under warmer scenario, but highlighted that in their control plots the flowering was even delayed, due to an observed delay of snow melt. Our data did not show evidences of parallel shifts between SM and flowering stages, either at the inter-specific level, or at the intra-growth forms level, except for deciduous shrubs, that could thus be identified as the most sensitive growth form concerning the flower buds (FB) and the first flowering day (FF).

Therefore, we could hypothesize that with warmer spring and earlier SM, the flowering stages FB and FF will show a plastic response and move earlier in the season.

III.6.A.d. ***Influence of photoperiod on the phenology of alpine plants***

The role of photoperiodism on phenology and growth of alpine tundra plants is still unclear. Laboratory manipulation experiments provided some evidences of photoperiodic constrains on the development of alpine plants, particularly on flowering phenology (Prock & Korner, 1996; Keller & Korner, 2003; Heide, 2001; 2005). The photoperiodic control on alpine plants could be identified as a conservative strategy that allows them to profit from a growing season lengthening only at the beginning of the season (Gugger et al., 2015; Cannone & Dalle Fratte, 2016 submitted). Ernakovich et al. (2014) highlighted that, to understand how Arctic and alpine regions will respond to climate change, the different photoperiodic limitation (due to different latitude) should be taken into account, since it could drive to divergent responses, particularly in spring and autumn, with consequences on species interaction and cascade effects on community structure and functions. Therefore, even if the effect of photoperiod has been hypothesized, little is known on the quantitative ranges of this limitation, which allows phenophases to be more/less plastic in response to the inter-annual variability of climate (and thus the capability of adaptation to climate change).

Our analyses emphasized the importance of photoperiod as the main factor influencing plant phenology for some of our analyzed phenophases: main flowering (MF), seed development (SD), seed ripening (SR), and leaf senescence (LS), thus confirming previous studies from Keller & Korner (2003), or more recent investigations on phenotypic plasticity (e.g., Anderson et al., 2012; Gugger et al., 2015), and underlying that the photoperiod has to be considered when evaluating the effects of climate change in alpine terrains.

The photoperiod provided the first signal to plant (daylight length) and fixed the ranges of normal natural variation of flowering phenology (MF photoperiod = 11.9-15.8 light hours), while other climatic factors (mainly SM and TDD, depending on the phenophase) regulated the inter-annual variability that we observed. Hulber et al. (2010) stressed the dominance of climatic factors for high elevation alpine plants, compared to photoperiod. However, as hypothesized by Iler et al. (2013) in a future climate change scenario, warming could be too rapid, and plants limited by photoperiod will not have time enough for a genetic adaptation, and could exhibit non-linear responses to climate.

Concerning the MF, we found that photoperiod was coupled with SM and air TDD cumulated since SM, thus confirming other investigations of alpine plants (e.g. Hulber et al., 2010; Petraglia et al., 2014a), where temperature and the timing action of snowmelt have been associated to flowering phenology. However, it should be noted that, the extreme year 2007 did not provide evidence of any extreme in MF, both at inter-specific level as well as at the intra-growth forms level, thus highlighting a low plasticity of flowering stages. Differently from the alpine areas, in the Arctic, air temperature coupled with SM play the most important role on shaping flowering phenology (e.g. Bjorkman et al., 2015; Rosa et al., 2015) also because the Arctic summer is characterized by 24 hours of light and, therefore, in this context photoperiod does not exert any effect.

Among all the flowering stages, we found large differences in the trends with time over the study period: FB and FF were the least sensitive stages (only exception: deciduous shrubs, showing a flowering shift), while for the MF we observed an advance over time for 50% of the selected growth forms: deciduous dwarf shrubs, deciduous shrubs and graminoids.

Only deciduous shrubs, shifted simultaneously their flowering phenology among the subsequent phenophases (i.e. shifts of FB, FF and MF), which makes this growth form potentially more adaptable to changes in climate and could also explain their observed large expansion in the last sixty years among both alpine and polar ecosystems (e.g. Cannone et al., 2007; Elmendorf et al., 2012b).

These results thus confirmed previous observations that the start (FF) and peak (MF) of flowering phenology can respond to climate in different ways, independently of one other (CaraDonna et al., 2014). However, we found a strong relation between FF and MF (both inter-specific and intra-growth forms level), that allowed us to hypothesize that, even if the shifts of flowering stages were not coherent each other, in the future, with more rapid and robust changes in climate, we should observe comparable shifts among all the flowering stages.

According to literature data, warming can influence the sexual reproduction (Cao et al., 2016), seed set (Straka & Stazosmki, 2016), and seed longevity of alpine plants (Bernareggi et al., 2015; 2016). Consequently, under autumn warming scenario the seed germination is expected to increase for alpine plants (Mondoni et al., 2012; 2015) with survival rates quantified of 60-75% for autumn germinated seedlings (Mondoni et al., 2015). Our data emphasized that also for seed development (SD) and ripening (SR), some conservative strategies related to photoperiod have been adopted by alpine plants: indeed, the photoperiod was the main predictor of both SD and SR. Orsenigo et al. (2015) found by laboratory simulation that autumn heat waves could alter the germination phenology by eliciting an anomalous germination immediately after seed dispersal. However, they concluded that is not possible to generalize across species about the effects that autumn heat waves have on germination since their species-specific deep dormancy state, indeed they found increase of germination of almost 50% of species (on a dataset of 48 species). Thus, alpine plants will be able to germinate when the seeds will be ripen and disperse in time, which depends on the photoperiodic limitation.

Despite its large photoperiodic limitation, SD was one of the most sensitive phenophases: it showed the largest advance with time considering either the inter-specific level or the intra-growth forms level. As explained above for MF, photoperiod exerts its limiting action on SD within a daylight length range (11.3-15.8 light hours), thus allowing a certain degree of adaptability of alpine species to the inter-annual climatic variation. In this context, the most adaptable growth forms to change in climate were deciduous dwarf shrubs, evergreen dwarf shrubs and graminoids.

According to the GRMs analyses, both SM and air TDD cumulated since SM were identified as secondary factors (exerting limited influence compared to photoperiod), that could help to explain the inter-annual variability of SD. We also observed a strong relation with the MF, which allowed us to hypothesize that shifts of the flowering season could induce changes in the timing of seed development.

The SR again showed a stronger influence from the photoperiod, stressing the conservative strategy of the alpine species, which prevent plants to ripe seeds in non-favorable climatic condition. However, concerning SR we observed a delay with time (opposite to SD) at the inter-specific level. This is consistent with the observations of Mondoni et al. (2012; 2015) that climate warming would lead to a shift from spring to autumn germination. Hence, alpine plants can have a larger temporal niche available for their seeds dispersal and germination, depending on their specie-specific requirements of the dormancy state (Osernigo et al., 2015).

Similarly to SD, also for SR both the SM and air TDD since SM were identified as secondary factors, which allowed to hypothesize that in an autumn warming scenario, alpine plants could be able to exploit longer growing season and warmer autumn temperatures, potentially enhancing their reproductive efficiency. An earlier onset of the growing season is often associated with heat waves and warming, and corresponds to an earlier snow melt and to a decrease of soil moisture, which may result in a rapid die off of the seedlings that don’t have roots developed enough to resist to a drought period (Orsenigo et al., 2015).
Moreover, under warmer climates alpine plants would be able to produce seeds with an extended resistance to heat stress and changed germination responses (Bernareggi et al., 2015; 2016), and this could be related to the longer time available for seed development and ripening, which could allow plants to develop more adapted seeds.

At the intra-growth forms level, we found a delay of the SR only for evergreen shrubs, which lead in more time request for seed ripening, stressing the capability of this growth form to exploit longer growing season caused by autumn warming.

Concerning LS, we found a strong relation with the photoperiod, that we already discussed in the paper Cannone & Dalle Fratte (2016 submitted), see chap. III.5.B.j.

At the inter-specific level, we observed a delay of LS, and thus a lengthening of the growing season (e.g. Menzel et al., 2006a). In 2015, the extreme drought and warm summer condition (see Cannone & Dalle Fratte 2016, submitted) led to an extreme advance of senescence, that was recorded mainly by forbs and graminoids (according to De Boeck et al., 2016), while deciduous dwarf shrubs and deciduous shrubs were less sensitive.

However, the comparison of the growth forms highlighted that forbs were less plastic than graminoids, which enforce the observations from European Alps (Cannone & Pignatti, 2014), as well as from Arctic tundra (Elmendorf et al., 2012b), that graminoids are more competitive (plastic growth form) compared to forbs (aplastic growth form).

Thus, in a climate change scenario the different growth forms will show different responses that may implicate cascading effects in terms of species composition, community structure as well as biodiversity, and ecosystem processes (such as biogeochemistry). A better knowledge of the limitations/adaptability of alpine plants life cycle could help to fill the knowledge gap about plasticity of these ecosystems that could be used for mitigation and adaptation strategies, with novel implementation on the management plans of these vulnerable ecosystems.

III.6.B. Ground surface temperature (GST) and snow cover monitoring

MAGST and BTS variability have been discussed concerning the influence of solar radiation, snow cover, humidity, and vegetation (e.g. Ishikiwa & Hirakawa, 2000; Heggem et al., 2006; Bonnaventure & Lewkowicz, 2008).

The MAGST in our study showed a large inter-annual variability (1.7°C), which was almost comparable to findings from Pogliotti et al. (2015) over an almost comparable time series (7 years) despite the latter is referred to an higher altitude site (around 3000 m a.s.l.) in the Western Italian Alps.

Our data emphasized the importance of the snow cover duration (SCD) on regulating the MAGST at the inter-site level and inter-annual level, thus confirming that the snow cover duration is the main factor controlling the ground surface temperature (e.g. Zhang, 2005) especially in the alpine terrains.

Indeed, the combined effect of snow with topography can lead to large heterogeneity in the MAGST, also within few meters that can exceed the inter-annual variability (e.g. Gubler et al., 2011; Rodder & Kneisel, 2012; Gisnas et al., 2014; Pogliotti et al., 2015). In 2010, we recorded for example an intra-annual and inter-site variability of 3.0°C.

On the other hand, also the inter-annual variability can be influenced by many parameters: snow cover, topography, geology and surface grain size, vegetation cover and thickness of the organic layer (e.g. Gruber & Haeberli, 2009; Gubler et al., 2011; Scherrer & Korner, 2011, Cannone & Guglielmin, 2009; Guglielmin et al., 2012). The best predictor of the MAGST in our study was the snow cover duration (SCD) (according to Pogliotti et al., 2015), and consequently we found evidences of strong relations with the vegetation communities, which are related to the snow distribution (e.g. Galen & Stanton, 1995).

At the intra-surface types level, the bare ground exhibited the largest intra-annual variability of MAGST, while vegetated soils showed lower and almost comparable variability. At the intra-surface types level, the maximum MAGST was identified for *Rhododendron ferrugineum* and *Carex curvula* (3.3°C), while *Cerastium uniflorum* showed the minimum MAGST, even lower than bare grounds.

Our data highlight the buffering effect of the vegetation, that lead vegetated soils to be warmer compared to air temperature (N-factor>1.00). The N-factor that we identified for our selected alpine surface types, differed from those of Klene et al. (2001) from Arctic tundra plants (vegetation N-factors<1.00), highlighting that other factors other than the vegetation can influence the soil thermal offset.

There were also differences between vegetated surface types and bare ground in the snow season, as showed by the N-factor FDD: close to zero for the vegetated soils (except for *Cerastium uniflorum*), and higher for the bare ground, which highlight that the vegetation presence influence the thermal conditions of the ground also in the snow season.

However, during winter the main factor controlling the soil temperature is the snow cover (e.g. Zhang, 2005; Pogliotti et al., 2015). The thermal insulation of snow cover has been identified to be from 60 and 100 cm (e.g. Haberli, 1973; Keller & Gubler, 1993; Guglielmin et al., 2003; Zhang, 2005; Staub & Delaloye, 2016). Both the BTS obtained from daily record of GST as well as the FDD computed on the snow season period, highlighted a strong relation with the beginning date of snow cover deeper than 80 cm (BD>80). In particular this effect was evident in the last winter (2016), where the BD>80 was delayed of more than one month respect the mean, leading in a strong cooling of the GST (evident at both inter-sites and intra-surface types level, except for *Salix herbacea*). Indeed, according to literature data, a thin snow cover in autumn promotes an efficient ground cooling (e.g. Keller & Gubler, 1993; Guglielmin, 2004).

According to our data, the pioneer species (i.e. *Cerastium uniflorum*) occurred with permafrost presence, as tested by BTS. Also *Salix herbacea* for some years showed a possible permafrost occurrence. Such results are extremely important for mapping mountain permafrost distribution, since actual model normally do not consider vegetation as a factor to be included in permafrost modeling (Keller et al., 1998; Wright et al., 2003; Guglielmin et al., 2003), or included vegetated areas as proxy of permafrost free areas (Boeckli et al., 2012).

Our findings highlighted also that the shrublands expansion that we are experiencing in the Alps due to climate change at the expenses of grasslands, could produce a further warming of ground temperatures (up to 1.5 °C for example when comparing MAGST of *R.ferrugineum* and bare ground), only due to the higher buffering effect of the shrubs respect barren ground or other vegetation cover types (e.g. grasslands), with potentially strong implications on soil carbon fluxes and nutrient cycling.

III.6.C. Manipulation experiments on alpine vegetation

Nitrogen (N) and phosphorous (P), are the two most essential and growth-limiting elements in terrestrial ecosystems (Elser et al., 2007). Climate warming may induce increased nutrient soil organic matter mineralization (e.g. Chapin et al., 1995; Cornelissen et al., 2014) and the recent increase in atmosphere due to anthropogenic activity could enhance nutrient availability through N deposition. These items raise the question of how terrestrial ecosystems will respond (Chapin et al., 1995; Elser et al., 2007, Petraglia et al., 2014b; Li et al., 2016).

Nitrogen addition demonstrates that most alpine plants are particularly responsive to increased N supply (Schappi & Korner, 1996; Heer & Korner, 2002). Our data indicated clear evidences of N but also of P limitation of alpine terrestrial ecosystems, involving also different plant traits and phenological events (e.g. Li et al., 2016).

The consequences of an excessive N load, can be altered growth, altered organism chemistry composition, shifted phenology, changed nutrient cycling and, ultimately, alteration in plant community composition (Xia, 2008; Xi et al., 2016), even if it is still lacking an adequate knowledge of the impacts of nutrients on plant phenology (Jochner et al. 2013). Thus, our study could help to fill this gap about relations between seasonality and nutrient availability.

Petraglia et al. (2014b), studying only one forb species for 3 years (*Gnaphalium supinum*, typical of snowbeds), found evidences that the flowering effort was limited by P, while the flowering date was advanced by P supply. Our data indicated longer duration of MF with xNPK addition, caused mainly by a delay of the MF completion, thus confirming that alpine snowbeds are strongly P-limited, and that they will be more able than grasslands in exploiting new resources to optimize their flowering phenology. Therefore, our results suggest that allocation of resources to reproductive structures is stimulated by P (e.g. Petraglia et al. 2014b).

However, we observed different responses among the vegetation communities (according to Liancourt et al., 2009). Grassland community showed higher sensitivity to the xN addition, which exerted a reduction of the MF duration (-12 days). Also in this case the effect was mainly driven by an earliest MF completion. For grasslands, we could thus hypothesize that a larger nitrate supply could exert negative impact on the flowering duration with important consequences on the temporal niche competition among communities.

The other phenological stage that we analyzed was the LS. Since we observed a strong photoperiod constrain on LS, it was not surprising that LS showed low responses to treatments.
However, since plants from low fertile environments display specific and adaptive mechanisms for nutrient resorption from senescing leaves and facilitate transport of photosynthetic products to other part of the plant (Aerts et al., 2007; Freschet et al., 2010; Lang et al., 2014), we could hypothesize that a change of available nutrients could influence LS, at least for some community types.
In particular, we found snowbed to be highly sensitive to the ammonium sulfate (xN), which exerted a negative input on LS (advance of onset of LS).

We also observed a strong effect on snowbeds from flower removal (FL) thus highlighting that snowbed species can show higher efficiency concerning the allocation of energetic resources between vegetative and reproductive organs (e.g. Obeso et al., 2002). There are very few studies on the reproductive organ removals (Obeso et al., 2002; Xiao et al., 2016), but our results indicated that non-flowering years could lead in positive responses on the allocation of nutrient to vegetative development (for snowbeds).

The nutrient availability strongly influenced the vegetative development, as observed for the leaf length (LLmax), the plant height (Hmax) and the above ground biomass (ABG). At the inter-specific level, xNPK involved an increase of the LLmax and Hmax, while both xNPK and urea additions increased the production of the ABG. A strong N and P co-limitation were thus identified for many of the analyzed vegetative plant traits, thus confirming other literature data (e.g. Bowman et al., 2006; Davidson et al., 2004; Huang et al., 2012; Li et al., 2015).

Carry over effects were also observed from the first year of addition. Indeed, we observed longer shoots with xNPK, thus confirming finding from the long-term monitoring, which indicated carry over effects following an extreme event of LS, caused by a prolonged drought and hot period.

Snowbed communities are among the most threatened by current climate change, indeed they show high sensitivity to changing of environmental parameters, especially of snow cover. However, their positive response to altered nutrient availability, allow hypothesizing that non-linear changes could be expected under future anthropogenic related climate change scenario.

III.7. Supplementary material

Table S1. Topographic characterization of the permanent plots. Legend: B = bottom of the valley; IRG = inactive rock glacier; FIRG = foot of the inactive rock glacier; ARG = active rock glacier; M = lateral moraine.

Plot ID	altitude m a.s.l.	slope (°)	Aspect (sectors)	Aspect (°N)	Localization	Plot ID	Altitude m a.s.l.	slope (°)	Aspect (sectors)	Aspect (°N)	Localization
P1	2357	7	E	90	B	P37	2499	15	N	360	ARG
P2	2360	6	E	90	B	P38	2511	5	NE	45	ARG
P3	2364	10	NE	45	B	P39	2519	3	E/NE	67	ARG
P4	2369	11	N	360	B	P40	2515	15	N	360	ARG
P5	2424	5	N	360	IRG	P41	2519	10	E/NE	67	ARG
P6	2411	5	N	360	IRG	P42	2523	2	E/NE	67	ARG
P7	2414	10	W	270	IRG	P43	2530	30	NE	45	ARG
P8	2410	10	NE	45	IRG	P44	2518	3	S	180	ARG
P9	2502	3	SE	135	ARG	P45	2524	10	NE	45	ARG
P10	2505	5	E	90	ARG	P46	2544	5	NW	315	ARG
P11	2513	1	SE	135	ARG	P47	2515	1	SE	135	ARG
P12	2528	35	NW	315	ARG	P48	2516	5	N	360	ARG
P13	2537	10	NE	45	ARG	P49	2504	1	SE	135	ARG
P14	2570	30	N	360	ARG	P50	2496	10	S	180	ARG
P15	2544	1	E/NE	67	ARG	P51	2510	4	N	360	ARG
P16	2545	40	N	360	ARG	P52	2596	14	NE	45	ARG
P17	2528	35	NE	45	ARG	G1	2510	4	N	360	ARG
P18	2498	2	SW	225	M	G2	2491	3	NE	45	ARG
P19	2493	4	E	90	M	G3	2497	3	NE	45	ARG
P20	2470	30	SE	135	M	G4	2488	7	SE	135	ARG
P22	2375	2	E	90	B	G5	2491	3	N	360	ARG
P23	2388	3	W	270	B	G6	2464	12	SE	135	ARG
P24	2390	6	W	270	FIRG	G7	2440	5	W	180	ARG
P25	2389	3	E	90	FIRG	G8	2515	20	N	360	ARG
P27	2431	3	SE	135	M	G9	2513	10	SE	135	ARG
P28	2470	7	SE	135	M	G10	2506	11	NE	45	ARG
P29	2495	10	E	90	M	G11	2518	3	E/NE	67	ARG
P30	2375	2	S/SW	202	M	G12	2520	17	SE	135	ARG
P31	2510	7	E	90	M	G13	2516	13	NW	315	ARG
P32	2492	2	NE	45	ARG	G14	2519	8	N	360	ARG
P33	2497	10	SE	135	ARG	G15	2521	20	SW	225	ARG
P34	2485	1	SE	135	ARG	G16	2527	7	NW	315	ARG
P35	2494	3	N	360	ARG	G17	2538	1	SW	225	ARG
P36	2500	10	N/NE	22	ARG	G18	2540	6	N	360	ARG
						G19	2577	5	N	360	ARG

Table S2. List of the monitored species at the Foscagno long-term phenology monitoring and manipulation experiments (nomenclature according to Conti et al., 2005).

species name	family name	italian name	english name	elevation range (m a.s.l.)	Chorolgy	growth form	Raunkier
Agrostis alpina Scop.	Poaceae	Cappelini delle Alpi	Bentgrass	1700-2800	Orof.SouthEruopean	graminoid	H caesp
Anthoxanthum alpinum A. Löve et D.Löve	Poaceae	Paleo alpino	Vernalgrasses	1200-2800	Arctic-Alpine (Euroasiatic)	graminoid	H caesp
Helictochloa versicolor (Vill.) Romero Zarco	Poaceae	Avena screziata	Alpine Oat Grass	1800-3000	Orof.SouthEruopean	graminoid	H caesp
Bistorta vivipara (L.) Delarbre	Polygonaceae	Poligono viviparo	Alpine Bistort	1500-2800	Circumb. Arctic-Alpine	forb	G rhiz
Cardamine resedifolia L.	Crucifereae	Billeri pennato	Mignonette-leaved Bitter Cress	1500-2600 (3500)	Alpine-MidEuropean	forb	H scap
Carex curvula All. subsp. *curvula*	Cyperaceae	Carice ricurva	Tufted Sedge	1900-2800	Orof.SouthEruopean	graminoid	H caesp
Carex sempervirens Vill.	Cyperacea	Carice sempreverde	Evergreen Sedge	1600-2700	Orof.SouthEruopean	graminoid	H caesp
Cerastium uniflorum Clairv.	Caryophillaceae	Peverina dei ghiaioni	One-flowered Chickweed	1800-3400	Alpine endemic	forb	Ch pulv
Doronicum clusii (All.) Tausch	Compositae	Doronico di Clusius	Clusius' Doronicum	2000-3000 (3300)	Orof.SouthEruopean	forb	G Rhiz
Empetrum hermaphroditum Hagerup	Empetraceae	Moretta comune	Crowberry	1200-3000	Circumb. Arctic-Alpine	shrub (ev.)	Ch frut
Geum reptans L.	Rosaceae	Cariofillata delle pietraie	Creeping Mountain Avens	2000-3400	Orof.SouthEasthernEruopean	forb	H rept
Gnaphalium supinum L.	Asteraceae	Canapicchia glaciale	Dwarf cudweed	2200-3000	Circumb. Arctic-Alpine	forb	H scap
Juniperus communis L. var. saxatilis Pall.	Cupressaceae	Ginepro nano	Dwarf Juniper	1500-2500	Arctic-Alpine (Euroasiatic)	shrub (ev.)	NP
Kalmia procumbens (L.) Gift, Kron & Stevens ex Galasso, Banfi & F. Conti	Ericaceae	Azalea alpina	Creeping Azalea	1600-2400 (3000)	Circumb. Arctic-Alpine	dwarf shrub (ev.)	Ch rept
Leontodon helveticus Mérat emend. Widder	Compositae	Dente di leone dei graniti	Granite hawkbits	1800-2700	Orof.SouthWestEruopean	forb	H ros
Leucanthemopsis alpina (L.) Heywood	Compositae	Margherita alpina	Alpine Chrysanthemum	1700-3600	Orof.SouthWestEruopean	forb	H scap
Ligusticum mutellina (L.) Crantz	Apiaceae	Motellina delle Alpi	Alpine Lovage	1800-2600	Orof.SouthEruopean	forb	H scap
Luzula alpinopilosa (Chaix) Breistr. subsp. *alpinopilosa*	Juncaceae	Erba lucciola dei ghiacciai	Alpine woodrush	1900-3000	Orof.SouthEruopean	graminoid	H scap
Nardus stricta L.	Poaceae	Nardo rigido, Cervino	Matgrass	1200-2500	Orof.SouthEruopean	graminoid	H caesp
Oxyria digyna (L.) Hill	Polygonaceae	Acetosa soldanella	Mountain Sorrel	2400-2900 (3200)	Circumb. Arctic-Alpine	forb	H caesp
Poa alpina L. subsp. *alpina*	Poaceae	Fienarola alpina	Alpine Meadow Grass	1500-2700 (3600)	Circumb. Arctic-Alpine	graminoid	H caesp
Poa laxa Haenke subsp. *laxa*	Poaceae	Fienarola ciodola	Short-leaved Spear Grass	2000-3600	Orof.SouthEruopean	graminoid	H caesp
Potentialla aurea (L.) subsp. *Aurea*	Rosaceae	Cinquefoglia fior d'oro	Golden Cinquefoil	1800-2900	Orof.SouthEruopean	forb	H scap
Ranunculus glacialis L.	Ranunculaceae	Ranuncolo dei ghiacciai	Glacial Buttercup	2000-3500 (4200)	Arctic-Alpine (European)	forb	H scap
Rhododendron ferrugineum L.	Ericaceae	Rododendro rosso	Rusty Alpenrose	1600-2300 (3000)	Circumbor.	shrub (ev.)	Ch frut
Salix herbacea L.	Salicaceae	Salice erbaceo	Dwarf willow	2000-3000	Circumb. Arctic-Alpine	dwar shrub (dec.)	Ch frut
Senecio incanus subsp. *carniolicus* (Willd.) Br-Bl.	Compositae	Senecio della carnia	Eastern Downy Ragwort	1800-2600 (3000)	Alpine endemic	forb	H scap
Soldanella pusilla Baumg.	Primulaceae	Soldanella della silice	Alpine Snowbell	1900-2800	Orof.SouthEruopean	forb	H ros
Vaccinium uliginosum L. subsp. *microphyllum (Lange) Tolm.*	Ericaceae	Mirtillo falso	Bog Whortleberry	1300-2500 (3000)	Circumbor.	shrub (dec.)	Ch frut
Veronica alpina L.	Scrophulariaceae	Veronica alpina	Alpine Speedwell	1500-3000 (3200)	Arctic-Alpine (Euroasiatic)	forb	H scap

Table S3. Distribution of species among the permanent plots. Permanent plots not listed correspond to bare ground soils. Community types: Sn = Snowbed, Sh = Shrubland, DSh = Dwarf Shrubland, Gr = Grassland, Pi = Pioneer.

			plot ID	P1	P2	P3	P4	P5	P7	P8	P12	P13	P14	P15	P17	P18	P19	P20	P22	P23	P24	P27	P28	P29	P30	P31	P33	P34	P35	P36	P39	P40	P42	P43	P44	P45	P46	P47	P48	P50	P51	G2	G3	G5	G6	G7	G8	G9	G10	G11	G13	G15	G16	G17	G18
			communities	Sn	Sh	Sh	DSh	Sh	DSh	Sh	Pi	Sn	Sn	Pi	Pi	Gr	Gr	Sh	Gr	Sh	Sh	Gr	Gr	Gr	Gr	DSh	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Sn	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Pi	Sh	Sh	Pi	Pi	Pi	Pi
species name	**growth form**	**replicates**		2	2	1	4	2	2	1	1	1	1	1	2	1	3	1	5	4	3	5	1	2	2	4	2	1	1	2	3	2	1	3	3	4	3	6	2	1	1	3	1	2	3	1	3	4	6	5	3	4	3	3	4
Agrostis alpina	graminoids	3		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Anthoxanthum alpinum	graminoids	6		-	-	-	-	-	-	-	-	-	-	-	-	-	x		x	x	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Helictochloa versicolor	graminoids	3		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Cardamine resedifolia	forbs	4		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x	-	-	x	-	-	-
Carex curvula	graminoids	11		-	x	-	x	x	-	-	-	-	-	-	-	x	x	-	x	-	-	x	-	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Cerastium uniflorum	forbs	9		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	x	-	-	x	x	x	x	-	-	x	-	-	-	-	-	-	-	x	-	-	-	-	-	x	-
Doronicum clusii	forbs	3		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	x	-	-	-	x	-	-	-
Empetrum hermaphroditum	ev.dwarf shrubs	3		-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geum reptans	forbs	14		-	-	-	-	-	-	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	-	x	-	x	x	-	-	-	-	x	x	x	-	x	-	-	-	-	-	x	-	-
Juniperus communis	ev.shrubs	3		-	-	x	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kalmia procumbens	ev.dwarf shrubs	6		-	-	-	x	-	x	-	-	-	-	-	-	-	-	-	x	-	-	-	-	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leucanthemopsis alpina	forbs	15		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	x	x	x	-	x	-	-	-	x	x	-	-	x	-	-	x	x	x	-	x	-	-	-	-	-	x
Oxyria digyna	forbs	7		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	x	x	x	x
Poa alpina	graminoids	4		-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x
Poa laxa	graminoids	11		-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	-	-	-	-	x	-	-	-	x	-	x	x	x	-	-	x	-	x	-
Ranunculus glacialis	forbs	3		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	x
Rhododendron ferrugineum	ev.shrubs	5		-	x	-	x	-	-	-	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
Salix herbacea	dec.dwarf shrubs	7		x	-	-	-	x	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Senecio carniolicus	forbs	9		-	-	-	-	-	-	x	-	-	-	-	-	-	x	-	-	x	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x	x	x	-	-	-	-
Vaccinium uliginosum	dec.shrubs	4		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-
Veronica alpina	forbs	3		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-

Figure S4. Spatial distribution of plots with graminoids species.

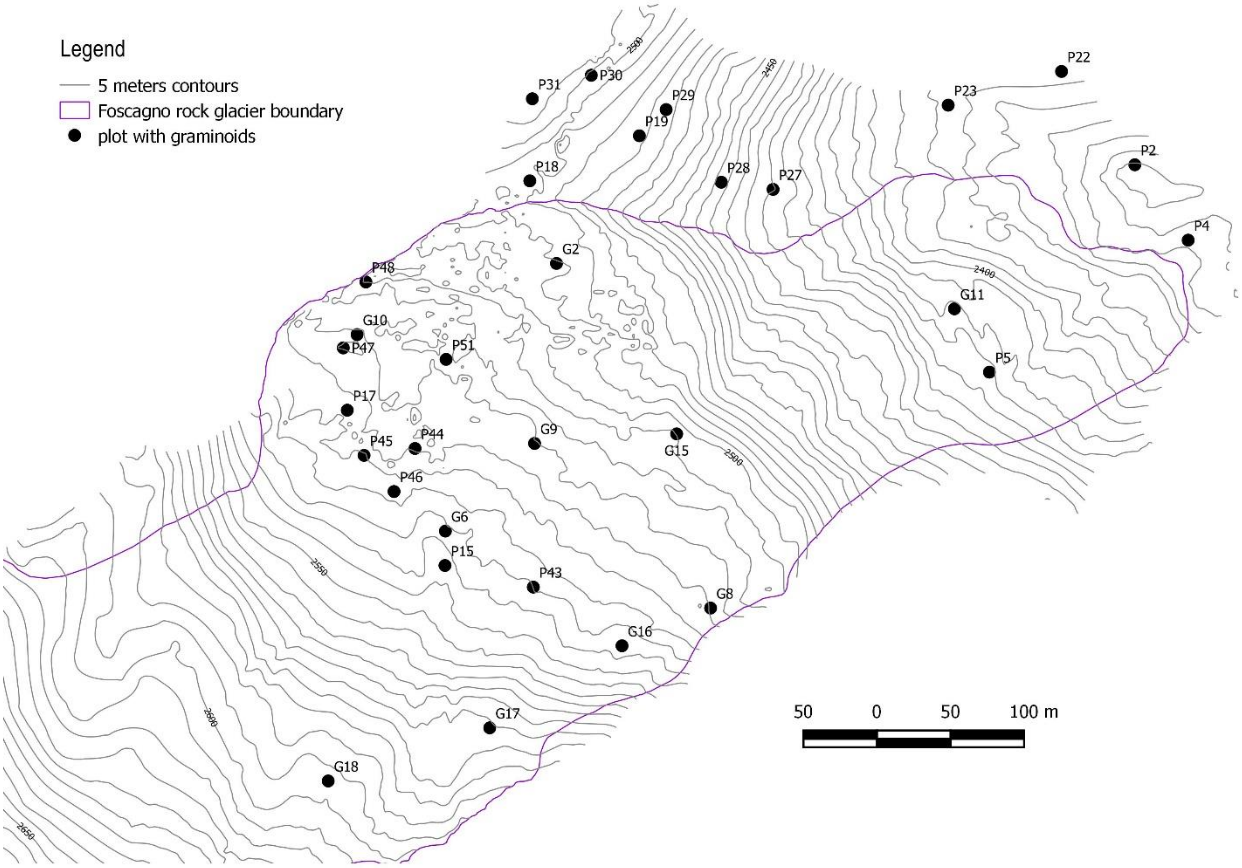

Figure S5. Spatial distribution of plots with forbs species.

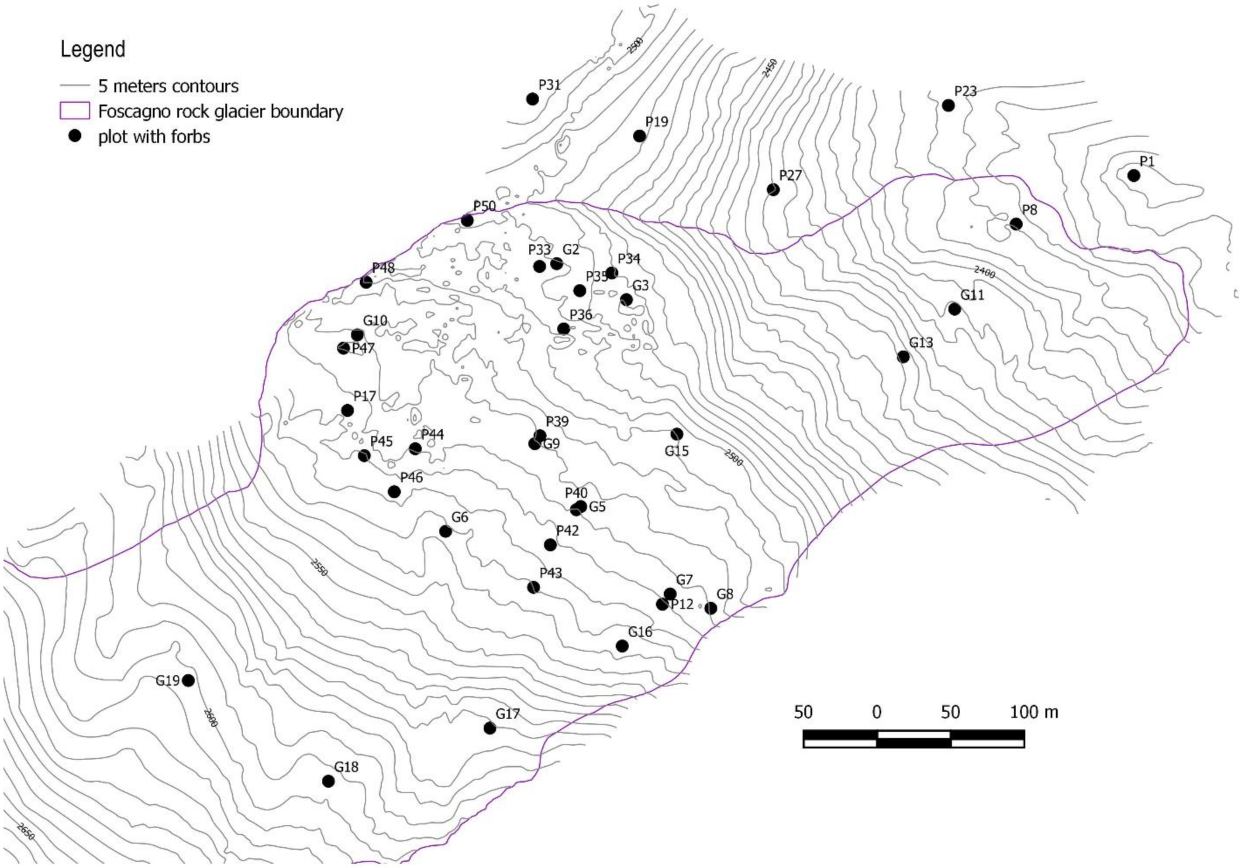

Figure S6. Spatial distribution of plots with evergreen shrubs species

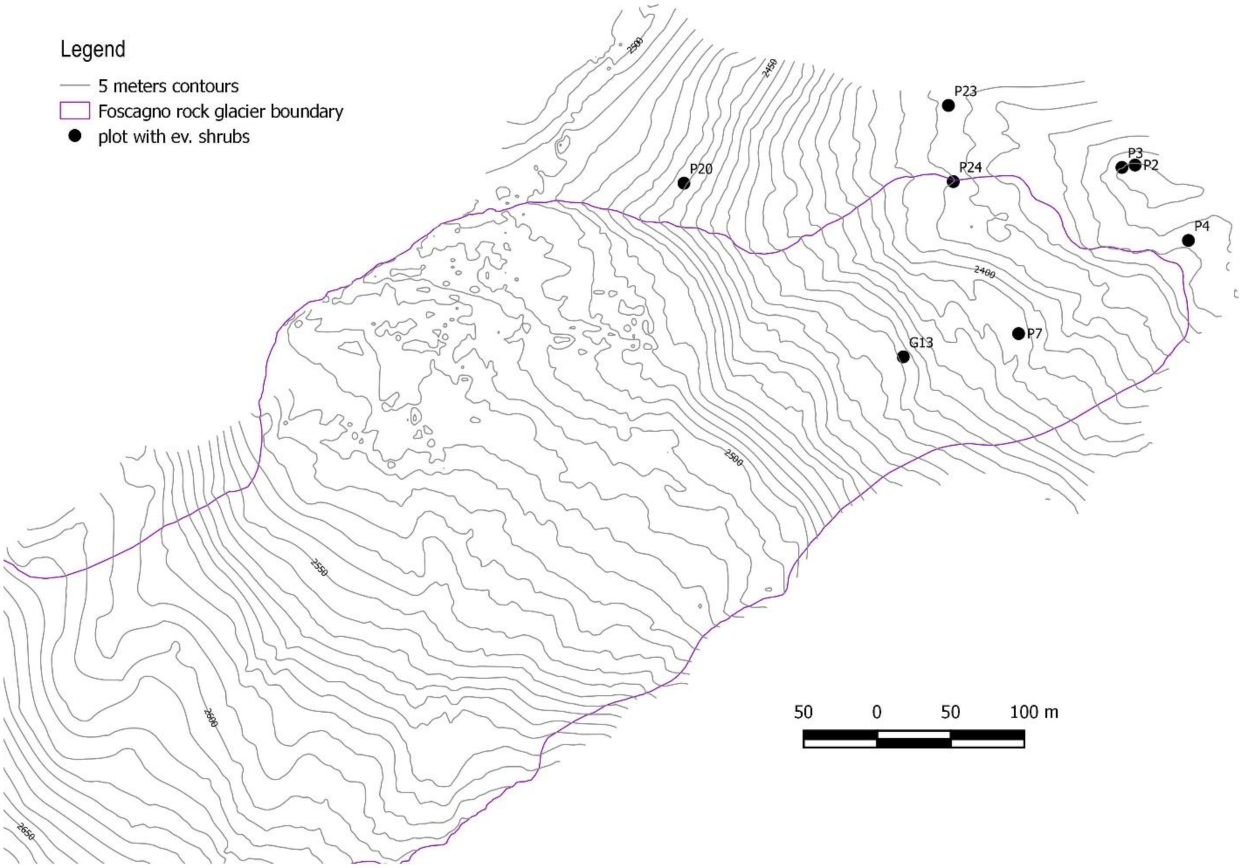

Figure S7. Spatial distribution of plots with evergreen dwarf shrubs species

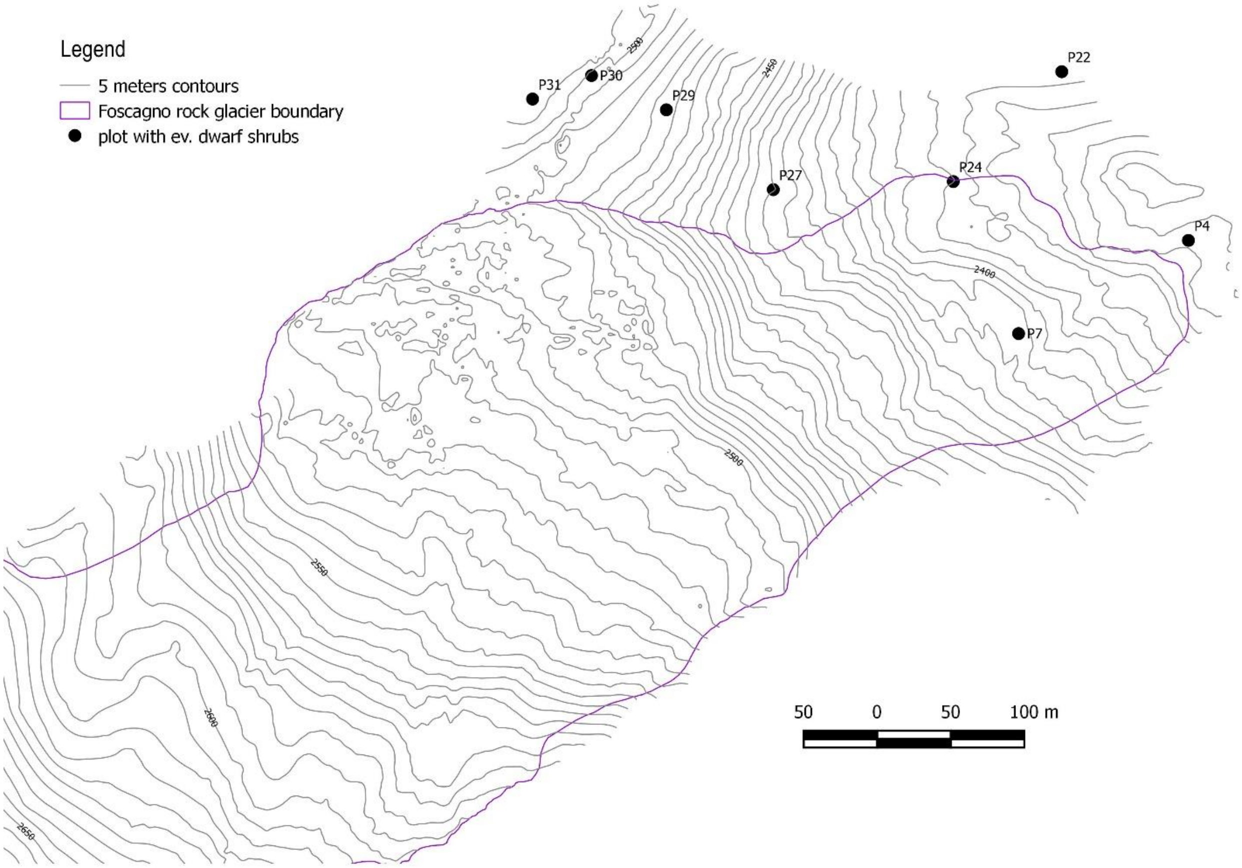

Figure S8. Spatial distribution of plots with deciduous shrubs species

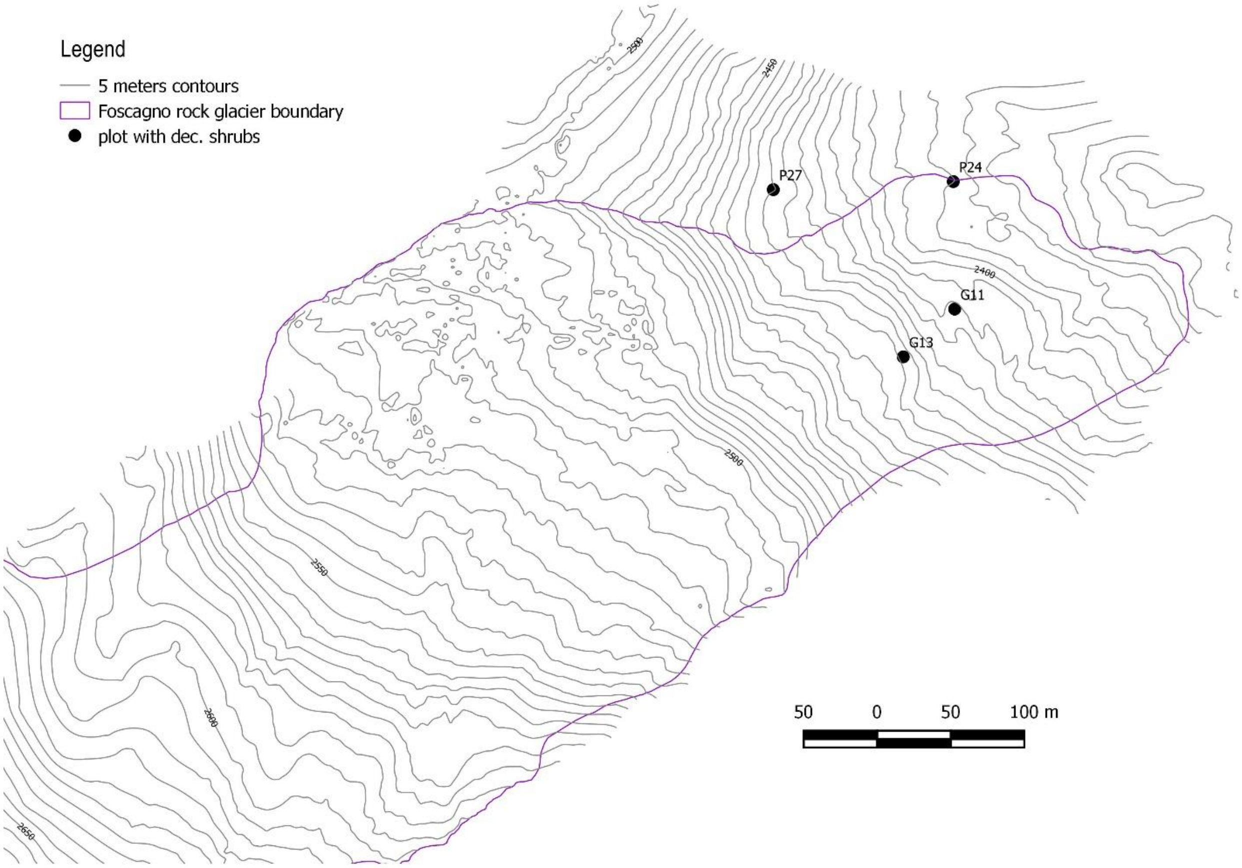

Figure S9. Spatial distribution of plots with deciduous dwarf shrubs species

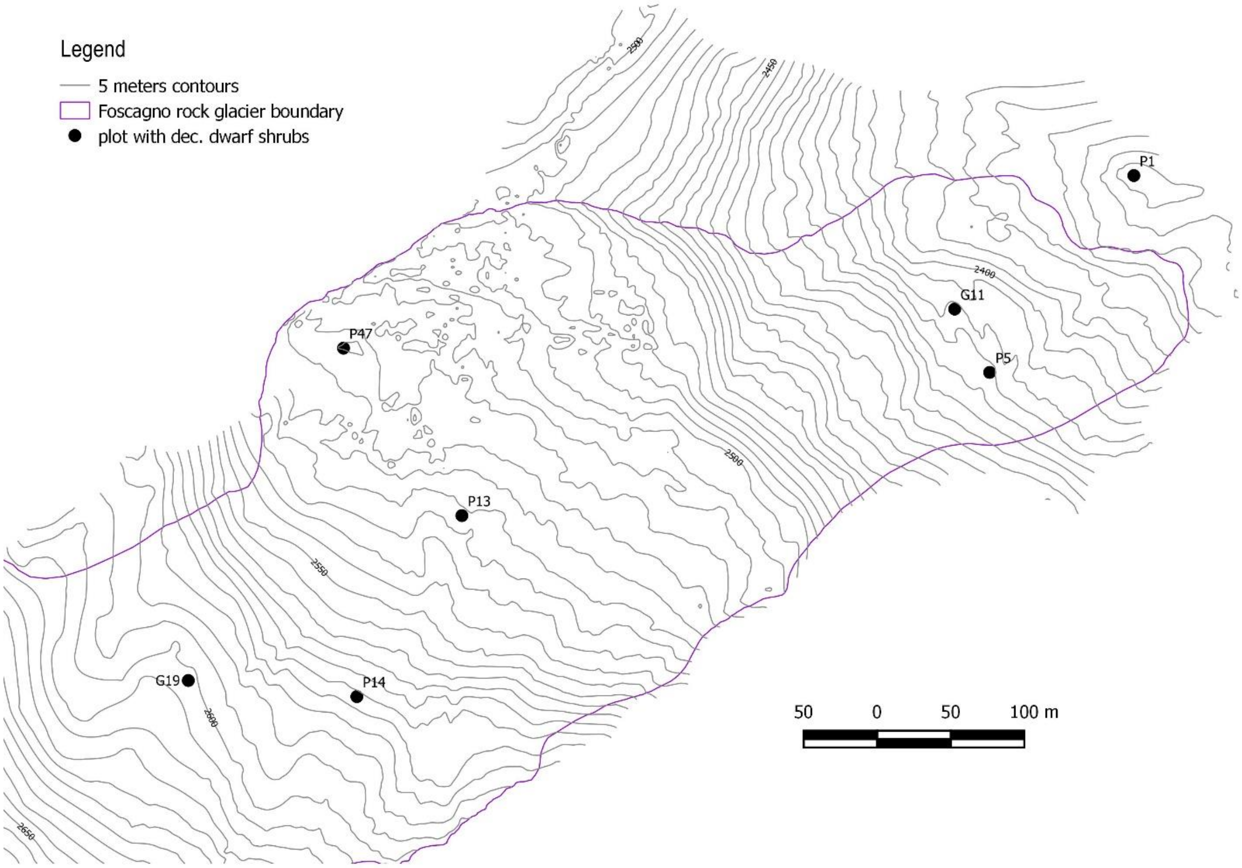

Table S4. Main topographic, ecological and edaphic characteristics of the study sites. Global radiation is the mean value over the study period.

Vegetation cover	**Location ID**	**Elevation (m a.s.l.)**	**Slope (°)**	**Aspect**	**Global radiation (Wh/m^2)**	**Vegetation cover (%)**	**Vegetation height (mm)**	**Morphology**	**Surface grain size (%)**			
									Blocks	**Pebbles**	**Gravel**	**Fine material**
evergreen shrubs *(Rhododendron ferrugineum)*	P20	2461	33	SE	1340162	100	310	slope	80	0	0	20
	P23	2388	13	E	1003087	100	400	ridge	15	30	20	35
deciduous shrubs *(Vaccinium uliginosum)*	G11	2411	20	N	1215093	100	50	slope	0	20	40	40
	P27	2429	12	SE	972297	100	90	slope	0	25	65	10
evergreen dwarf shrubs *(Kalmia procumbens)*	P31	2505	15	SE	1273640	100	35	slope	0	0	0	0
deciduous dwarf shrubs *(Salix herbacea)*	G19	2609	5	N	1427208	75	15	slope	20	25	30	25
	P47	2514	7	SE	1330307	100	28	furrow	0	40	10	50
Graminoids *(Carex curvula)*	P29	2478	13	E	1247685	90	90	slope	0	20	5	75
forbs *(Cerastium uniflorum)*	G17	2576	7	N	1001582	50	20	furrow	35	25	35	5
	P39	2514	15	NE	1253806	100	55	ridge	15	65	20	0
bare ground	P32	2494	18	N	1323637	0	0	ridge	5	65	25	5
	P41	2521	24	N	1103166	0	0	furrow	70	30	0	0
	P52	2609	9	E	1036110	0	0	furrow	100	0	0	0

Table S5. List of the selected species for the phenology monitoring at the manipulation experiments.

species	**growth form**	**snowbed**	**grassland**
Salix herbacea	deciduous dwarf shrubs	x	
Vaccinium uliginosum	deciduous shrubs		x
Cardamine resedifolia	forbs	x	
Gnaphalium supinum	forbs	x	
Soldanella pusilla	forbs	x	x
Veronica alpina	forbs	x	
Leontodon helveticus	forbs		x
Ligusticum mutellina	forbs		x
Bistorta vivipara	forbs		x
Potentilla aurea	forbs		x
Agrostis alpina	graminoids	x	
Luzula alpinopilosa	graminoids	x	
Anthoxanthum alpinum	graminoids		x
Carex curvula	graminoids		x
Carex sempervirens	graminoids		x
Nardus stricta	graminoids		x

IV. CONTINENTAL ANTARCTICA

IV.1. Introduction

In Continental Antarctica, there is a shortage of data available on vegetation changes (but see Guglielmin et al., 2014). In Victoria Land, Brabyn et al. (2005) showed that, in the period 1960-2004 vegetation expanded with an increase of algae, likely driven in this case by local alteration of water supply. Other examples indicate a generalized increase of lichen vegetation and a concomitant decrease of bryophytes due to drying climate (Melick & Seppelt, 1997; Johansson & Thor, 2008).

Changes in the active layer thickness (ALT) strongly influence the water table, thus altering the moisture availability (Guglielmin et al., 2014). Active layer changes can also indirectly modify the vegetation through variation of the frost heave, cryoturbation, ice segregation or gelifluction disturbance (Cannone et al., 2007; 2015).

Continental Antarctica is the last pristine environments on Earth, that provides a unique opportunity to assess the natural dynamics and responses of cryptogamic vegetation without the disturbance effect due to the competition with vascular plants or any other biotic disturbance (such as in Maritime Antarctica, in the Arctic or in the Alps).

Moreover, while along Antarctica Peninsula a strong warming occurred in the last decades with tangible effects such as glaciers retreat and permafrost degradation, in Continental Antarctica a cooling or almost stable temperature was coupled with an increase of ground surface temperature, mainly attributable to changes in the summer radiation (e.g. Guglielmin & Cannone, 2012). This dichotomy between active layer thickness and air temperature trends can produce large unexpected and unmodelled impacts on ecosystems, which make this area of great interest.

In Victoria Land, Continental Antarctica, a long-term monitoring network of vegetation-snow-soil temperature was established in 2002/2003 across a latitudinal gradient 73-77°S (Cannone, 2006). One of the sites of this network (see chapter IV.4.B, Guglielmin et al., 2014) represent the longest near continuous dataset (since 1999) of permafrost and active layer temperature in Antarctica (e.g. Guglielmin, 2004; 2006).

In the paper attached (chapter IV.4.B, Guglielmin et al., 2014) we focused on the impacts of recent climatic changes in Victoria Land, attempting to: a) identify the patterns of spatial and temporal active layer variability, b) analyze the changes of the associated vegetation, c) identify the climatic forcing of active layer and vegetation changes.

Moreover, during the Antarctic summer 2014/2015 we implemented the long-term monitoring network with some manipulation experiments in order to evaluate the response of Antarctic terrestrial ecosystems to climate change. The experiments were performed at 5 sites located over a latitudinal transect (73°S-77°S) and consisted in the addition of: snow, water, urea, ammonium sulfate, NPK, guano, as well as manipulation of snow accumulation by snow fences, of soil temperatures by open top chambers and of precipitation by snow shield.

In the next chapters we thus evaluated the results from the first year of these experiments providing the starting point for the next years monitoring.

For the nomenclature of mosses and lichen species we referred to the most recent literature (Øvstedal and Smith, 2001; Olech, 2004; Castello, 2003; Ochyra et al., 2008; Olech & Singh, 2010) and current nomenclatural rules (following Eriksson et al., 2001), while for the nomenclature of vegetation communities we used the classification proposed by Cannone & Seppelt (2008) for the Victoria Land vegetation.

IV.2. Study area

IV.2.A. The Victoria Land

The foreign activity for this PhD was carried out in Victoria Land (continental Antarctica), in the area surroundings the Italian Antarctic Research Station ‘Mario Zucchelli’ (MZS), with the logistic support of the Italian Antarctic Program (PNRA). The study area was located along a coastal latitudinal gradient in Victoria Land, in the Ross sector, East Antarctica.

In the frame of the SCAR project EBA (Evolution and Biodiversity in Antarctica) and, in cooperation with the LGP (Latitudinal Gradient Project), a monitoring network was established in 2002 and 2003 to assess the impacts of climate change on vegetation, soils, and permafrost in Victoria Land (Continental Antarctica) across a latitudinal gradient (Cannone, 2006). Among the sites of this network we selected five locations, distributed along the coast from Apostrophe Island (73°30′S, 167°50′E) in Northern Victoria Land to Finger Point (Granite Harbour) (77°00′S, 162°26′E) in Southern Victoria Land (Fig. IV.2.1). All sites are located along the coast, with the exception of Tarn Flat, which is inland on the slope area just before the plateau. They have a similar altitudinal range (10-250 m a.s.l.) so that comparable data, not influenced by elevation, are obtained for assessing relationships along the latitudinal gradient.

Since 1999, at Boulder Clay (close to MZS), a CALM (Circum Polar Active Layer Monitoring) grid (Nelson et al., 2008) was installed for the monitoring of Antarctic terrestrial ecosystems and relations between permafrost –active layer thickness and vegetation communities dynamics (Guglielmin, 2006).

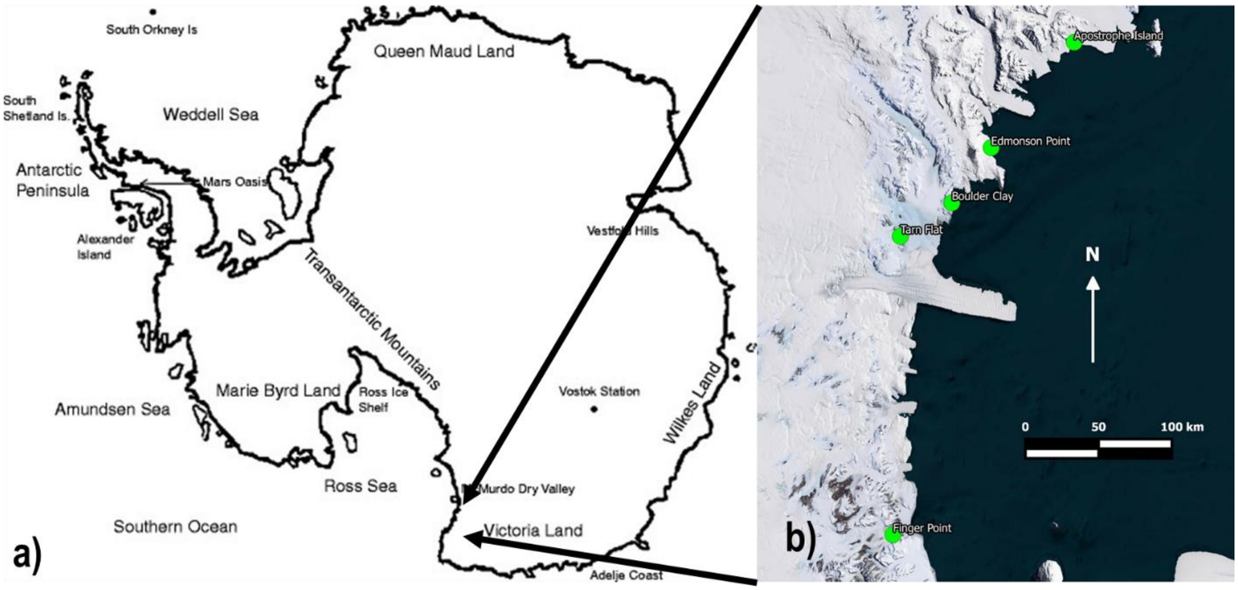

Figure IV.2.1 Location of the study area of Victoria Land (a) with a zoom on the study sites (b).

Recently in Continental Antarctica a strong active layer thickening (mainly attributed to the increase of incoming radiation) was documented in Terra Nova Bay area, despite the absence of any air warming since 1996, showing an opposite trend respect the Antarctic Peninsula and other sectors of the Antarctic continent (Guglielmin & Cannone, 2012; Guglielmin et al., 2014).

Table IV.2.1 Location and main characteristics of the study sites (adapted from Cannone, 2006)

Sites	Coordinates	Elevation (m a.s.l.)	Location	Lithology
Apostrophe Island	73°30'S 167°50'E	50	Coast	Gabbro and morainic deposits
Edmonson Point	74°30'S 165°07'E	10-50	Coast	Metamorphic rocks
Boulder Clay	74°30'S 164°05'E	250	Coast	Granite ad morainic deposits
Tarn Flat	73°31'S 167°25'E	20-100	Inland	Granite and morainic deposits
Finger Point	77°00'S 162°26'E	20-50	Coast	Granite and morainic deposits

IV.2.B. Geography and climate

Victoria Land is located in the Ross sector of continental Antarctica, and extents from Cape Hallet (72°S) along the coast to the dry valleys (77°S), and connects to the transantarctic mountains (Fig. IV.2.1).

Figure IV.2.2. Antarctic regions showing vegetation zones. Picture taken by Longton (1988).

Although the climate has cooled slightly in the last decade, in Northern Victoria Land, active layer thickness is currently slowly increasing, probably due to an increase in radiation received at ground level (Guglielmin & Cannone, 2012; Guglielmin et al., 2014).

This region is part of the “frigid” vegetation zone, according to Longton (1988) (Fig. IV.2.2). The climate of this region is cold and arid, namely frigid Antarctic (Øvstedal & Smith 2001), characterized by a mean annual air temperature of -15°C, while the mean summer air temperature (December–February) ranges between -0.1 and -2.0°C (Cannone & Guglielmin, 2012). The monthly mean air temperature ranges from -25.9°C (August) and -0.1°C in January. (Singh et al, 2015).

Further south in Victoria Land the climate is drier and colder with a mean annual air temperature of -17.4°C at McMurdo Station (77°50’S, 166°40’E). The monthly mean air temperature at McMurdo Station ranges between -27.9°C (August) and -1°C (January).

Precipitation, always in the form of snow, is very low and ranges between 100 and 200 mm per year (Grigioni et al., 1992, Monaghan et al., 2006), resulting in condition of extreme aridity.

IV.2.C. Geology and geomorphology

All sites are located in ice-free areas, most of them very close to the glacial boundaries (i.e. Boulder Clay and Apostrophe Island). In all sites there is continuous permafrost, with an active layer varying in thickness from zero to more than 100 cm, depending on the year and the site location (Guglielmin & French, 2004).
Cannone et al. (2008) provided a detailed description of the chemical and physical characteristics of the soils of the selected locations.

The chosen sites represent the most common environmental conditions, and almost all the rock substrates were sampled (i.e. granite, basalts, gabbro, metamorphic rocks, morainic and marine deposits). The soils of Victoria Land are Gelisols, while in the Dry Valleys of Southern Victoria Land Anhyortels and Anhyturbels are prevalent (Bockheim, 2002), and in Northern Victoria Land data on the soil classification are still lacking.

Lithology is strongly related to several chemical parameters (Cannone et al., 2008), notably extractable Al, Fe, Ca, K, but is unrelated to grain-size distribution. Consequently different chemistry of the surface-soil layer (including nitrate, organic carbon, C/N ratio), water content, and also the active-layer depth, influence the vegetation composition and distribution (Cannone et al., 2008).

Some sites (i.e. Edmonson Point) have ornithogenic soils, mainly due to the presence of penguins. In some sites there is a large occurrence of patterned ground (Guglielmin & French, 2004). More detailed description of edaphic characteristic of each location are given below (see chapter II.2.e.)
Measurements of the ground thermal regime and of the active layer thickness were carried out in some permanent plots of the long-term monitoring network (Guglielmin et al., 2005; Cannone & Guglielmin, 2009). As demonstrated for Maritime Antarctica (Cannone et al., 2006; Guglielmin et

al., 2008; 2012) the diverse vegetation types exerted different buffering effects on the surface energy balance and were associated with changed active layer thickness. Changes of the surface energy balance induced by the warming of air temperature and/or changes in precipitation might be able to induce significant modifications both of the vegetation and of the associated physical environment (Guglielmin et al., 2014). In particular the active layer would be altered and, therefore, also the ground moisture and free water availability, with potential impacts on the terrestrial ecosystems.

IV.2.D. Flora and vegetation

The vegetation of continental Antarctica is exclusively composed of cryptogams (microfungi, cyanobacteria, algae, lichens, bryophytes), with lichens and bryophytes being the dominant components of most terrestrial ecosystems.

Previous descriptions of the moss and lichen flora and of the main vegetation communities have been provided (e.g. Kappen, 1985; Castello & Nimis, 1995; Seppelt et al., 1995; 1996: Seppelt & Green, 1998; Smith, 1999; Cannone, 2005; Cannone & Seppelt, 2008).
Victoria Land (Ross sector) is characterized by the highest levels of biodiversity (in terms of species richness, α diversity) among the different sectors of continental Antarctica, with the documented occurrence of c. 57 species of lichens (Castello & Nimis, 2000; Cannone & Seppelt, 2008) (although some papers report up to 92 lichen species, see Castello 2003) and of 14 species of bryophytes (Ochyra et al., 2008; Cannone et al., 2013).

The latitudinal transect allows to study most of the widespread formations and vegetation communities in Victoria Land (Table IV.2.2). The vegetation of the Victoria Land monitoring network (Cannone, 2006) includes four main vegetation types, dominated by (a) mosses, (b) mosses encrusted by epiphytic lichens, (c) macrolichens, and (d) scattered epilithic lichens and mosses, respectively.

These contrasting communities offer different potential sensitivity to climate change. Monitoring of the dynamics of the hydrophilic bryophyte communities and of their target species (*Bryum pseudotriquetrum*, *Ceratodon purpureus* and *Syntrichia magellanica*) compared to those of xerophilic species and communities (i.e. *Syntrichia sarconeurum*) could indicate changes of ground moisture and of active layer thickness. The dynamics and distribution patterns of chionophylous species such as *Pseudephebe minuscula* and *Usnea* spp., should provide important information on the snow cover regime and on its potential alterations in the future. The scattered vegetation on barren grounds could allow analyzing the community dynamics and the species turnover in those open communities dominated by abiotic factors and lacking intraspecific and interspecific competition.

Vegetation communities and species are more influenced by the coast–inland gradient and by the water availability (associated with ground moisture and snow), than by the latitudinal gradient (Cannone & Seppelt, 2008). Hot spots of biodiversity occurred at sites where the availability of suitable ecological niches allows vegetation colonization and development.

The floristic classification proposed by Cannone & Seppelt (2008), distinguishes six different orders which could be grouped in two main classes of vegetation: a) dominated by lichens (orders 1, 2, 5 of Table IV.2.2 and b) mainly dominated by bryophytes (orders 3, 4, 6 of Table IV.2.2).

The sequence of associations within each alliance emphasizes ecological requirements, often indicative of a range of moisture and/or nutrient regime. The distribution of bryophytes is compatible with a gradient in ground moisture.

Recent data on soil properties in different vegetation and permafrost conditions in continental Antarctica (Cannone et al. 2008) show that *Bryum* ssp., *Ceratodon purpureus and Syntrichia magellanica* are generally found where ground moisture is relatively high (25%), while *Schistidium antarctici* and *Syntrichia sarconeurum* generally occur where soil moisture is lower (13%). However, in many localities in Victoria Land species show adaptation to variable ground moisture conditions (e.g. *C.purpureus* and B.*pseudotriquetrum* are able to tolerate also relatively dry conditions according to Selkirk & Seppelt 1987).

Table IV.2.2 Floristic classification of Victoria Land (according to Cannone & Seppelt, 2008).

Formation	**Order**	**Alliance**	**Association**
Macrolichens	1. *Usnea-Umbilicaria*	1. *Usnea-Umbilicaria*	1A. *Usnea sphacelata*
			1B. *Usnea antarctica-Umbilicaria decussata*
Macrolichens and microlichens	2. *Buellia frigia - Physcia caesia - Xanthoria ssp.*	2A. *Buellia frigida*	2A.1. *Prasiola crispa-Xhantoria mawsonii*
			2A.2 *Buellia frigida*
			2A.3 *Rhizoplaca melanopthalma*
		2B. *Xhantoria elegans-Physcia caesia*	2B. *Xhantoria elegans-Physcia caesia*
Mixed macrolichens and bryophites	3. *Pseudephebe minuscula - Lecidella siplei* - Bryophytes	3A. *Lecidella siplei -* Bryophytes *(B.pseudotriquetum, B.argenteum, Hennediella)*	3A. *Lecidella siplei - Bryophytes (B.pseudotriquetum, B.argenteum, Hennediella)*
		3B. *Pseudephebe minuscula - Lecidella siplei* - Bryophytes	3B. *Pseudephebe minuscula - Lecidella siplei –* Bryophytes
Lichen encrusted Bryophytes	4. *Physcia caesia - Candelariella flava - Xhantoria mawsonii -* Bryophytes	4. *Physcia caesia - Candelariella flava - Xhantoria mawsonii –* Bryophytes (*Schistidium - Syntrichia - Bryum*)	4A.1. Epiphytic lichen encrusted *S.antarctici*
			4A.2. Epiphytic lichen encrusted *B.argenteum*
			4A.3. Epiphytic lichen encrusted *S.sarconeurum*
Microlichens	5. *Lecidea - Rhizocarpon - Rhizoplaca - Lecanora*	5. *Lecidea - Rhizocarpon - Rhizoplaca - Lecanora*	5. *Lecidea - Rhizocarpon - Rhizoplaca - Lecanora*
Pure Bryophytes	6. *Bryum ssp - Ceratodon - Cyanobacteria*	6A. *Bryum ssp - Ceratodon - Cyanobacteria*	6A.1. *Bryum argeteum - Cyanobacteria*
			6A.2. *Cyanobacteria - B.argeteum - Ceratodon*

IV.2.E. Description of the latitudinal transect

The study sites were selected within a long-term monitoring network (Cannone, 2006). They represent the most common soil and vegetation types in Victoria Land. See table 1, p. 4 in Cannone et al. (2008) for details on soil types and table 4, p. 7 in Cannone & Seppelt, (2008) for details on vegetation types. The main edaphic characteristics of sites are summarized in Table IV.2.1.

Apostrophe Island

Apostrophe Island is the northernmost location of the network (Fig. IV.2.3). It is a small ice-covered island lying close of Spatulate Ridge in Lady Newnes Bay. The scattered pioneer vegetation is composed of *Bryum argenteum*, *Caloplaca athallina and Candelariella flava* growing on the gravel where no soil disturbance is visible. However, periglacial features are frequent on the island, with typical patterned ground with extensive epilithic macrolichen vegetation containing *Usnea sphacelata*, *Umbilicaria decussata*, *Bryum subrotundifolium* and *Buellia frigida*. Here, two plots of the long-term monitoring are installed: PP7 and PP8. PP7 is representative of bare ground condition, with only some pioneer vegetation, while PP8 is installed on the macrolichen – bryophytes communities. Manipulation experiments were installed in the surroundings of the permanent plots.

Figure IV.2.3. Photo of Apostrophe Island. © PNRA.

Edmonson Point

Edmonson Point is a rounded, largely ice-free point lying below Mount Melbourne along the west side of Wood Bay (Fig. IV.2.4). It is an Antarctic special protected area (ASPA 165) because of its terrestrial and freshwater ecosystems. The volcanic lithology and substrates are nutrientenriched by colonies of Adélie penguins and south polar skuas. The site contains a diverse range of freshwater habitats supporting algae, cyanobacteria and bryophytes. The study area was placed distant enough from the coast, attempting to avoid any influence from the penguin rockery.

At Edmonson Point three plots were installed among the long-term monitoring network, representing the range of different vegetation types, without any direct influence of the penguin rookery. Two plots (PP1, PP2) were installed on closed bryophyte and cyanobacteria vegetation, on wet and temporarily inundated surfaces with ornithogenic soils. *Bryum pseudotriquetrum Bryum argenteum, Ceratodon purpureus* and *Cyanobacteria* covered the area with more permanent water, and *Syntrichia magellanica*, *Ceratodon purpureus*, *Bryum argenteum* and *Rhizoplaca melanophthalma* occupied the temporarily inundated site at the foot of the slope. The third plot (PP3) was located on the upper slope, on bare ground. Manipulation experiments were installed in the surroundings of the permanent plots, and on the northern coast of the island.

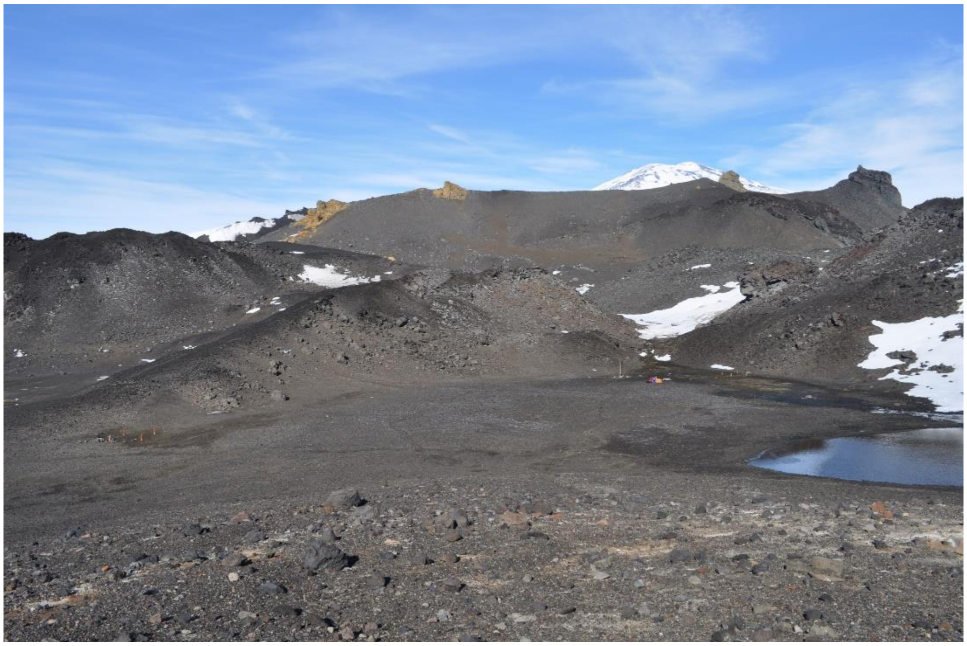

Figure IV.2.4. Photo of Edmonson Point. © PNRA.

Boulder Clay

Named unofficially "boulder clay" (74°44' S, 164° 01' E, 205 m a.s.l.), it is an ice-free area located about 6 km south of the Italian station (MZS) on a very gentle slope (5°) with southeastern exposure (Fig. IV.2.5).

Lithologically, a Late Glacial ablation till overlies the body of a dead glacier (Guglielmin et al., 1997). Surface features include perennially ice-covered ponds with icing blisters and frost mounds, frost-fissure polygons and debris islands (Guglielmin et al., 1997, French & Guglielmin, 1999; 2000; Forte et al., 2016). The till matrix is generally silty sand, with small patches of clayey silt. Vegetation is very scarce (less than 5% of the surface is covered by vegetation), composed mainly of patches of mosses and epilithic lichens (Cannone et al., 2008). The boulder clay site represents the longest (since 1999) near-continuous data series of permafrost and active layer temperature monitoring in Antarctica (Guglielmin, 2004; 2006; Guglielmin & Cannone 2012; Guglielmin et al., 2014). The vegetation of Boulder Clay belongs to different community types, ranging from different types of epilithic lichen communities, to bryophytes dominated communities both with pure bryophytes as well as with lichen encrusted bryophytes.

Two plots are installed at Boulder Clay from the long-term monitoring. The first (PP10) was on loose morainic deposits colonized by scattered bryophytes (*Bryum subrotundifolium, Schistidium antarctici*) with terricolous and epiphytic lichens (*Lecidella siplei*). The second (PP11) was in epilithic vegetation (*Umbilicaria decussata, Usnea sphacelata, Buellia frigida, Pseudephebe minuscula*) on the pebbles, large boulders and outcropping bedrock that were widespread in this proglacial area.

Both plots were located within the CALM grid area, which was installed for the monitoring of active layer thickness (e.g. Guglielmin, 2006; Guglielmin et al., 2014). Manipulation experiments were installed close to the CALM grid and to the permafrost monitoring station (Guglielmin & Cannone, 2012).

Figure IV.2.5. Photo of Boulder Clay. © PNRA.

Tarn Flat

The Tarn Flat area is the largest ice-free area (ca. 11 × 9 km) north to the McMurdo Dry Valley in Victoria Land (Antarctica) and is not far from the Italian Antarctic Research Station (MZS) (Fig. IV.2.6).

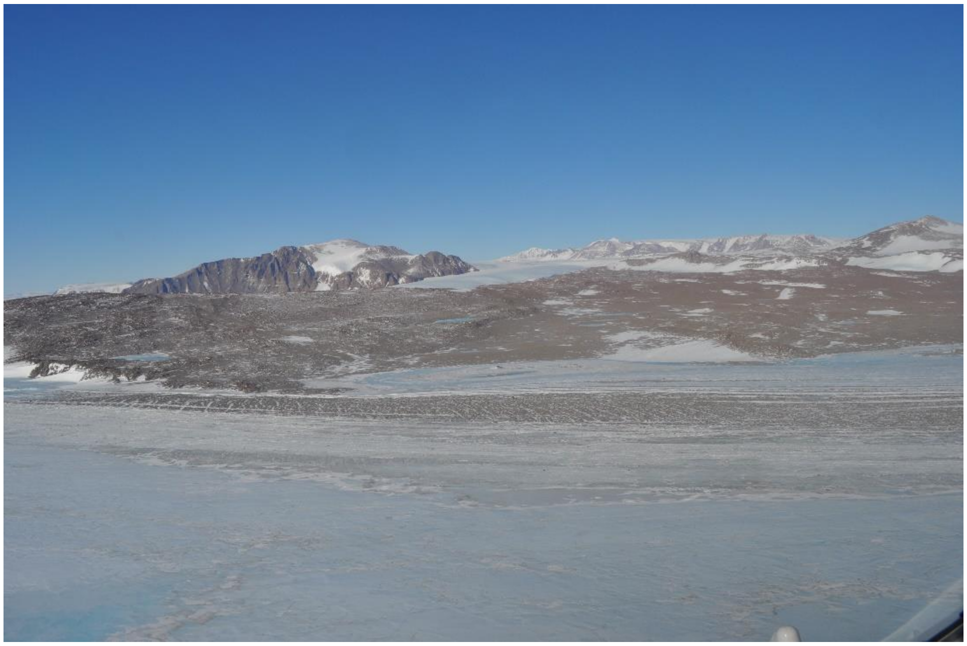

Figure IV.2.6. Photo of Tarn Flat. © PNRA.

Figure IV.2.7. Photo of Finger Point. © PNRA.

This ice-free area is characterized by Late Wisconsin glacial deposits, with some spectacular eskers at lower elevations, and by outcropping Ordovician granites overlaid by sparse erratic boulders. It presents a very large number of lakes and ponds (64) that have dimensions from a few tens to several hundreds of meters.

Tarn Flat was selected to represent the conditions of an inland site characterized by a very large proglacial ice-free area with morainic sediments. The prevailing vegetation was scattered terricolous and epilithic lichen vegetation (*Lecidella siplei*, *Lecidea cancriformis*) both on the main surface of hydric and younger grounds (PP17) and on the upper part of the slope (PP14). Manipulation experiments were installed in the surroundings of the permanent plots.

Finger Point

Finger Point is the southernmost site of the permanent plot network (Cannone, 2006) (Fig. IV.2.7): in this area three different sites, were selected that were representative of different ecology and habitats.

The first plot (PP9) was located on closed bryophyte vegetation (*Schistidium antarctici, Bryum argenteum*) covered by terricolous and epiphytic lichens (*Lecidella siplei, Buellia papillata*), the second plot (PP18) was established on outcropping bedrock with epilithic macrolichen and crustose lichens community with *Buellia frigida*, *Xanthoria elegans* and *Umbilicaria decussate*, and the last plot was located on barren ground with very scattered epilithic and terricolous/epiphitic lichens (PP19) with dominance of *Lecidella siplei*.

Manipulation experiments were installed in the surroundings of the permanent plots.

IV.3. Materials and Methods

IV.3.A. Manipulation experiments in Continental Antarctica

During the Antarctic summer 2014/2015 we installed some manipulation experiments in Victoria Land, in order to evaluate the responses of Antarctic terrestrial ecosystems to climate change.

Our experiments focused on the manipulation of different parameters, with a mono-factorial design: soil thermal regime, snow thickness, precipitation, fertilization (addition of different nutrient types), irrigation (water and snow addition).

We replicated these experiments in 5 locations located along a latitudinal transect in Victoria Land (Apostrophe Island, Edmonson Point, Boulder Clay, Tarn Flat and Finger Point) (Table IV.3.1 and see chap. IV.2.E for more information on the study sites).

Table IV.3.1. List of the manipulation experiments that we installed in Victoria Land.

Site	experiment	Mosses (n)	Bare ground (n)
Apostrophe Island	OTC	3	1
	Snow shield	1	1
	Snow fence x10	1	
	Additions x6	1	1
Edmonson Point	OTC	8	2
	Snow shield	3	2
	Snow fence x10	1	
	Additions x6	4	4
Boulder Clay	OTC	3	1
	Snow shield	1	1
	Snow fence x10	1	
	Additions x6	1	1
Tarn Flat	OTC	3	1
	Snow shield	1	1
	Snow fence x10	1	
	Additions x6	1	1
Finger Point	OTC	3	1
	Snow shield	1	1
	Snow fence x10	1	
	Additions x6	1	1

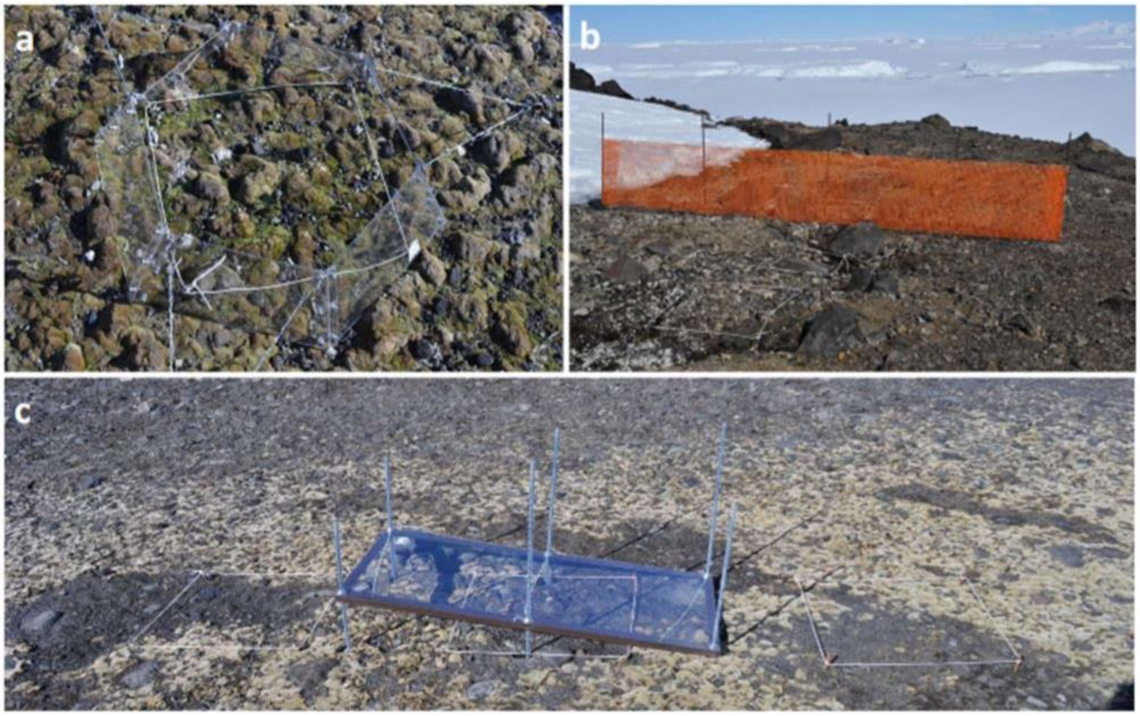

Figure IV.3.1. Example of the structures installed for the manipulation of a) soil temperature (open top chamber, OTC), b) snow thickness (snow fence) and c) precipitation (snow shield).

In total, we installed (Fig. IV.3.1):
a) 26 Open Top Chambers (OTCs): polycarbonate hexagonal greenhouses open at the summit, which contribute to increase the soil temperature. The OTCs were installed according to the ITEX (International Tundra Experiment) protocol (Molau & Edlund, 1996);
b) 13 snow shields (SS): polycarbonate sheets installed subparallel to the soil surface and open on the borders, to recreate a drought scenario;
c) 5 snow fences (SF): plastic barriers installed perpendicular to the main wind direction, to manipulate the snow depth changes due to the wind effects (snow erosion, transport, accumulation).

The fertilization was carried out with four different treatments:

- Urea (xU);
- Ammonium Sulphate (xN);
- phostrogen (xNPK, equivalent of the Plant Food used at the Foscagno valley ME);
- Penguin guano (xG, previously sterilized in laboratory).

Simultaneously to the fertilizations, we carried out also the following additions:

- Snow addition (xS)
- Water addition(xW).

Based on previous analysis of the minimum area of the continental Antarctica vegetation communities (Cannone, 2004), for each of these experiments we installed a plot of 50x50cm.

Moreover, in the proximity of each of these structures (OTCs and SS) we installed a control plot (cc), kept to evolve without any treatment. For the SS the control plot was on the windward side of the shield, while another plot was installed on the leeward side of the shield (Fig. IV.3.1).

The fertilization and manipulation (Fig. IV.3.2) of the soil water regime (indicated as "additions" in table IV.3.1) were performed on 16 replicates (each replicate consisting of the 6 treatments listed above), 8 replicates on vegetated soils and 8 with non-vegetated soils.

Indeed, we run our experiments installing for the same location at least one sub-replicate on bare ground and one on vegetated sites (mosses or mosses-lichens depending on the site). The vegetated plots were selected in order to incorporate the most dominant vegetation (cryptogamic) community of each site (see chap. IV.2).

The minimum configuration that was installed in each location was the following (in Apostrophe Island, Boulder Clay, Tarn Flat and Finger Point): 4 OTCs (mosses n=3; bare ground n=1), 2 snow shields (mosses n=1; bare ground n=1); 1 snow fence (main vegetation cover of each location); 2 replicates of additions (mosses n=1; bare ground n=1) (Table IV.3.1).
In Edmonson Point, we could install more replicates: 10 OTCs (mosses n=8; bare ground n=2); 5 snow shields (mosses n=3, bare ground n=2), 1 snow fence (mosses) and 8 replicates of additions (mosses n=4; bare ground n=4).

In each location we dug at least one soil trench up to the permafrost table, and collected sample at different depth (2 and 10 cm, and at the permafrost table) in order to describe the main soils characteristics, providing a baseline for future investigation.

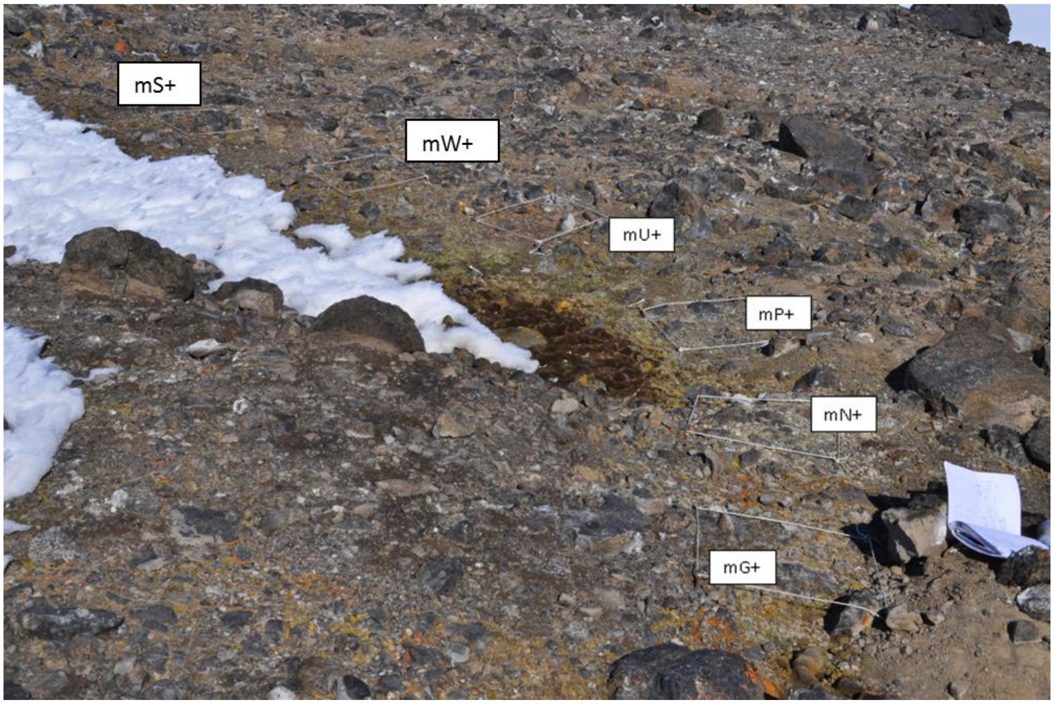

Figure IV.3.2. Example of one of the additions replicate: G = penguin guano, N = ammonium sulphate, P = Phostrogen – NPK, U =Urea, W = water, S = snow.

For the amount of fertilizer addition for each single experiment we referred to Wasley et al., (2006): Urea = 45g, ammonium sulfate = 45g, NPK=25g. Similarly, we added 50 g of guano, collected at the penguin rockery of Edmonson Point. All the nutrients were sterilized in the base before the addition.

The fertilizer was diluted in 300 mL of water that was obtained by sample of snow taken from each site (and melted in the laboratory). Only in Edmonson Point, since there was a larger amount of liquid water we could use the water from a spring not so far from our experiments.

The water amount of each single treatment (xW) was of 3.5L, according to preliminary laboratory analysis of the water holding capacity of sample collected in each site. Concerning the addition of snow (xS) consisted in addition of snow taken in each location close to the plot, and compacted on the plot to reach 10 cm of snow cover thickness on the entire plot surface.

At the addition sites, we collected for each plot the surface soil (<2 cm) at the border of the plot, in different moments of the experiments: before the treatments and at the end of the season. We separated the biomass when present, stored the samples at -20°C, and brought in Italy for further investigation. Therefore, the additions were executed also on the area outside from the plot, covering a15 cm band all around the plot.

To know the effect of the structures installed on soil temperature, we installed some data loggers with two-channels thermistors (Hobo Onset U23, accuracy ±0.2°C, resolution ±0.02°C). In total we installed data loggers in: 9 OTCs, with one sensor in the middle of the chamber and one sensor outside in the control plot (in 1 OTC at Finger Point, Apostrophe Island, Tarn Flat, Boulder Clay and 5 OTCs at Edmonson Point); 5 snow shields, with one sensor under the shield and the other one in the leeward side (a shed in every location); 1 snow fence (Edmonson Point) with two sensors in the leeward side and two sensors in the windward side, at different distances from the barrier.

Moreover, as a baseline for future monitoring, we run a phytosociological survey (PS 50x50cm and PS 5x5cm) and a point intercept (PI 5x5cm) for each of the installed plot.

IV.3.B. Permafrost warming and vegetation changes in Continental Antarctica

This work was carried out at four study sites located across a latitudinal gradient from Apostrophe Island (73°30'S, 167°50'E) to Prior Island (75°41'S, 162°52'E).

At Victoria Land, since 2002, a long-term monitoring network of vegetation was established in order to assess the impacts of climate change on vegetation (Cannone, 2006). One of the selected site was Boulder Clay, which represents the longest near-continuous data series of permafrost and active layer temperature in Antarctica (Guglielmin, 2004; 2006). Since 1999, a 100x100m circumpolar active layer monitoring (CALM) grid (Nelson et al., 2008) was established at this site (see Guglielmin, 2006).

We thus analyzed a) the patterns of spatial and temporal active layer variability, b) changes of associated vegetation and c) climatic factors of active layer and vegetation changes.

More detailed information about methods concerning this section, are provided in the paper Guglielmin et al. (2014), see next chapter IV.4.B.

IV.4. Results

IV.4.A. Evaluation of the effects after one year of ME in Continental Antarctica

In the following chapter, we provided a preliminary assessment of the effects on the ground surface temperature (GST) after one year of climate change simulation in Victoria Land, continental Antarctica.

Snow fences

The installed snow fences exerted a strong influence on the snow cover distribution. The effect was relevant both in terms of snow thickness and snow duration, even if we could not quantify the effect directly for all the sites, since the snow cover was already disappeared in many of the study sites at the beginning of the summer of the second year of the experiments.

Moreover, since the study sites are located in remote places, it was not easy to survey with high frequency the sites to make measures of snow cover thickness.

Comparing the snow thickness data that we could collect in the last summer (only 3 day of measures) in Apostrophe Island, we observed a larger snow accumulation in the leeward site of the fence (Fig. IV.4.1.).

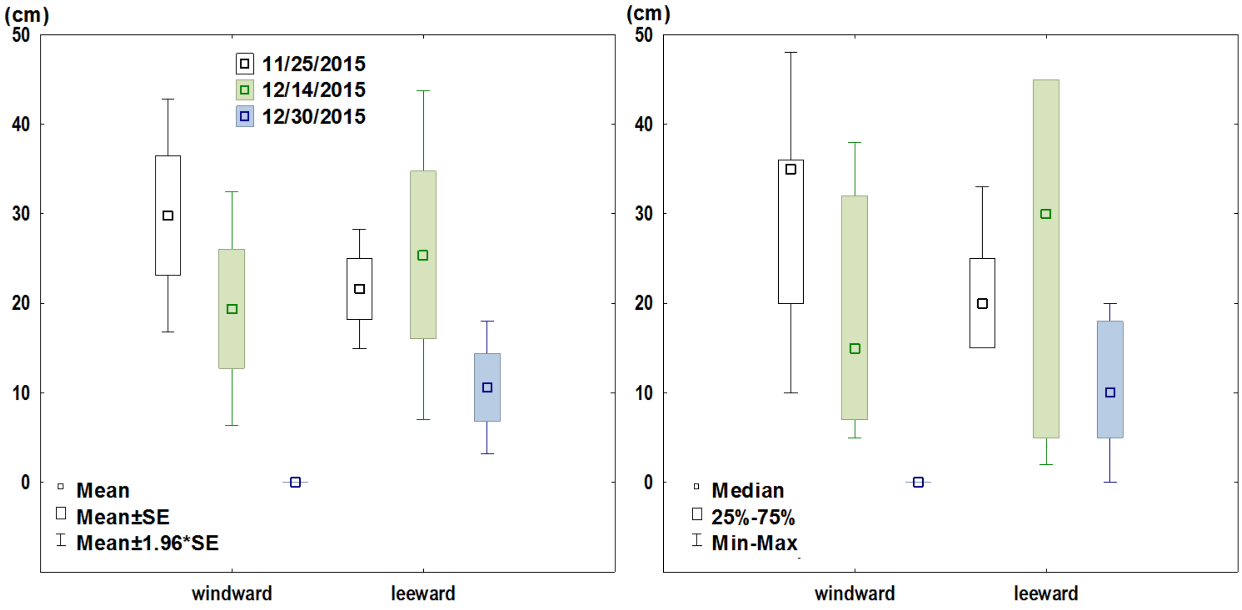

Figure IV.4.1. Snow thickness measured in the summer 2015/2016 at the snow fence in Apostrophe Island.

This effect was more evident going towards the melting date: at the end of December, the windward side was already snow free in all the plots, while the leeward sites already had snow in 3 plots.

The effect of the enhanced snow cover in the leeward sites was also clearly visible when analyzing the data from the temperature loggers installed at Edmonson Point.

Considering the MAGST over the first year of the experiment, the leeward side was warmer (+1.3 °C) compared to the windward side. A larger amount of snow cover on the leeward side, lead at least to 4 main responses (Fig. IV.4.2):
1) longer period of zero curtain effect (ZCE) at the beginning of winter season, most likely related to higher snow cover thickness;
2) more buffered temperature during all the freezing period, thus indicating a presence of an insulating snow cover layer;
3) higher temperature in Fall and Winter, but lower in Spring;
4) later SM, and later start of thawing season (almost 10 days later).

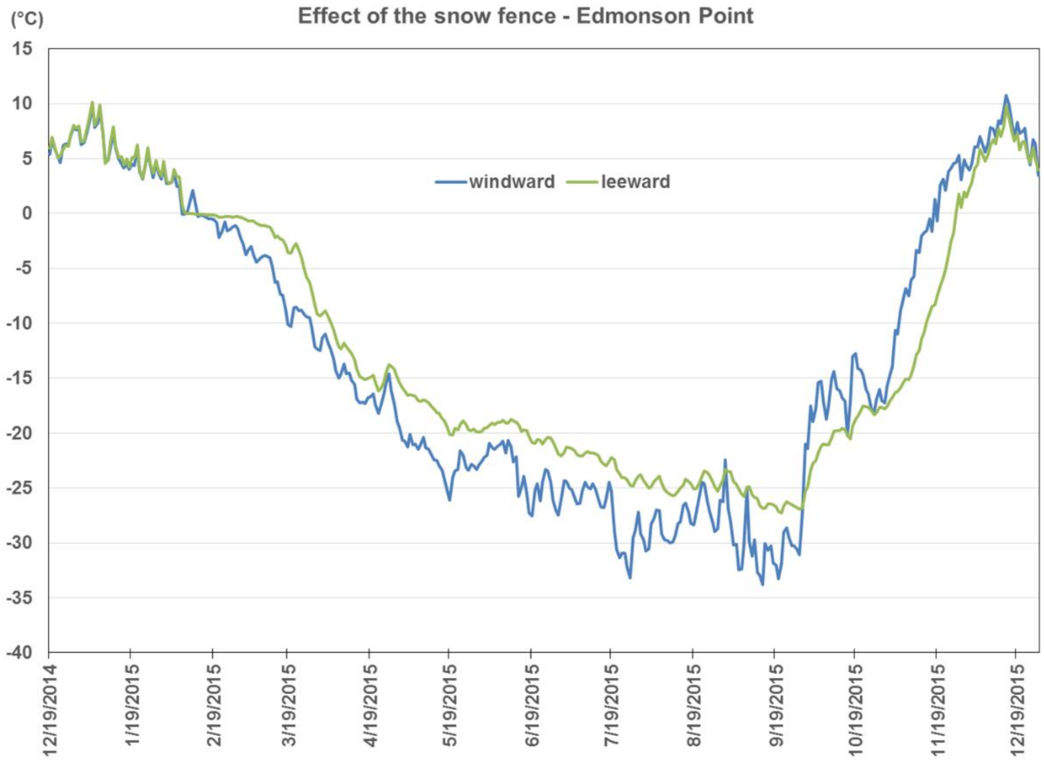

Figure IV.4.2. Comparison of the effects of windward and leeward sides on the mean daily GST recorded at the snow fence in Edmonson Point.

Snow shields (SS) and open top chambers (OTCs)

After one year of treatments, we observed a positive effect on the MAGST for all our replicates (considering both OTCs and SS).

We lost data only from one OTC in Apostrophe I., due to the damage of the skuas (Table IV.4.1).

The OTC exerted a larger variability (concerning their effect compared to the cc), ranging from +0.1 to +1.1°C, while the SS ranged from +0.2 to +0.9°C. There was also a large intra-site variability of the effects of OTC: according to the data collected at Edmonson Point, the effect of the OTCs ranged from 0.1 to 0.8 °C (Table IV.4.1).

Table IV.4.1. Effects of the open top chamber (OTC) and of the snow shields (SS) on the MAGST, computed as difference compared to the control plots (cc).

types	location	ID	Treatment - cc
OTC	Edmonson Point	EP1_m_OTC1	+0.1
		EP2_m_OTC	+0.5
		EP3_m_OTC	+0.6
		EP4_m_OTC	+0.2
		EP5_m_OTC1	+0.8
	Boulder Clay	BC_m_OTC1	+0.5
	Tarn Flat	TF_m_OTC	+0.9
	Finger Point	FG_m_OTC1	+1.1
SS	Apostrophe I.	AI_m_SS	+0.2
	Edmonson Point	EP5_m_SS	+0.2
	Boulder Clay	BC_m_SS	+0.5
	Tarn Flat	TF_m_SS	+0.9
	Finger Point	FG_m_SS	+0.7

Finger Point and Tarn Flat were the locations that documented the largest effects of both OTCs and SS (Table IV.4.1).

Interestingly, over all our manipulation experiments (ME) the largest increase of temperature was caused by the snow fence comparing the leeward side to the windward side (+1.3°C), thus highlighting the role of snow cover changes more than air temperature changes.

In some cases, we observed a longer persistence of the snow cover inside the chambers (similarly to other ME in Antarctica, see Bokhorst et al., 2011; 2013). At Boulder Clay for example, in two OTCs we measured at the end of November: 1) 20 cm of snow inside than chamber compared to zero of the cc; 2) 10 cm inside the OTC compared to zero of the cc. In these two cases, the effect of the longer snow cover lasted one week.

Concerning the SS instead, we did not observe such a clear effect of different melting rates. Indeed, most likely this phenomena was caused by different heat fluxes inside the OTCs, which are closed on all sides, compared to the SS, were the air is free to move.

The effect of a more persistent snow cover will increase the MAGST with the OTC (since we observed a clear increase of MAGST at the leeward side of the snow fence experiment), and it will be a factor to be considered in terms of changed water regime and local humidity.

Comparing two structures of the same site (Boulder Clay), we found some differences. Indeed, while the trend of the control plot of the OTC (OTC-cc) and of the leeward plot of the SS (SS-lee) was very similar (as could be expected for the snow free season), the OTC in general exerted a warmer effect on the mean daily GST during the thawing season compared to the SS (Fig. V.4.3).

All the plots recorded the same period of ZC. However, in the OTC and in the SS there was a prolonged period with temperatures of few decimals lower than zero (not properly a ZC period), thus indicating that some snow was probably accumulated (Fig. V.4.3).

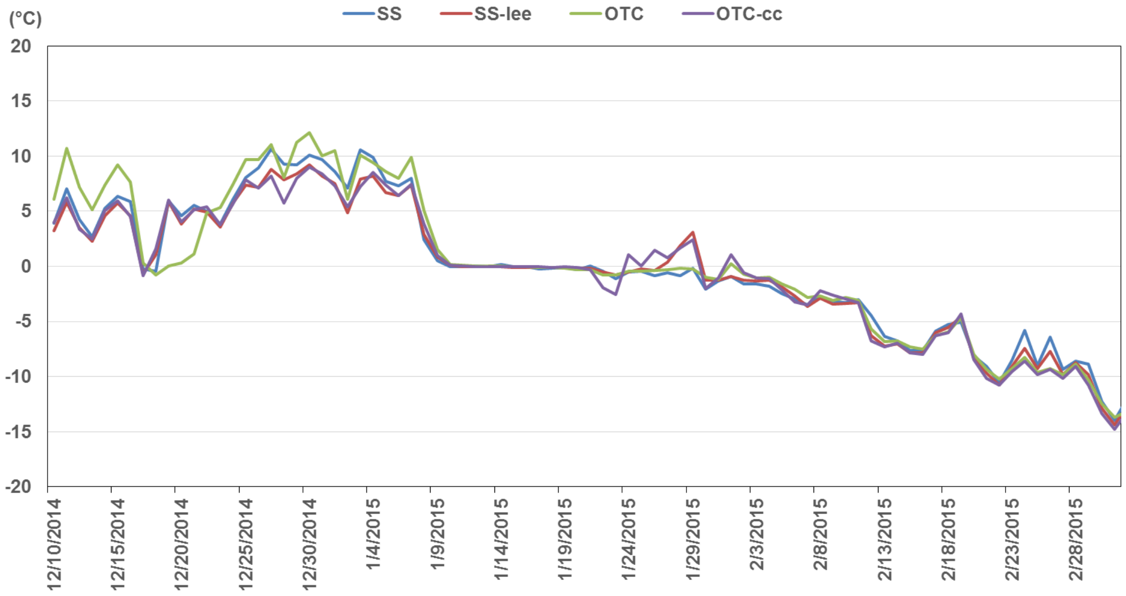

Figure V.4.3. Comparison of the effects of a snow shield (SS) and an open top chamber (OTC) from Boulder Clay, at the beginning of the freezing season.

Other manipulation experiments

Concerning the additions (nutrient, water and snow additions), we could not provide any preliminary assessment after only one year of activities. Indeed, the responses that will be evaluated in these sites (change in vegetation composition, biomass, microbial activity and community composition, etc…) require longer time to be evident (e.g. Wasley et al., 2006).

IV.4.B. Permafrost warming and vegetation changes in Continental Antarctica

Given the high biodiversity of cryptogamic flora in Antarctica (e.g. Cannone & Seppelt, 2008; Convey et al., 2014; Singh et al., 2015) there is a urge need to understand relationships of mosses and lichens with climate and environmental change currently occurring in Antarctica.

Continental Antarctica provides a unique opportunity to assess the natural dynamics and responses of cryptogams without the disturbance effect due to the competition with vascular plants or biotic disturbances.

While along Antarctic Peninsula a strong warming coupled with large retreat of glaciers occurred (Turner et al., 2007), in continental Antarctica a cooling or almost stable temperature trend have been detected (e.g. Doran et al., 2002; Guglielmin & Cannone, 2012). However, recent observations highlighted that permafrost is warming also in this region due to the increase of total summer radiation, with a summer surface temperature warming trend of 0.31°C per year coupled with an active layer thickening of 1 cm per year (since 1997) (Guglielmin & Cannone, 2012),

In the following paper (Guglielmin et al., 2014) we aim to investigate the patterns of spatial and temporal variability of the active layer thickness and of the associated vegetation (over the period 2002-2013), and to identify the climatic forcing factors of active layer and vegetation changes.

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Permafrost warming and vegetation changes in continental Antarctica

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Abstract

Continental Antarctica represents the last pristine environment on Earth and is one of the most suitable contexts to analyze the relations between climate, active layer and vegetation. In 2000 we started long-term monitoring of the climate, permafrost, active layer and vegetation in Victoria Land, continental Antarctica. Our data confirm the stability of mean annual and summer air temperature, of snow cover, and an increasing trend of summer incoming short wave radiation. The active layer thickness is increasing at a rate of 0.3 cm y^{-1}. The active layer is characterized by large annual and spatial differences. The latter are due to scarce vegetation, a patchy and very thin organic layer and large spatial differences in snow accumulation.

The active layer thickening, probably due to the increase of incoming short wave radiation, produced a general decrease of the ground water content due to the better drainage of the ground. The resultant drying may be responsible for the decline of mosses in xeric sites, while it provided better conditions for mosses in hydric sites, following the species-specific water requirements. An increase of lichen vegetation was observed where the climate drying occurred. This evidence emphasizes that the Antarctic continent is experiencing changes that are in total contrast to the changes reported from maritime Antarctica.

Keywords: climate change, active layer, permafrost, vegetation, Antarctica, mosses, snow, ground water content, incoming radiation

S Online supplementary data available from stacks.iop.org/ERL/9/045001/mmedia

1. Introduction

The high-latitude areas of both hemispheres are expected to be highly sensitive to the impacts of climate change. Vegetation, the active layer, and the underlying permafrost are key environmental components of terrestrial ecosystems.

Since the 1990s, permafrost has generally warmed across the Northern Hemisphere (Christiansen *et al* 2012, Romanovsky *et al* 2011): it exhibited smaller warming rates in warm (close to 0 °C) or ice-rich permafrost, while in other areas (such as the higher altitudes of Central Asia) it has shown a rate of increase of up to 0.5 °C decade^{-1} since the early 1990s (e.g., Zhao *et al* 2010). However, since the 1990s, trends have been weak in several sites, including Alaska (e.g. Osterkamp 2008), northern Canada (e.g. Smith *et al* 2005) and Antarctica (McMurdo Dry Valleys) (Guglielmin *et al* 2011). Since the 1990s, a progressive increase of the active layer thickness (ALT) has been recorded in all regions, with the exception of northern Alaska, the western Canadian Arctic, and West Siberia (Christiansen *et al* 2012). In continental Antarctica, in northern Victoria Land, the active layer thickened by 1 cm y^{-1} from 1996 to 2009 (Guglielmin and Cannone 2012), while in the McMurdo Sound (southern Victoria Land) no clear trend was recognized from 1999 to 2007 (Adlam *et al* 2010).

Permafrost warming and active layer thickening were mainly attributed to air warming, although in several cases the role of snow cover, soil properties and the overlying vegetation were emphasized (e.g. Osterkamp 2007, Romanovsky *et al* 2007, Fedorov and Konstantinov 2008, Haeberli *et al* 2010, Romanovsky *et al* 2010). In particular, the active layer thickness does not always follow the trend of the underlying permafrost and, in general, appears much more closely related to the trend of summer air temperature (e.g. Osterkamp 2008, Streletskiy *et al* 2008) or to summer radiation (Guglielmin and Cannone 2012).

Vegetation affects the energy balance of the soil and, therefore, vegetation changes can have feedbacks on the active layer thickness and underlying permafrost temperature (Walker *et al* 2003, Guglielmin and Cannone 2012). Traditionally in the Arctic, vegetation is considered an important factor that greatly affects the energy balance and, consequently, the active layer (e.g. Klene *et al* 2001), and also because different vegetation associations produce a different organic layer thickness (Mazhitova *et al* 2004, Smith *et al* 2009). In continental Antarctica, despite its scattered coverage, the cryptogamic vegetation provides an insulating effect on the ground surface temperature (GST), with a net cooling. The degree of cooling varies with differences in vegetation type, structure, coverage and thickness (Cannone and Guglielmin 2009).

Conversely, active layer changes can indirectly modify the overlying vegetation through variations of the frost heave, cryoturbation, ice segregation or gelifluction disturbance, or through the different water availability linked to the active layer thickness (Cannone *et al* 2007, 2014).

Relating to the impacts of recent climate change on vegetation, in maritime Antarctica a large increase of the two native Antarctic vascular plants (*Deschampsia antarctica*, *Colobanthus quitensis*) has been documented in the past 30–50 years in response to air warming (Parnikoza *et al* 2009, Torres Mellado *et al* 2011) and probably also to increased precipitation and active layer thickening (Cannone *et al* 2014).

There is a shortage of data available on vegetation changes in continental Antarctica. In Victoria Land the only example of long-term vegetation monitoring, carried out at Cape Hallett (Brabyn *et al* 2005), showed that, in the period 1960–2004, vegetation expanded (with an increase of algae), although it was not possible to associate this change with long-term temperature increases, while it is likely that it was driven by local alterations of water supply. In other sectors of continental Antarctica, in Wilkes Land, there was a generalized increase of lichen vegetation and a concomitant decrease of bryophytes due to a drying climate (period 1960–1990; Melick and Seppelt 1997). In Dronning Maud, Johansson and Thor (2008) reported an increase in both lichen species density and abundance and a slight increase of lichen taxa of their permanent plots for the period 1992–2002.

In one of the few areas of the world in which air warming does not exist (Victoria Land, Ross sector, continental Antarctica) we aim to: (a) identify the patterns of spatial and temporal active layer variability; (b) analyze the changes of the associated vegetation; (c) identify the climatic forcing factors of active layer and vegetation changes.

2. Material and methods

2.1. Study sites

This work was carried out at four study sites located across a latitudinal gradient from Apostrophe Island (73°30′S 167°50′E) to Prior Island (75°41′S 162°52′E) (figure 1(A)). The sites are ice-free areas located along the coast, with similar altitudinal ranges (50–150 m.a.s.l.), allowing one to achieve comparable data not influenced by differences in elevation. At all sites there is continuous permafrost with an active layer varying in thickness from zero to more than 100 cm depending on the year and the site location. Detailed descriptions of the chemical and physical characteristics of the soils are available in Cannone *et al* (2008).

The vegetation of Victoria Land is composed exclusively of cryptogams. Previous descriptions of the moss and lichen flora and of the main vegetation communities have been provided (e.g. Kappen 1985, Castello and Nimis 1995, Seppelt *et al* 1995, 1996, Seppelt and Green 1998, Smith 1999, Cannone 2005, Cannone and Seppelt 2008). At Victoria Land, since 2002, a long-term monitoring network of vegetation was established (Cannone 2006). The vegetation of the Victoria Land monitoring network includes four main vegetation types, dominated by (a) mosses, (b) mosses encrusted by epiphytic lichens, (c) macrolichens, and (d) scattered epilithic lichens and mosses, respectively.

The climate of the area surrounding the Italian Antarctic Research Station 'Mario Zucchelli' (MZS) is characterized by a mean annual air temperature of −13.9 °C (Frezzotti *et al* 2001). Precipitation, always in the form of snow, is very low and ranges between 100 and 200 mm (Grigioni *et al* 1992, Monaghan *et al* 2006).

The main study site, named unofficially boulder clay, is located close to MZS, in northern Victoria Land. Boulder clay (74°44′45″S 164°01′17″E, 205 m.a.s.l.) is an ice-free area located about 6 km south of the Italian station on a very gentle slope (5°) with southeastern exposure. Lithologically, a Late Glacial ablation till overlies a body of dead glacier (Guglielmin *et al* 1997). Surface features include perennially ice-covered ponds with icing blisters and frost mounds, frost-fissure polygons and debris islands (Guglielmin *et al* 1997, French and Guglielmin 1999, 2000). The till matrix is generally silty sand, with small patches of clayey silt. Vegetation is very scarce (less than 5% of the surface is covered by vegetation), composed mainly of patches of mosses and epilithic lichens (Cannone *et al* 2008). The boulder clay site represents the longest near-continuous data series of permafrost and active layer temperature in Antarctica (Guglielmin 2004, 2006). Since 1999, a 100 × 100 m circumpolar active layer monitoring (CALM) grid (Nelson *et al* 2008) was established at this site. Details of the active layer and GST spatial variability were given in a previous paper (Guglielmin 2006).

The other three sites (Apostrophe Island, 73°30′S 167°50′E; Edmonson Point, 74°19′S 165°07′E and Prior Island 75°41′S 162°52′E) were selected within a long-term monitoring network (Cannone 2006) for this investigation (figure 1(A)). They represent the most common soil and vegetation types in Victoria Land (see table 1, p. 4 in Cannone *et al* 2008 for details on soil types and table 4, p. 7 in Cannone and Seppelt 2008 for details on vegetation types).

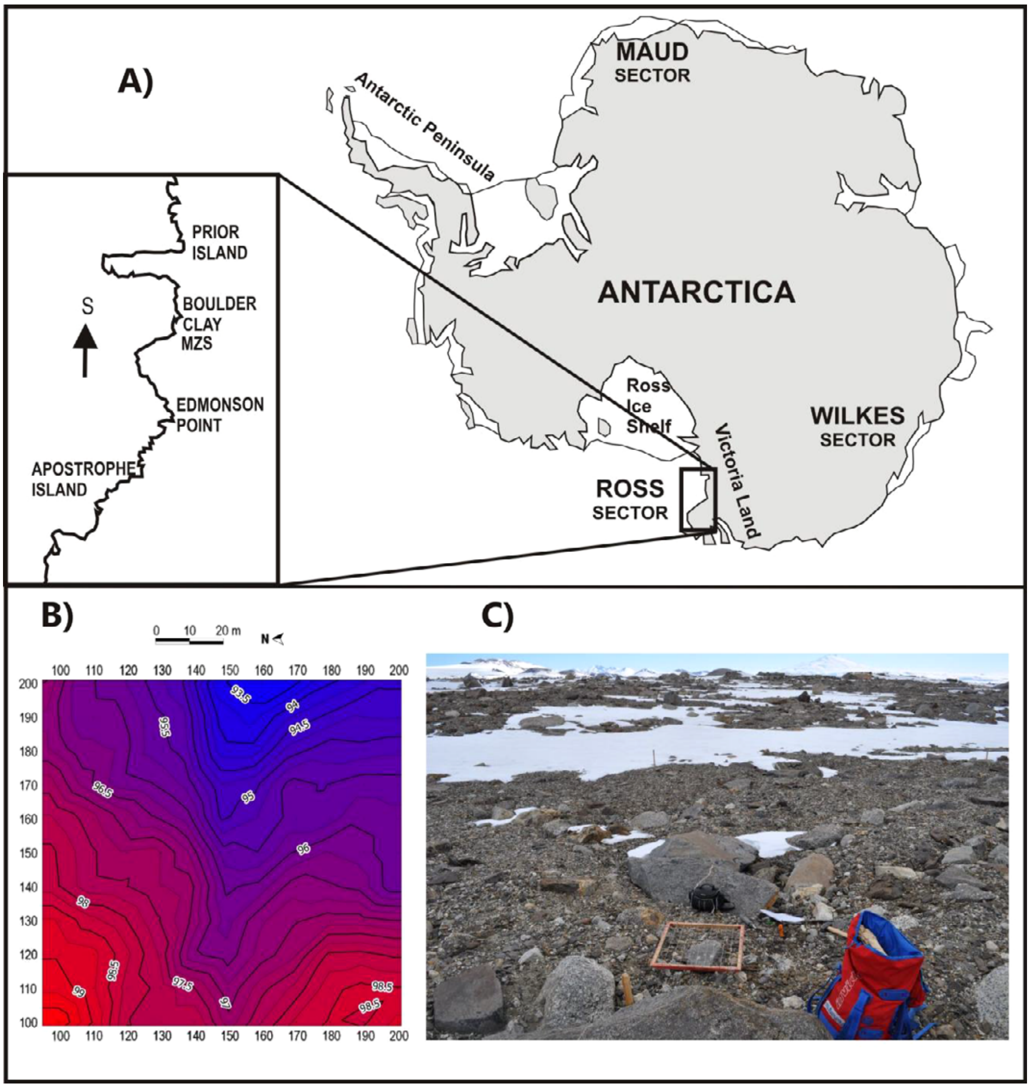

Figure 1. Study area: (A) The study sites are located in Victoria Land (continental Antarctica) in the Ross sector, along a coastal latitudinal transect from Apostrophe Island to Prior Island; (B) Digital Elevation Model (DEM) of the boulder clay CALM grid; (C) view of the boulder clay CALM grid with a special focus on the depression where snow cover accumulates. In the background the active volcano Mt. Melbourne is visible.

3. Field surveys

3.1. Active layer

Active layer measurements were performed within the boulder clay CALM grid, which is a 100 m × 100 m grid (figures 1(B) and (C)). The measurements were carried out on each of the 121 grid points marked in the field by a wooden stake, through two different methods: (a) ground probing according to the CALM protocol (Nelson *et al* 2008) and (b) measurement of the thermal profiles (down to a depth of 30 cm) according to Guglielmin (2006). In the second case the active layer thickness was then calculated as the 0 °C depth by extrapolating from the two deepest temperature measurements (Guglielmin 2006). Here we used only the data obtained by the second method because, due to the coarse grain size, the data achieved by probing are less consistent (Guglielmin 2006). At the same time also the snow cover (cm) was manually recorded at the same 121 points: these data are referred to the long-lasting snow cover still occurring at the date of the measurements. Due to logistical constraints, it was not possible to perform the active layer, ground temperature at 10 cm depth (GT10) and snow cover measurements every year.

Ground surface temperatures were monitored at 2 cm depth at boulder clay (permafrost station, see Guglielmin 2006, Guglielmin and Cannone 2012), Prior Island, Apostrophe Island and Edmonson Point. The thermistors have an accuracy of 0.1 °C at boulder clay station and 0.2 °C at the other sites, with a resolution of 0.01 °C. Temperatures were measured every 10 min. At boulder clay station uninterrupted monitoring has continued since 1996, while at the other sites a summer monitoring was carried out in the season 2001/2002 and, since December 2009, a continuous monitoring is ongoing. Air temperature and incoming solar radiation were recorded by the PNRA (Progetto Nazionale Ricerche Antartide) AWS Eneide (74°41′S 164°05′E) located in the middle of the coastal latitudinal gradient (data are kindly

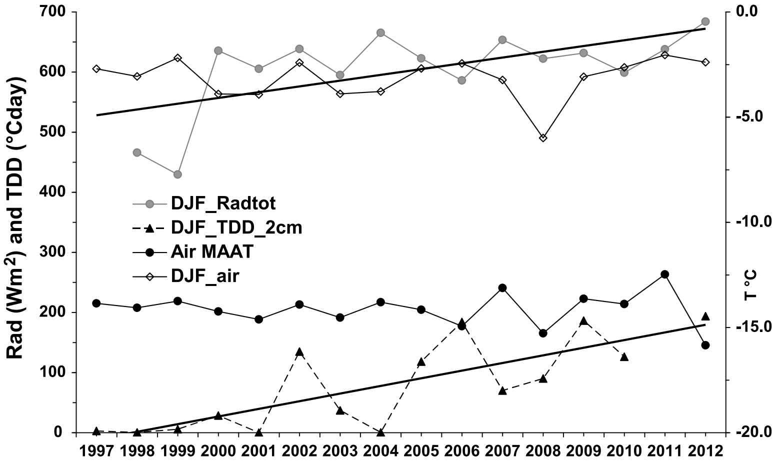

Figure 2. Climate trends in the period 1996–2012 with special reference to: mean annual air temperature (Air MAAT) and summer air temperature (DJF_air), summer total incoming radiation (DJF_Radtot) and the summer soil thawing degree days (DJF_TDD_2 cm). All data are kindly provided by the AWS Eneide with the exception of DJF_TDD_2 cm, which was provided by the boulder clay Permafrost station.

provided by Meteo-Climatological Observatory of PNRA, www.climantartide.it).

3.2. Vegetation survey

The vegetation survey was carried out in the CALM grid at boulder clay in 2002 and 2012/13. In 2002 the survey was carried out in all the 121 nodes of the grid on 50 cm × 50 cm plots. For each plot the total vegetation cover (%), list of species, and percentage cover of each species was recorded. In 2012/13, due to logistical constraints, the survey was carried out on only 25 nodes of the grid selected randomly, using the same method adopted in 2002, in order to provide comparable data.

The permanent plots located at boulder clay (PP10, PP11), Prior Island (PP5, PP6), Edmonson Point (PP1, PP2 and PP3) and Apostrophe Island (PP7) were installed in 2001/2002 (Cannone 2006) and analyzed according to the protocol by Cannone (2004). In 2011/12/13 the permanent plots were re-surveyed to analyze the eventual changes that occurred in more than 10 years.

4. Statistical and GIS analyses

The analyses of the trends with time of the main climatic parameters were carried out by linear regression. To assess which factors affected active layer thickness, snow cover, ground temperature at 10 cm (GT10) and the main vegetation parameters (total coverage, etc) within the boulder clay CALM grid, we carried out general regression models (GRM) with backward stepwise selection. All these computations were carried out using the software Statistica 6.0 produced by StatSoft®. The vegetation changes occurred in the boulder clay CALM grid and their interactions with the main environmental factors were analyzed by means of multivariate analysis (RDA, Redundancy Analysis). In particular, for the RDA the data were log transformed, the scaling was made through the inter-species correlation, the standardization by species was centered, and the sample standardization was normal and the significance of the first ordination axis was performed by Monte Carlo test ($p < 0.05$). The vegetation changes occurring in the selected permanent plots were analyzed by means of multivariate analysis (RDA, Redundancy Analysis). In particular, for the RDA the data were square-root transformed, the standardization by species was centered, without standardization by samples, and the significance of the first ordination axis was performed by Monte Carlo test ($p < 0.01$). The multivariate analyses were performed using the software CANOCO for Windows (Ter Braak and Smilauer 1998). A table with the eigenvalues and the percentage of variance was reported for each analysis (Supplementary Table 1 available at stacks.iop.org/ERL/9/045001/mmedia).

To illustrate the spatial variability of snow cover, GT10, active layer thickness and vegetation, maps were prepared using the triangulation with a linear interpolation algorithm (Hinkel and Nelson 2003, Mazhitova *et al* 2004) available in commercial software (QGis 1.8.0). The normalized index of active layer variability (INV, see figure 6) was determined according to Hinkel and Nelson (2003).

5. Results

5.1. Climate

In the period 1996–2012, the mean annual air temperature (MAAT) (figure 2) ranged between −15.3 °C (2008) and −12.5 °C (2011), with an almost stable trend ($\beta = +0.035\,°\mathrm{C\ y^{-1}}$), although not statistically significant. In the same period, summer air temperature (DJF-Air) (figure 2) ranged between −6 °C (2008) and −2 °C (2011), being apparently stable (without any statistically significant trend). Only during fall (MAM_air) was there a statistically significant warming of air temperature ($R = 0.64$, $p < 0.01$; $\beta = +0.16\,°\mathrm{C\ y^{-1}}$), compensated by a decreasing spring air temperature ($\beta = -0.21\,°\mathrm{C\ y^{-1}}$, although not statistically significant).

The total summer incoming short wave radiation (DJF_Radtot) (figure 2) showed a statistically significant increase ($R = 0.61$; $p = 0.013$; $\beta = +9601$), although this

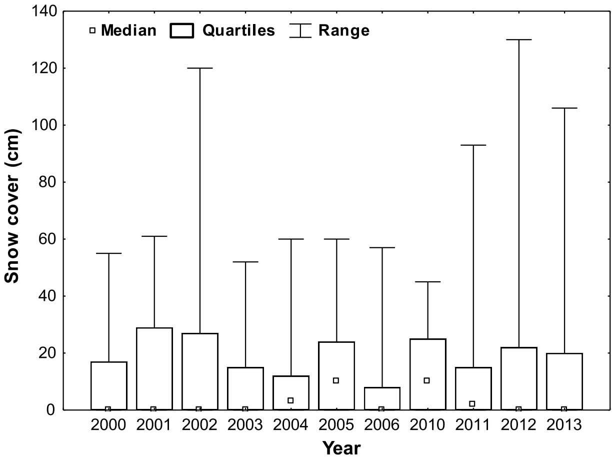

Figure 3. Snow cover thickness (cm) (median, quartiles and range) at the boulder clay CALM grid (100 m × 100 m, 121 nodes) in the period 2000–2013.

trend is less pronounced than that recorded until 2009 ($p = 0.031$; $\beta = +12\,621$; Guglielmin and Cannone 2012).

The snow cover data are available since 2000 at the boulder clay CALM grid, with only three years lacking (2007–2009). Snow cover showed a relatively large inter-annual variability, both relating to the mean (6–18 cm) as well as the maximum values (<50–130 cm) (figure 3), but showed no apparent trend in the selected period. Snow cover distribution is strongly controlled by the meso-morphological features (figures 1(B) and (C)) and, in particular, by the central E–W oriented depression that acts always as the main accumulation zone (figures 1(B) and 4). The possible spatial variations are related to micro-morphological features (<10 m), such as big boulders, and some small concavities and convexities that produce snow accumulation, mainly N–S or NE–SW oriented, when the prevailing wind blows from the NW, as it did in 2013.

5.2. Active layer

At the boulder clay CALM grid, the active layer thickness showed a large variability (figure 5), both for its mean values (from 2 to 18 cm) and its ranges (maximum values between 23 and 92 cm), with a slight increasing trend (+0.3 cm y^{-1}, $p < 0.05$). For all years (with the exception of 2001), at intra-annual level, the active layer thickness was strictly linked to the ground temperature at a depth of 10 cm (data not shown), as tested by linear regression ($p < 0.01$, β ranging between +0.11 and +0.3, depending on the specific year).

The linkage of the active layer thickness at boulder clay with the ground temperature is testified also by the summer thawing degree days of the ground surface temperature (DJF soil TDD) recorded at the boulder clay permafrost station, which exhibited a statistically significant increase ($R = 0.75$, $p < 0.01$; $\beta = +11.45$), although with a less pronounced trend than until 2009 ($p < 0.01$; $\beta = +13$; Guglielmin and Cannone 2012).

The INV showed a wide variability, with values ranging between 0 and 827%, with an annual mean of 142% (if we include also the nodes never thawed) in the examined period or with a range between 0 and 387% and a mean of 67.8%: considering only the nodes that every year were thawed.

Considering the sites located along the latitudinal transect, the ground surface temperature (GST) and the thawing degree days (TDD) showed contrasting patterns (table 1), with a significant increase in the plots hosting barren ground (PP3, Edmonson Point, PP6, Prior Island), as well as in the plots characterized by the occurrence of moss-dominated vegetation with high coverage and high soil water content (PP1, PP2, Edmonson Point). On the other hand, GST decreased in the plots characterized by the dominance of epilithic lichens, mainly on blocks (PP7, Apostrophe Island, PP11, boulder clay).

At these sites, the soil total organic carbon (TOC) increased since 2002 (table 1). The soil water content showed contrasting patterns, with a slight increase or stability in the driest plots (PP6, Prior Island and PP10, boulder clay) and a strong decrease in the wettest plots (PP1, PP2, PP3, Edmonson Point) (table 1).

5.3. Vegetation

The vegetation of the boulder clay CALM grid was composed exclusively of cryptogams (mosses; epilithic, epiphytic and ubiquitous lichens; cyanobacteria and algae), occurring in discontinuous and scattered patches. According to the survey carried out in 2002, almost all of the 121 nodes of the CALM grid were characterized by the occurrence of communities dominated by mosses with epiphytic lichens and cyanobacteria colonizing the sediments with finer grain size, coupled with communities dominated by epilithic lichens, mainly occurring on pebbles and blocks. In 2002 the dominant moss species were *Schistidium antarctici*, followed by *Bryum argenteum*, while other species such as *Syntrichia princeps* and *Ceratodon purpureus* occurred only sporadically across the grid. Several epiphytic lichens were associated with *Schistidium antarctici* and other moss species, such as *Buellia grimmiae, B. papillata*, *Candelariella flava* and *Leproloma* spp. Cyanobacteria occurred both associated with the moss-dominated communities, as well as alone as crusts on the finer sediments. The epilithic communities were mainly composed of crustose lichens (dominated by the placodioid *Buellia frigida*), but included also foliose (mainly *Umbilicaria decussata*) and fruticose lichens (*Usnea antartica*).

Analyzing the vegetation changes in the selected 25 nodes of the CALM grid, since 2002 there was a generalized decline of vegetation, both for the total coverage and for the coverage of the main groups of cryptogams (mosses, cyanobacteria), with the exception of lichens (figure 7).

The spatial distribution of vegetation within the selected 25 CALM grid nodes (figure 8) showed that the vegetated areas almost coincide between 2002 and 2013 and that their coverage was almost stable (although with slight decreases of mosses and increases of lichens).

The multivariate analyses (RDA) (figure 9) emphasized that the floristic composition of vegetation changed slightly comparing 2002 and 2013, with two main groups of species: (a) the community dominated by *Schistidium antartici* is

Table 1. Main vegetation and soil characteristics in 2002 and 2013 at the selected permanent plots at Edmonson Point (PP1, PP2, PP3), Prior Island (PP5, PP6), Apostrophe Island (PP7) and boulder clay (PP10, PP11). Legend: ND = not determined.

	PP1		PP2		PP3		PP5		PP6		PP7		PP10		PP11	
	2002	2013	2002	2013	2002	2013	2002	2013	2002	2013	2002	2013	2002	2013	2002	2013
Total coverage (%)	83.75	94.5	88.13	88.06	0	0	17.8	24.3	1.8	3.8	45.4	49.5	3.6	3.2	19.5	21.5
Mosses (%)	58.46	73.1	82.64	79.5	0	0	0.5	0.5	0.03	0.2	3	3.39	1.47	1.15	0.38	0.43
Lichens (%)	0	0.69	5.29	5.97	0	0	17.08	22.89	1.3	1.57	45.87	50.6	2.08	2.08	19.15	19.84
Cyanobacteria (%)	25.94	23.5	0	15.19	0	0	0	0.007	0	0	0	0.16	0	0.11	0	0
Algae (%)	0	3.22	0.05	0.16	0	0	0.1	1.08	0.73	2.04	0	0	0	0	0	0
Water (%)	30.3	19	27.6	13.7	16	3.08	ND	4.8	0.7	0.77	7	5.2	0.9	1.46	ND	4.35
TOC (%)	1.6	2.9	0.5	1.1	0.1	0.46	ND	4	4	7.35	0.3	1.74	0.2	0.78	ND	0.56
GST (°C)	3.8	4.1	2.8	5.3	5.3	7.8	1.9	−0.3	1.7	2.8	7.3	4.5	−0.1	0.5	ND	ND
TDD	126	135.5	134	265	250.5	370.1	169.9	111.9	151.2	258.2	234.5	152.5	39	119	ND	ND

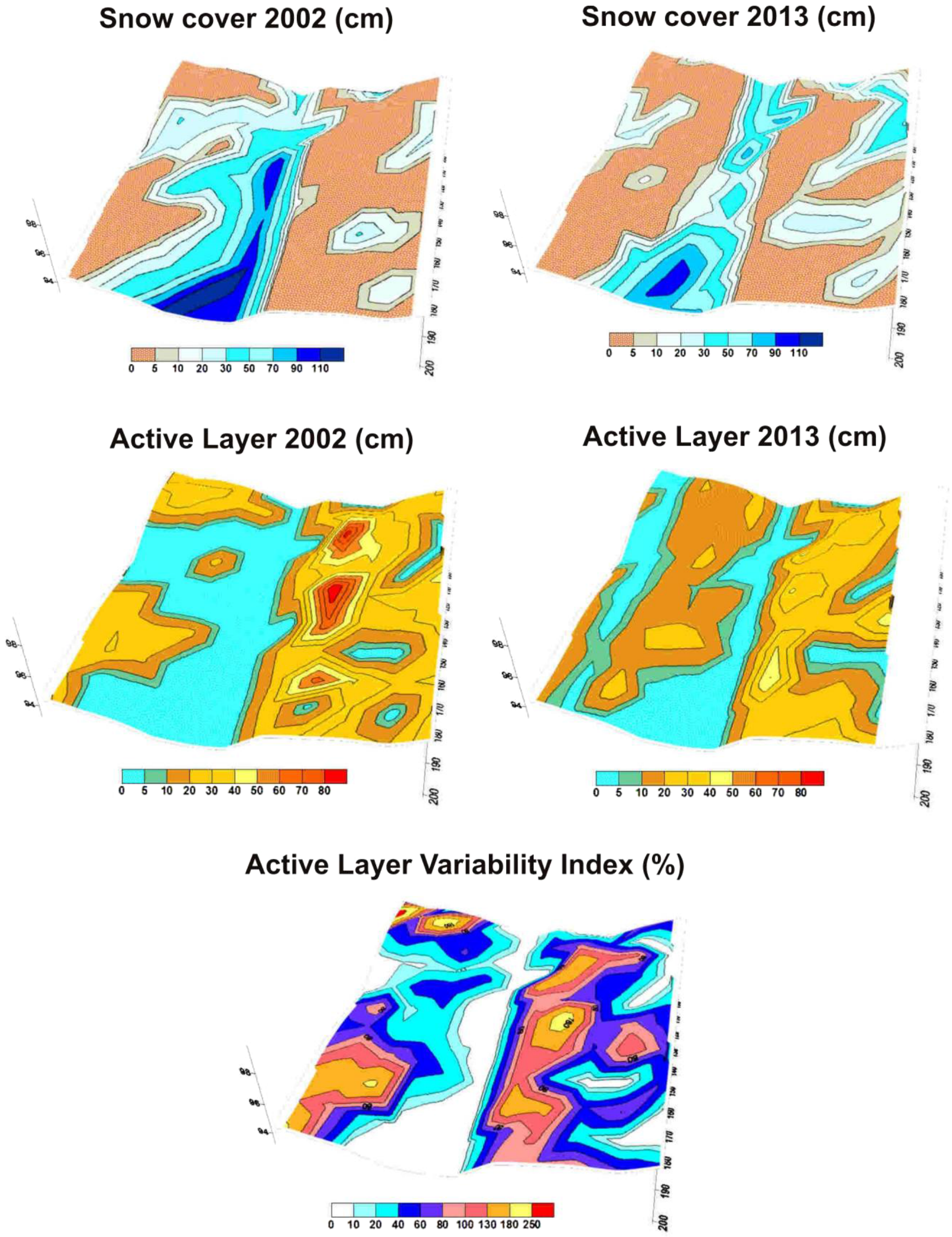

Figure 4. Changes of snow cover (cm), active layer thickness comparing 2002 and 2013 within the boulder clay CALM grid and active layer variability index (INV) computed for the selected period.

preferentially associated with sites with less snow cover, higher topographic position, thicker active layer and higher GT10, (b) the communities of epilithic lichens (*Buellia frigida, Umbilicaria decussata*), are mainly associated with the availability of blocks, larger snow accumulation and thinner active layer. Closer to the origin, the community dominated by *Bryum argenteum* and epiphytic lichens showed wide ecological requirements. The shift between the 2002 and 2012 sites in the site graph (figure 9) emphasized that in the 10-year period the vegetation changed slightly. In most cases these changes depended on the decrease of coverage of one or more species, while the floristic composition within the plot remained relatively stable.

Considering the sites located along the latitudinal transect, vegetation exhibited contrasting patterns too (table 1), although different from those of the environmental abiotic factors. Indeed, both the southernmost plots located at Prior Island (PP5, PP6), the northernmost plots of Apostrophe Island (PP7) and the plot with highest moss coverage and soil water content of Edmonson Point (PP1) were characterized by a large vegetation increase (total vegetation coverage). The intra-plot patterns of mosses and lichens mainly reflected the original vegetation composition of each plot (e.g. lichens increased in

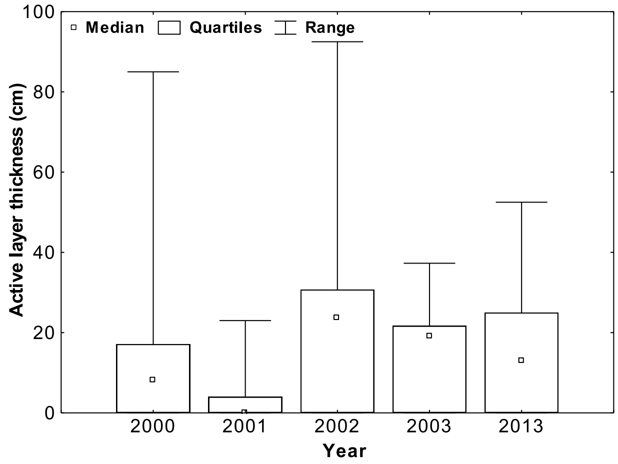

Figure 5. Active layer thickness (cm) (median, quartiles and range) measured at the boulder clay CALM grid (100 m × 100 m, 121 nodes) in the period 2000–2013 (please note that there is a gap between the 2003 and 2013 measurements).

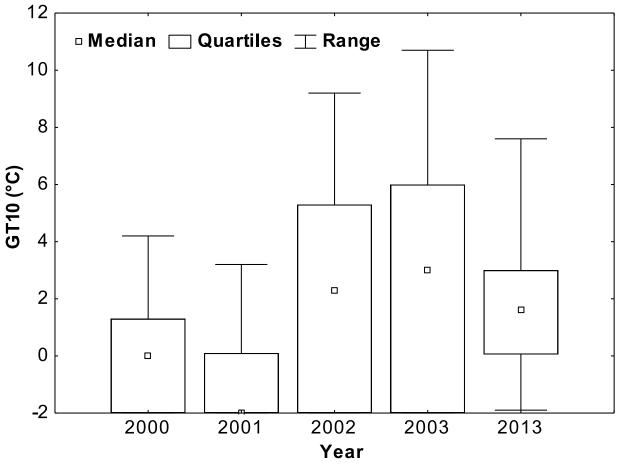

Figure 6. Ground temperature at 10 cm depth (°C) (median, quartiles and range) measured at the boulder clay CALM grid (100 m × 100 m, 121 nodes) in the period 2000–2013 (please note that there is a gap between the 2003 and 2013 measurements).

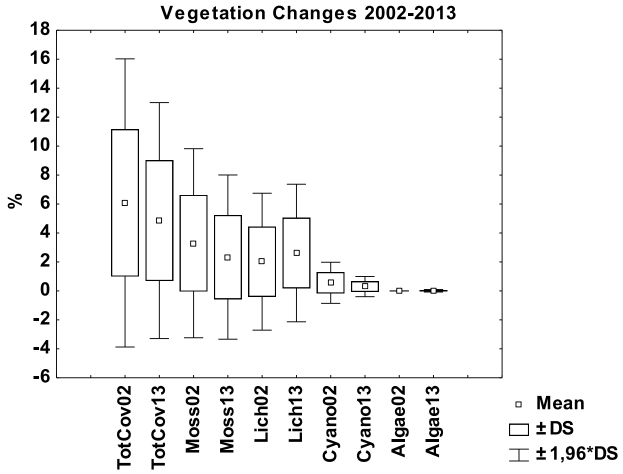

Figure 7. Vegetation changes (mean, mean ± standard deviation and range) at the boulder clay CALM grid (100 m × 100 m, 25 selected nodes) comparing 2002 and 2013 for: (a) total vegetation coverage (%); (b) total mosses (%); (c) total lichens (%); (d) cyanobacteria (%).

Table 2. Environmental and climatic factors that statistically significantly affect, respectively, the active layer thickness (cm) and the snow cover (cm) within the boulder clay CALM grid as tested by GRM with backward stepwise selection. The factors without statistically significant importance (height, blocks, pebbles, gravel, year) are not shown.

	Active layer thickness			Snow		
	F	p	R	F	p	R
Aspect (°)				3.2	<0.001	
Slope (°)				29.6	<0.001	
Sand (%)				4.034	0.04	
Snow (cm)	85.8	<0.001				
MAAT (°C)				5.8	0.01	
DJF_air (°C)	27.9	<0.001				
SON_air (°C)				10.8	0.001	
MAM_air (°C)				8.7	0.003	
DJF_rad (W m^{-2})	22.3	<0.001				
Full model	70.6	<0.001	0.66	6.1	<0.001	0.26

plots mainly composed of lichen vegetation, while mosses did the same in plots mainly dominated by mosses). There was also an increase of algae in half of the selected plots, independently of the values of soil water content.

Also the RDA allowed one to emphasize the changes occurring in the selected permanent plots in the period 2002–2013 (figure 10). As could be expected, the higher values of total coverage, mosses and cyanobacteria were associated with higher soil water contents, differently from lichens. The sites were split into two main clusters: one dominated by lichen vegetation (on the left part of the graph) and one mainly dominated by mosses and cyanobacteria (right part of the graph). Moreover, lichens showed a preference for sites with lower GST and TDD, in a similar way to the lichens occurring in the boulder clay CALM grid (figure 9). The shifts of the sites in the graph emphasized the changes occurring since 2002 and due to changes of both the environmental parameters and the vegetation (see also table 1).

5.4. Climate–active layer–vegetation interactions

Among the main environmental and climatic factors affecting the active layer thickness across the entire boulder clay CALM grid were snow cover, summer air temperature and summer incoming short wave radiation (table 2), as tested by GRM. Analyzing the factors affecting snow cover, the most important were slope, and spring and fall air temperature (table 2).

The snow patterns and persistence, especially in the central depression, control the GT10, ALT patterns and INV,

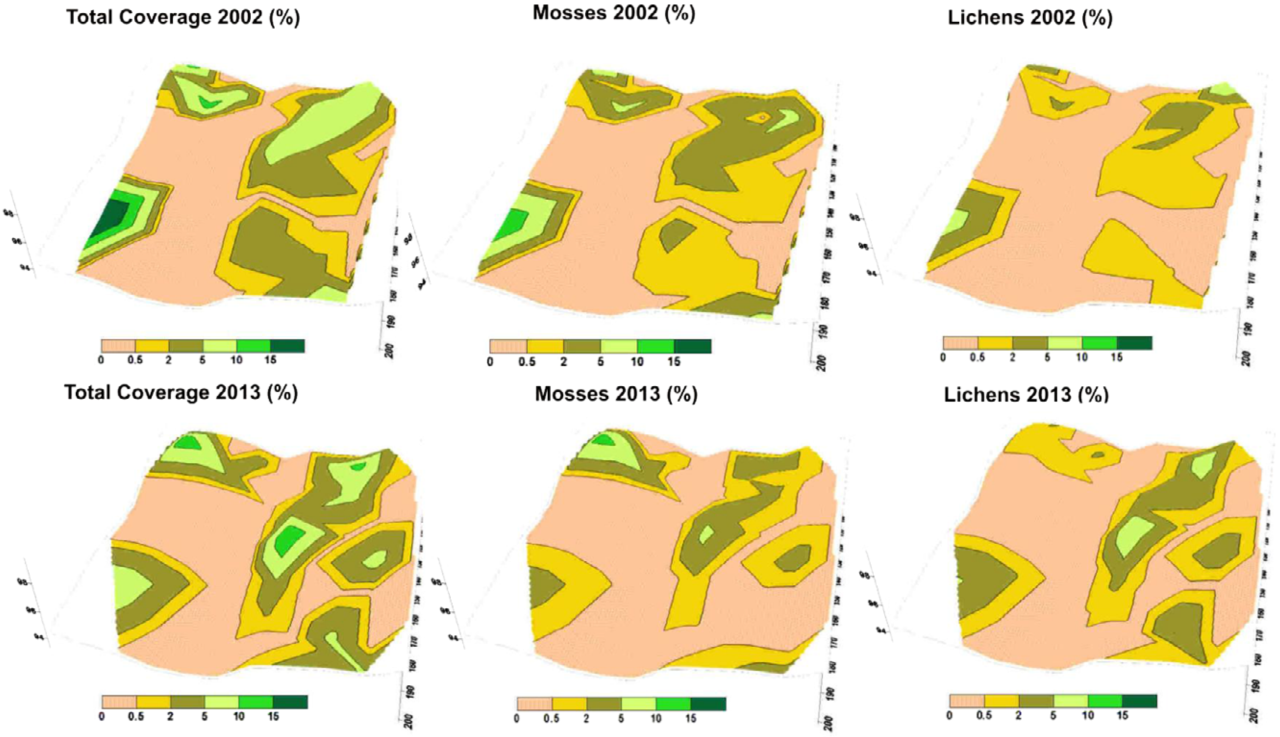

Figure 8. Spatial variation of total vegetation coverage (%), total mosses (%) and total lichens (%) for the 25 selected nodes within the boulder clay CALM grid (100 m × 100 m) comparing 2002–2013.

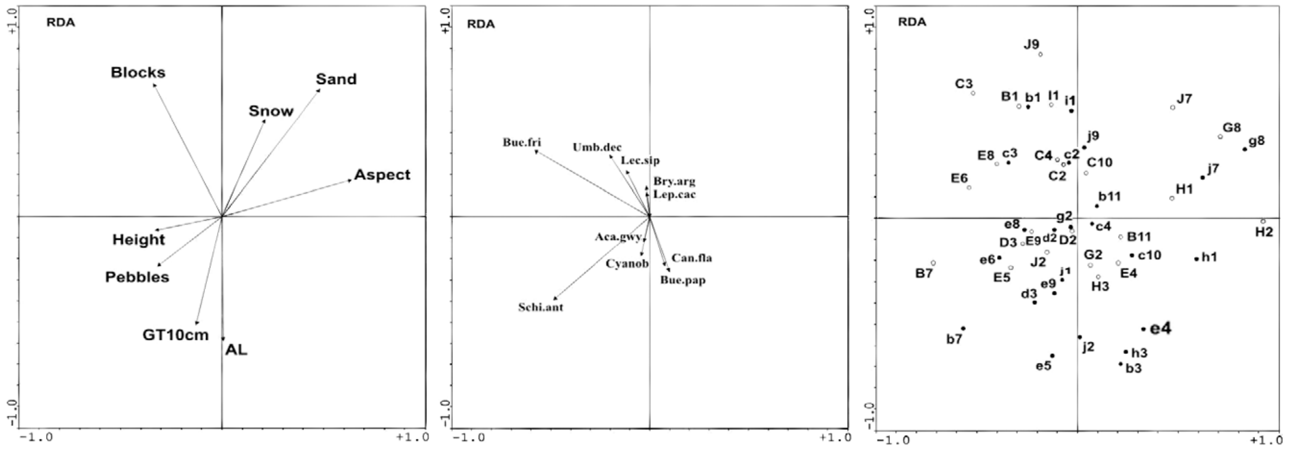

Figure 9. Redundancy analysis (RDA) of the 25 selected nodes of the boulder clay CALM grid in the period 2002–2013, with the plots showing the interactions among: (a) environmental variables; (b) species; (c) sites. Legend: white dots and small letters refer to sites in 2002; black dots and capital letters refer to sites in 2013.

because the ground never thaws when snow persists for all the summer.

Analyzing at intra-annual level which were the most important environmental factors (elevation referred to the origin of the grid, slope, aspect, surface texture, active layer thickness, GT10, snow) affecting vegetation distribution, we found that the only factor exerting a statistically significant influence ($p < 0.05$) in 2002 was the occurrence of blocks (total vegetation coverage and lichens), while in 2012 they were sand (total coverage, mosses), blocks and active layer thickness (lichens) (data not shown).

6. Discussion

6.1. Climate

Our data confirm on a longer time span (until 2012/13) the trend of stability of the mean annual air temperature (MAAT) already outlined by Chapman and Walsh (2007) for the period 1958–2002. According to our results, the air temperature trends observed until 2009 in fall (warming) and spring (cooling) are enhanced, while the trends of both summer incoming radiation and summer soil TDD are less pronounced than in 2009 (Guglielmin and Cannone 2012). The trend of

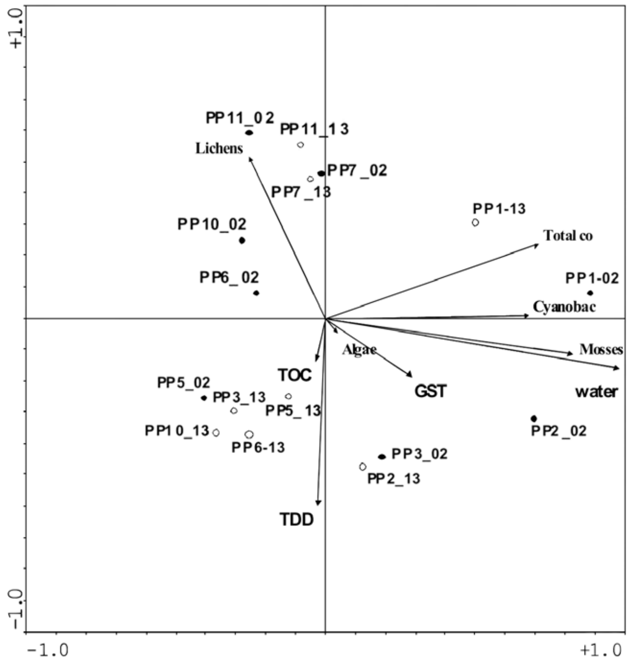

Figure 10. Redundancy analysis (RDA) of the permanent plot sites (PP1, PP2, Edmonson Point; PP5, PP6, Prior Island; PP7 Apostrophe Island; PP10, PP11 boulder clay) in the period 2002–2013, with the triplot showing the interactions among environmental variables, species and sites. Legend: black dots refer to sites in 2002; white dots refer to sites in 2013.

solar radiation increase detected by Doran *et al* (2002) was further confirmed by Hoffman (2010) in the Dry Valleys and Guglielmin and Cannone (2012) in northern Victoria Land.

The observed air temperature stability despite the increase of short wave summer radiation could be explained at a local scale as an albedo effect (Gardiner 1987). The coastal areas of continental Antarctica (including also our study sites), are characterized by the predominance of snow and ice coverage with high albedo (0.6–0.9) with respect to sediment or bedrock outcrops, as well as by a high-speed wind regime. As a consequence, the influence of incoming short wave radiation on air temperature is negligible, but not on the ground temperature (due to the lower albedo allowing more energy to be absorbed).

Indeed, the effect of differential albedo coupled with the increase of incoming radiation promoted an increase of the melting of buried ice in the past decade also in the McMurdo Valley (Fountain *et al* 2014) despite a decrease of air temperature.

Moreover, the processes/trends observed at our study site as well as in the McMurdo Dry Valley could be related to a process occurring at a regional scale. Indeed, what is now happening is the opposite of what happened along the coastal areas of Antarctica between 1959 and 1988. In that period a decrease of short wave incoming radiation occurred in association with an increase of air temperature (Stanhill and Cohen 1997).

At our study site, the snow cover showed no trend relating to its mean depth (figure 3), confirming what was reported by Monaghan *et al* (2006). However, there was a change of the spatial distribution patterns of snow cover within the CALM grid, likely related to a potential change of wind direction (figure 4), as the main part of the snow accumulated in the grid is drifted by the wind.

6.2. Active layer

Our results show that the active layer thickness is increasing, although the data of the monitoring of the boulder clay CALM grid (121 nodes) provide a trend (+0.3 cm y^{-1}) less pronounced than at the boulder clay permafrost monitoring station (+1 cm y^{-1} within the borehole until 2009) (Guglielmin and Cannone 2012). In the other monitoring sites of Victoria Land there are unfortunately insufficient data of active layer thickness dynamics due to logistical constraints.

The active layer increasing trend is a widespread process observed with different rates at several locations in the Northern Hemisphere, from northern Sweden (e.g., +0.7 to −1.3 cm y^{-1} in the period 1978–2006, with an acceleration since 1995, according to Åkerman and Johansson (2008) and more recently confirmed by Callaghan *et al* 2010), in the High Arctic (e.g. Svalbard Islands and Greenland, although not spatially and temporarily uniform, Christiansen *et al* 2010), in North America (e.g., +0.7–1 cm y^{-1} in Yukon, in the period 1985–2008, according to Burn and Zhang 2009), Russia (Drozdov *et al* 2012, Kaverin *et al* 2012) and in the north of East Siberia (Fyodorov-Davydov *et al* 2008). However, long-term observations of changes in ALT are less conclusive because often the active layer thickness exhibits substantial inter-annual fluctuations (e.g. Smith *et al* 2009, Popova and Shmakin 2009) and in several regions it remained substantially stable (e.g., North Slope of Alaska according to Streletskiy *et al* (2008), Shiklomanov *et al* (2010)). In continental Antarctica, only Adlam *et al* (2010) reported active layer thickness data at southern Victoria Land and, for the period 1999–2007, they did not recognize any apparent trend.

In terms of spatial variability, the active layer at the boulder clay CALM grid showed values of mean inter-annual INV much higher than those reported for sites with continuous permafrost at Bolvansky in Russia (Mazhitova *et al* 2004) or at Toolik Lake or Atqasuk in northern Alaska (Hinkel and Nelson 2003). The higher inter-annual variability is mainly concentrated in the upper and more wind exposed relief (SW corner) or on the gentle slope exposed to E–SE. The snow patterns control the INV because this value is lower where snow persists for a longer time. Differently from the Arctic sites, here the scattered vegetation and related scarce underlying organic layer (very thin) do not significantly affect the energy balance and the active layer thickness at the scale of the grid. In addition here the ice content in the ground is very homogeneous and therefore not so important in the INV values.

6.3. Vegetation

Within the boulder clay CALM grid the total vegetation cover decreased (mainly due to the reduction of mosses and cyanobacteria) while lichens increased. The decline of mosses can be related to the active layer thickening, increasing solar radiation and decrease of ground water availability. Indeed, only the xeric *Schistidium antarctici* persisted in this site, while the other moss species declined since 2002 (figure 9). Conversely, the epilithic lichens increased slightly because they are mainly located on blocks in sites were the drifted snow accumulates, providing water supply independently of the active layer thickness changes/dynamics (figures 4, 8).

In most of our selected study sites (with the exception of Edmonson Point) lichens exhibited a generalized increase. The lichen increase is mainly associated with a decrease of both GST and TDD (table 1, figure 10). Edmonson Point provides a different trend because this is a special site characterized by a much higher soil water content (about one order of magnitude more than the other sites), being a true ‘oasis’ in the polar desert (Bargagli *et al* 1999). At this site it is remarkable that mosses increased their coverage significantly where GST and TDD slightly increased, while they decreased their coverage where GST and TDD showed much larger increases.

In continental Antarctica there are very few examples of long-term monitoring of vegetation. In the Ross sector, for northern Victoria Land (Cape Hallett area), Brabyn *et al* (2005) reported that between 1968 and 2004 the total vegetation expanded (with an increase of algae) and they interpreted this change to be driven by local alterations of water supply, rather than by global warming. A trend of lichen expansion associated with drying conditions was described for Wilkes Land by Melick and Seppelt (1997) in the period 1960–1990. Also for Dronning Maud, another site of continental Antarctica geographically remote from Victoria Land, Johansson and Thor (2008), performing the monitoring of their permanent plots (period 1992–2002), observed that there was an increase of lichens both relating to the abundance, density and number of taxa. Although few, these examples provide evidence that where climate drying is occurring there is an increase of lichens, while there are contrasting patterns on moss responses, depending on their ecological requirements in terms of water availability, as the capability of contrasting water stress events is species-specific (Wasley *et al* 2006).

In maritime Antarctica, one of the three regions of the planet suffering the fastest climate warming, there are several examples of vegetation changes with evidence of enhanced cryptogamic (mosses and lichens) colonization of recently deglaciated areas; but, above all, vegetation changes concern the large expansion of the two native vascular plant species (*Deschampsia antarctica* and *Colobanthus quitensis*) (e.g. Fowbert and Smith 1994, Smith 1994, Parnikoza *et al* 2009, (Torres Mellado *et al* 2011), Cannone *et al* 2014).

In the polar regions of the northern Hemisphere, long-term manipulation experiments showed that warming induced a decrease in non-vascular plant biomass (both mosses and lichens), although the declining trend of non-vascular plants with warming has also been assumed to reflect competition with vascular plants instead of the effect of climatic drivers (e.g. Chapin *et al* 1995, Hobbie *et al* 1999, Cornelissen *et al* 2001, Elmendorf *et al* 2012).

Therefore, continental Antarctica provides a unique opportunity to assess the natural dynamics and responses of cryptogams without the disturbance effect due to the competition with vascular plants (such as in maritime Antarctica and in the Arctic), as well as the impact of grazing (such as in the Arctic, e.g. Joly *et al* 2009), or of fur seals and animal disturbance (such as in maritime Antarctica, e.g. Favero-Longo *et al* 2011).

6.4. Climate–active layer–vegetation interactions

Continental Antarctica represents the last pristine and most extreme environment on Earth and one of the most suitable contexts to analyze the relationship between active layer, vegetation and climate, and their dynamics (Cannone and Guglielmin 2009).

Our data showed that the snow distribution is the main driving factor (table 2) of the active layer thickness of the boulder clay CALM grid, with summer air temperature and summer short wave incoming radiation as secondary factors. The role of the snow cover in warming/cooling the ground surface and thickening/thinning of the active layer has been already pointed out in the Arctic (e.g. Osterkamp 2007, Romanovsky *et al* 2007, Fedorov and Konstantinov 2008). However, here the active layer thickness is increasing despite the substantial stability of snow cover. This could be explained by the increase of short wave incoming radiation, as demonstrated by Guglielmin and Cannone (2012) for the close boulder clay permafrost station (until 2009). In any case, here snow cover also exerts a ‘net warming effect’ due to its thermal insulating effect, as already reported in the Arctic (e.g. Goodrich 1982, Johansson *et al* 2013). In particular here the warming effect is mainly due to the prevailing negative air temperatures in spring and summer.

Concerning the active layer thickness in the other sites, the available data are not enough to compute trends. However, the increase of GST and TDD at Edmonson Point and in all the barren ground sites suggests that an increase of the active layer thickness is very likely. This trend is indirectly confirmed in all sites (except PP6) by the strong reduction of the ground water content, probably due to the better drainage triggered by the thickening of the active layer.

The buffering effect of the vegetation on GST and TDD and, probably also on the active layer, was observed in the vegetated plots, confirming previous results achieved by Cannone and Guglielmin (2009). Moreover, the better drainage and the decrease of the water content in the soil due to the active layer thickening may have produced the decline of mosses. The apparent paradox of the PP1 at Edmonson Point, in which mosses increased despite the decrease of the ground water content, can be explained considering that this site was water saturated in 2002, while now it is well hydrated but not saturated, being more compatible with the ecological requirements of the mosses.

The observed increase of total organic carbon (TOC) in the soil could affect the C cycle in the future; although, at the moment, its influence on the ground thermal conditions is negligible because the organic layer is too discontinuous and thin.

7. Conclusions

Despite the lack of air warming in continental Antarctica our data emphasize that ecosystem changes occurred rapidly, as they are already detectable in only 10 years.

The active layer is thickening at a rate comparable to areas in which air warming is occurring, emphasizing the role of solar radiation and snow cover. These factors are particularly important in extremely cold areas such as continental Antarctica, where the air temperature seldom exceeds 0 °C even in summer and vegetation is exclusively cryptogamic and patchy.

The thickening of the active layer produced a general decrease of the ground water content due to the better drainage of the ground and to the increase of the incoming solar radiation.

The resultant drying may be responsible for the decline of mosses in xeric sites (Prior Island, boulder clay), while they have provided better conditions for mosses in hydric sites (Edmonson Point), following the species-specific water requirements. This evidence emphasizes that the Antarctic continent is experiencing changes (climate, ecosystems) totally different from those of the Antarctic Peninsula and of maritime Antarctica.

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V. MARITIME ANTARCTICA

V.1. Introduction

In Maritime Antarctica there are several examples of vegetation changes in terms of spatial distribution, with evidence of enhanced cryptogamic (mosses and lichens) colonization of recently deglaciated areas (e.g. Favero Longo et al., 2012); but, above all, vegetation changes concern the large expansion of the two native vascular plant species (*Deschampsia antarctica* and *Colobanthus quitensis*) (e.g. Cannone et al., 2016a).

In Maritime Antarctica, Signy Island (South Orkney Island), has been recognized as a paradigmatic site for the assessment and monitoring of biological changes (Smith, 1990) and constitute the perfect site for the study of environmental, and consequently biological, changes in terrestrial ecosystem given its climatically and ecologically sensitivity (Smith, 1990; Cannone et al., 2016a) and the availability of previous field-based studies carried out in the 1960s and 1970s (e.g. Edward, 1972; Smith, 1972; Fenton, 1980; Fenton & Smith, 1982).

In this area of Antarctica, the air temperature warmed up at faster rates in the last decades compared to other regions of Antarctica (Convey, 2011). Indirect effects of climate warming, including changes in availability of key environmental resources and rapid changes in populations of both indigenous and alien species, could influence terrestrial ecosystems more than changes in temperature alone (e.g. Convey, 2013; Wasley et al., 2006; Favero-Longo et al., 2012).
Signy Island has experienced a dramatic increase in fur seal numbers over recent decades, which led to the damage of lowland terrestrial vegetation, with the eradication of the cryptogamic vegetation (Favero-Longo et al., 2012) or facilitation of vascular plants (Cannone, 2011; Cannone et al., 2016a).

Recent studies from Signy Island, demonstrated that the vegetation can strongly buffer the ground surface temperature (Guglielmin et al., 2012) and therefore changes in vegetation composition will affect the ground surface temperature. Moreover, it is essential to know the vegetation distribution and its dynamic for the future, since such ecosystems may act as a source for carbon release to the atmosphere at least until the “legacy” of organic matter and nutrients stored in the soils will be largely decomposed (Cannone et al., 2012).

Moss peat banks up to three meters have accumulated in several areas of the maritime Antarctica and their spatial distribution was documented in the late 1950s (e.g. Smith, 1972; Fenton, 1980; Fenton & Smith, 1982). Recent studies highlighted the relevant role of moss banks as archive of past and recent climatic change (e.g. Royles & Griffith, 2015). Recent warming and changing in water regime at Signy Island was reflected in increased rates of *Chorisodontium acyphillum* moss banks (Royles et al., 2012).

Here, we first analyzed the contemporary abundance and distribution of moss banks on the Island, as a baseline for future monitoring, assessing also their ecological requirements (see chapter V.4.A, Cannone et al., 2016b submitted).

After this first evaluation, based on comparison of the 1970s and 2011 surveys, we assessed long-term (around 40 years) and large-scale moss responses to climate change and identified the underlying ecological processes associated to changes (see chapter V.4.B, Cannone et al., 2016c submitted).

For the nomenclature of mosses species we referred to Ochyra et al. (2008), while for the therminology of ‘moss banks’ and their identification we used the methods proposed by the first description of the 1960s by Fenton & Smith (1982).

V.2. Study area

V.2.A. Signy Island

A supplementary activity of this PhD was done in order to assess the ecology and analyze the changes in spatial distribution in the last 50 years of the moss banks at Signy Island (Fig. V.2.1). Signy Island is one of the most important hot spots of terrestrial (and marine) biodiversity of Antarctic biome (Barnes et al., 2009) and one of the best paradigmatic example of polar cryptogam-dominated terrestrial ecosystems (Smith, 1990).

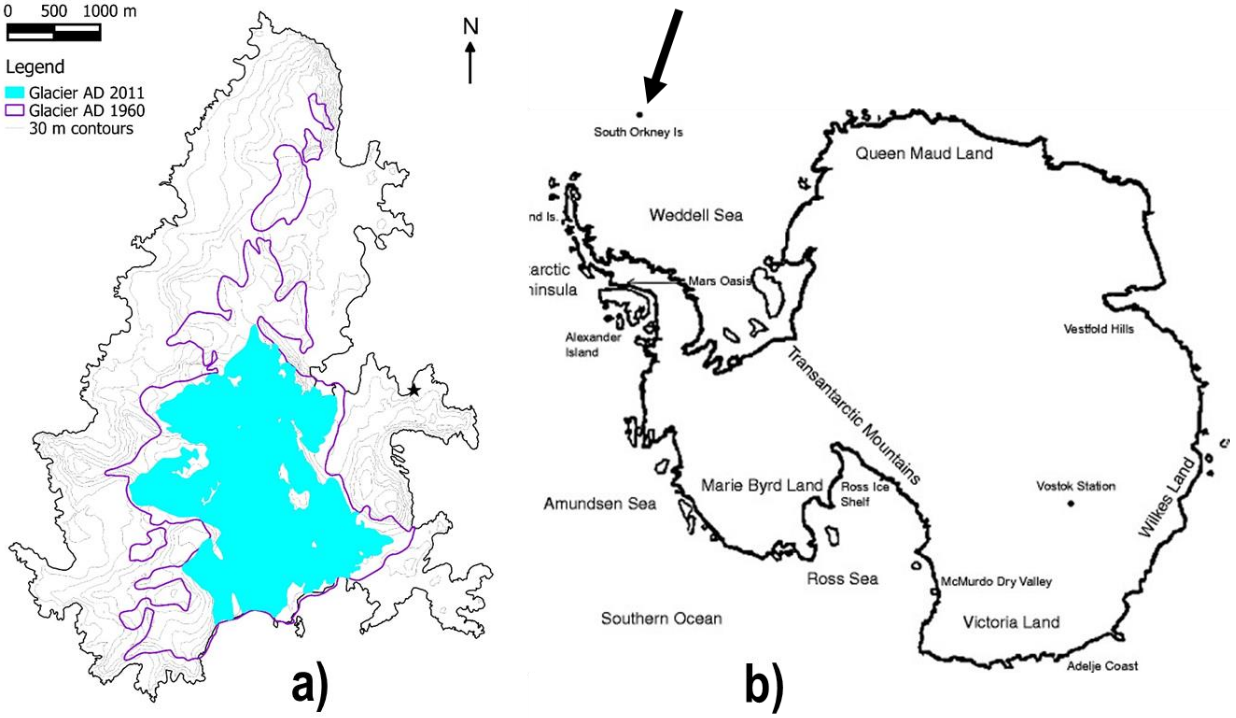

Figure V.2.1. Geographical location of Signy Island, indicated by the black arrow (b) and (a) zoom of the island. The black star indicate the BAS research base.

V.2.B. Geography and climate

Signy Island (60°43′S, 45°38′W) is located in the maritime Antarctica in the South Orkney Islands (Fig. V.2.1), and is characterized by a cold oceanic climate, with mean annual air temperatures of around −3.5 °C, mean monthly air temperatures above 0 °C for at least one (but up to three) months each summer, with an annual precipitation of around 400 mm (primarily in the form of summer rain) and average cloud cover of 6–7 oktas year-round (Guglielmin et al., 2012).

The island lies south of the much larger and higher Coronation Island, which generates regular Föhn winds, which bring moist misty air over Signy Island. Climatic records indicate a progressive warming of air temperatures of 2±1°C over the past 50 years (Turner et al., 2005), which accounts for the recent rapid shrinkage of the Signy ice cap (1m/y in the last 20 years), now covering about half of the island (Smith, 2007) (Fig. II.17).

V.2.C. Geology and geomorphology

The bedrock is mainly quartz-mica-schist, although marbles and amphibolites locally outcrop (Smith, 2007). The soils are mainly gelisols, with a prevalence of Psammoturbels, Haplorthels, Haploturbels, and Psammorthels. Histoturbels, Historthels, and Fibristels may occur in lowlands and on the western coast (Guglielmin et al., 2008).

Studies carried out from the 1960s and 1970s on Signy Island (Chambers, 1966a, 1966b, 1967, 1970; Holdgate et al., 1967; Collins et al., 1975) reported the occurrence of discontinuous permafrost with an active layer ranging between 40 cm and 2 m. More recently, a permafrost model (PERMDEM, Guglielmin et al., 2008b) based on the digital elevation model and the air lapse temperature shows that permafrost conditions in 2006 (Mean Annual Ground Surface Temperature, MAGST=0 °C) occurred over the entire island from the sea shoreline upward.

The geomorphology of the island is characterized mainly by periglacial landforms, which were described in detail and monitored by Chambers (1966a, 1966b, 1967, 1970). Low-centered sorted circles, sorted stripes and stone-banked lobes are the most widespread landforms.

Low-centered sorted circles occur preferentially in flat and depressed areas, at elevations lower than 80 m, and exhibit large variability in size, with diameters ranging between 2 and 5 m. At higher elevations high-centered sorted circles (ranging between 10 and 150 cm) occur, generally on flat summits. Unsorted circles are common, generally of similar size to the high-centered sorted circles, but these do not show a clear distribution pattern. Frost boils also occur in some depressed and peaty areas, with diameters ranging from 0.2 to 0.7 m. No ice wedge polygons or sand wedge polygons were found, although some poorly defined frost fissure polygons occur on the flat and highest ice-free areas of the island. Soil stripes are mainly sorted with a width ranging from 10 to 210 cm at the same site. Soil stripes are developed in till and on colluvial deposits where the slope is greater than 4°–6°. Transitional features from low-centered circles to sorted stripes are also present. Usually the coarse bands are raised with respect to the finer ones; although sometimes the opposite can occur, with unsorted stripes located close to the sorted ones (Guglielmin et al., 2012).

Gelifluction lobes are the most common periglacial feature: often occurring on the same slope with a high variability of shape and size from stone-banked terracettes, to lobes and stone streams (sensu Chambers). These gelifluction features are sometimes aggregated to form sheets. The gelifluction features are almost all stone-banked and develop on a wide range of slopes (always greater than 4°–5°), with frontal ramps between 0.5 and 3 m in height. On the western side of the island moss banked lobes, which can be over 3 m high at the frontal ramp, are widespread (Fig. V.2.2). Only one active rock glacier has been observed on the island, located just northward of Sombre Lake. The rock glacier shows a convex profile along the flow direction and a very steep frontal scarp, indicating the presence of ice within it (Guglielmin et al., 2008b).

Figure V.2.2. Moss banked lobes are widespread on the west coast of Signy Island. © PNRA.

II.3.d. Flora and vegetation

Vegetation on Signy Island is composed of both the Antarctic herb tundra formation, where the two native vascular plants *Deschampsia antarctica* Desv. and *Colobanthus quitensis* Bartl. occur, as well as the more common Antarctic non-vascular cryptogamic tundra formation (Gimingham & Smith, 1970; Smith, 1972; 1984).

Most of the island is covered by cryptogamic vegetation and, among the most widespread communities, are the *Usnea–Andreaea* association, distributed in the drier and more exposed sites while more barren ground is colonized by crustose and foliose lichens. Moss turf (e.g. *Polytrichum strictum-Chorisodontium acyphyllum* association) and cushion sub-formations (e.g. associations with *Sanionia uncinata* (Hedw.) Loeske) occur mainly in the wetter areas (Gimingham & Smith, 1970; Smith, 1972).

Communities of crustose lichens characterize littoral and supralittoral rocks, coastal rocks influenced by seabirds and inland dry rocks and soils at higher elevations (Smith, 1972; 1997; 2007).

Changes in cover of the dominant moss species (c. 15% of the island's bryophyte vegetation), have been monitored in adjacent fenced and unfenced areas, and correlated with both physical disturbance and changes in soil chemistry due to seawater and sweat washed out of the fur seals (Mg and Na increases) and to urine and excrement deposition (nitrate and ammonium increases) (Smith 1997). While more anecdotal observations on the general disappearance of macrolichens in seal-damaged areas has also been reported (Smith, 1988; 1997), changes in lichen variability and abundance have been only recently quantified (Favero-Longo et al., 2011; Favero-Longo et al., 2012).

Marine vertebrates play an important role both in the transfer of nutrients from marine to coastal terrestrial ecosystems in Antarctica, as well as by having direct impacts through trampling in the vicinity of breeding colonies and other large concentrations of animals. Lack of feeding competition (due to anthropogenic reductions in great whale populations), coupled with recent changes in krill-based food webs in the Southern Ocean (due to changes in the extent of winter sea ice), has resulted over the last 60 years in a rapid recovery and a distributional expansion of Antarctic fur seal (*Arctocephalus gazella* Peters 1875) populations, previously harvested almost to extinction at their main population centers on South Georgia and the South Shetland Islands (Waluda et al., 2010). At Signy Island, there has been a dramatic population increase, rapidly rising to over 10000 individuals towards the end of the 1980s with peaks of more than 20000 in 1994, 1995 and 2000 (Smith, 1988; 1997; Waluda et al., 2010)

The recent increase in summer populations of Antarctic fur seals is already known to have had major impacts on elements of the island’s vegetation. Due to excessive trampling and increased nutrient input, these highly mobile and gregarious marine mammals have caused the eutrophication of previously oligotrophic lake systems (Butler, 1999; Quayle & Convey, 2006) and the severe or complete destruction of c. 15% of the island’s bryophyte on terrestrial ecosystems (Smith, 2007). Cover of the dominant moss species has been reduced over large areas, and totally lost in others, and there has been a large increase in abundance of the nitrophilous alga *Prasiola crispa* (Lightfoot) Kutzing (Smith, 1990).

Signy Island thus provides a case study for the consequences related to the climate and anthropogenic driven increase of the Antarctic fur seal population on terrestrial and freshwater ecosystems (Smith, 1988; 1990; 1997; Butler, 1999).

V.3. Materials and methods

V.3.A. Spatial and temporal distribution of moss banks at Signy Island

At Signy Island, maritime Antarctica, a detailed survey of the spatial distribution and size of areas of bank-forming mosses was carried out during the 1970s across the entire island (Fenton & Smith, 1982).

During January-March 2011, we carried out a new field survey of the abundance and spatial distribution of moss banks, using methods consistent with those of Fenton & Smith (1982).

We then provided the contemporary abundance and spatial distribution of moss banks at Signy Island, in order to identify their ecological requirements and to provide a baseline for future monitoring.

Detailed information about the methods used in this section, were provided in the paper Cannone et al. (2016b submitted), see chapter V.4.A.

Moreover, these data were used also to assess the moss banks changes over more than 40 years, and to identify the processes underlying these changes, emphasizing the similarity of the ecological processes observed in Antarctica with those occurring in the Arctic as well as in high elevation alpine regions, see chap. V.4.B (Cannone et al., 2016c submitted).

V.4. Results

V.4.A. Ecology of moss banks at Signy Island (maritime Antarctica)

In the maritime Antarctica, one of the most dramatic air warming rates in the world has occurred over the last several decades (Turner et al., 2007). Together with local changes in precipitation, this has resulted in a rapid permafrost degradation (e.g. Guglielmin & Vieira, 2014), and a reduction in extent and thinning of many ice-fields and glaciers, exposing new terrain for colonization while, at the same time, altering patterns of water availability in terrestrial habitats (Convey & Smith, 2005).

Observations and environmental manipulation experiments further demonstrated the possibility of large and rapid species and community responses to such climate amelioration, with many species responding positively (Convey & Smith, 2005; Convey, 2011; Royles & Griffith, 2015; Cannone et al., 2016a).

Recent studies from Signy Island, demonstrated that the vegetation can strongly buffer the ground surface temperature (Guglielmin et al., 2012) and therefore changes in vegetation composition will affect the ground surface temperature. Moreover, it is essential to know the vegetation distribution and its dynamic for the future, since such ecosystems may act as a source for carbon release to the atmosphere at least until the “legacy” of organic matter and nutrients stored in the soils will be largely decomposed (Cannone et al., 2012).

Moss peat banks up to three meters have accumulated in several areas of the maritime Antarctica and their spatial distribution was documented in the late 1950s (e.g. Smith, 1972; Fenton, 1980; Fenton & Smith, 1982). Recent studies highlighted the relevant role of moss banks as archive of past and recent climatic change (e.g. Royles & Griffith, 2015). Recent warming and changing in water regime at Signy Island was reflected in increased rates of *Chorisodontium acyphillum* moss banks (Royles et al., 2012).

However, such recent analysis of moss banks ecology was restricted to a few set of samples. In the following paper (Cannone et al., 2016b submitted), we analyzed the spatial distribution of moss banks of all Signy Island, identifying their main ecological requirements, and providing thus a baseline for future investigation.

Ecology of moss banks at Signy Island (maritime Antarctica)

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Ecology of moss banks at Signy Island (maritime Antarctica)

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ABSTRACT

Mosses are dominant components of high latitude environments. Signy Island (maritime Antarctic) provides a paradigmatic example of polar cryptogam-dominated terrestrial ecosystems. In 2011 we mapped all moss banks, recording for each the associated key environmental factors (topography, biotic disturbance) and investigated their relationship with selected environmental factors including topography (elevation, slope, aspect), biotic disturbance (fur seals), deglaciation age of the surfaces, and snow cover (as a proxy of both the possibility of direct or indirect water supply as well as of the time the ground is snow-free in summer

We here provide a) the contemporary abundance and distribution patterns of moss banks as a baseline for future monitoring, and b) identify their ecological requirements.

Moss bank abundance and distribution are the result of the interaction of multiple abiotic and biotic factors, some relating to recent processes (a large recent increase in fur seal disturbance), and others to long-term landscape evolution (deglaciation age), all interacting with topography.

These findings allow a better understanding of the environmental value of this almost unique feature of maritime Antarctic vegetation and provide quantitative knowledge of their ecology.

KEYWORDS: Moss banks; Environmental factors; Maritime Antarctica; Topography; Fur seal; Deglaciation age.

INTRODUCTION

Mosses are ubiquitous components of plant communities in high latitude ecosystems, becoming dominant in terms of diversity and biomass in the High Arctic (Meltofte, 2013) and, particularly, in the Antarctic, where vegetation is dominated by cryptogams (Longton, 1988; Ochyra *et al.*, 2008; Convey, 2013; Cannone *et al.*, 2013). The importance of mosses is well demonstrated in key ecosystem processes relating to nutrient, carbon and water cycling, permafrost formation and thaw, and peat (carbon) accumulation. This is particularly the case in high latitude ecosystems where mosses contribute 30-50% of primary production (Turetsky *et al.*, 2010, 2012; Jorgenson *et al.*, 2010). Moreover, the sensitivity of mosses to changes in environmental conditions could be a key driver of high latitude terrestrial ecosystem responses to rapid contemporary climate change.

Signy Island (South Orkney Islands, maritime Antarctic) has been recognized as a paradigmatic example of polar cryptogam-dominated terrestrial ecosystems, illustrating the structure and dynamics of Antarctic ecosystems in general (Smith, 1990). A characteristic and unique feature of maritime Antarctic vegetation that is particularly well represented on Signy Island is the development of deep (1-3 m depth) moss banks (Collins, 1976; Fenton & Smith, 1982; Roads *et al.*, 2014), the formation of some dating back over 5000 years (Fenton, 1980). These are composed of the tall turf-forming mosses *Polytrichum strictum* Brid. and *Chorisodontium aciphyllum* (Hook.f. & Wilson) Broth, and are characterised by low humification and a lack of water saturation, receiving moisture supply mainly from precipitation (semi-ombrotrophic) (Fenton & Smith, 1982; Royles *et al.*, 2012).

In the 1970s the spatial distribution of these bank forming mosses on Signy Island was mapped in detail and hypotheses were developed relating to the main abiotic and biotic factors influencing them (Fenton & Smith, 1982). Several important environmental factors were identified by Fenton & Smith (1982), including: length of the time the ground is snow-free in summer; length of time the area has been free from permanent snow in the past; biotic disturbance; harshness of the environment (with specific reference to wind as a critical factor related to altitude); water supply; slope. However, these relationships were analyzed and described largely in a qualitative manner and based on examination of a restricted set of moss banks. Furthermore, after almost half a century of rapid regional climatic change (Smith, 1990; Royles *et al.*, 2012), the abundance and distribution patterns of this sensitive and key environmental component require updating, in order to provide a robust baseline for future monitoring and allow robust qualitative and quantitative assessments of future climate and environmental change impacts.

Here, we: I) provide an update of the abundance and distribution patterns of moss banks at Signy Island as baseline for their future monitoring; II) identify the ecological requirements of moss banks through analyzing their distribution patterns with respect to some key abiotic and biotic environmental factors including a) topography (elevation, slope, aspect), b) occurrence of biotic disturbance (fur seals), c) deglaciation age of the surfaces, d) snow cover (as a proxy both for the possibility of direct or indirect water supply, and of the time the ground is snow-free in summer).

STUDY AREA

Signy Island (60°43'S, 45°38'W; South Orkney Islands, maritime Antarctic) is characterised by a cold oceanic climate, with mean annual air temperature of −3.5 °C and annual precipitation of 400 mm, primarily as summer rain (Smith 1990, Royles et al. 2012). It is also characterised by prevailing westerly winds linked to the Southern Annular Mode (SAM, Zazulie *et al.*, 2010). Over the last 50 y Signy Island has experienced an increase of both air temperature and total annual precipitation (Turner *et al.*, 2009; Royles *et al.*, 2012; Cannone *et al.*, 2016). Signy Island also possesses a rapidly shrinking ice cap (losing >1 m/year in thickness over the last 20 y) (Favero-Longo *et al.*, 2012). Permafrost is continuous, with an active layer thickness ranging between 40 cm and more than 3 m (Guglielmin *et al.*, 2008, 2012), that has recently been deepening by *c.* 1 cm/year in response to increasing air temperature (Cannone *et al.*, 2006). The island's terrestrial habitats and its vegetation are well characterised, and are widely regarded as representative of the entire maritime Antarctic region, as well as of cryptogam-dominated fellfield habitats across the polar regions (Smith, 1972, 1984, 1990; Longton, 1988).

Since the late 1970s, when they were first recorded, Signy Island has experiences a very rapid increase in the numbers of resting and moulting fur seals (*Arctocephalus gazella* Peters 1875) (Waluda *et al.*, 2010). Fur seal activity can negatively impact vegetation, producing considerable damage by trampling/crushing (Smith, 1988), as well as though nitrogen release in faeces/urine (Favero-Longo *et al.*, 2011). It has also been recently documented that fur seals affected the spatial distribution of *Deschampsia antarctica* and *Colobanthus quitensis* on Signy Island, the two only native vascular plants occurring in the maritime Antarctic (Cannone *et al.*, 2016).

METHODS

A detailed survey of the spatial distribution and size of areas of bank-forming mosses across Signy Island was carried out during the 1970s across the entire island (Fenton & Smith, 1982). During January-March 2011, we carried out a new field survey of the abundance and spatial distribution of moss banks, using methods consistent with those of Fenton & Smith (1982).

For each area of moss bank we measured and recorded the following data: location (both by GPS and on the map), shape (shape of the area occupied by the moss bank as reported on the map), and moss bank depth (cm). We mapped the spatial distribution of moss banks recorded in 2011 using ArcGIS 9.2. Using the location of the centroid of each moss bank we computed the elevation (m a.s.l.), slope (°), aspect (divided into eight sectors: N; NE; E; SE; S; SW; W; NW) from the most recent digital elevation model (DEM) of Signy Island, which has a resolution of 7.5 m. In the field we also recorded the following data (information not recorded in the previous survey): a) dominant moss bank forming species (*C. aciphyllum* and/or *P. strictum*), b) maximum moss bank thickness, c) occurrence of vascular plant colonization, and d) presence/absence of fur seal disturbance, assessed on the basis of the visible health and indication of seal trampling/crushing and associated nitrogen release in faeces/urine (Favero-Longo *et al.*, 2011).

To assess the distribution patterns of moss banks with respect to elevation and slope, we used a non-parametric statistical approach based on the maximum and minimum values, median, 25% and 75% quartiles, providing a description of the core of the moss distribution (Maggini *et al.*, 2011).

The distribution of moss banks was plotted against the deglaciation age of the surfaces according to the reconstruction provided by Smith (1990), to assess the existence of any relationship with the Holocene deglaciation age of the surfaces, and to verify whether recent and ongoing deglaciation could provide suitable surfaces for future moss bank colonization and development.

To assess whether moss bank distribution was linked to long-lasting snow cover, we analyzed an infrared image taken over the entire island in summer (December 2010). Using this image we performed an unsupervised classification analysis using ArcMap 10.1 multivariate tools, in order to identify the areas covered by long-lasting snow. Once the snow polygons for the island had been identified, we investigated the relationship between the snow and moss distribution by considering three classes: 1) no interaction, 2) direct interaction between moss banks and snow cover with direct water supply from snow melting, (3) indirect interaction as the moss bank was separated by ≥ 10 m from the snow boundary, with the potential for indirect water supply from snow melting.

RESULTS

In 2011 we recorded a total of 310 moss banks across the entire island (Fig. 1), occurring at elevations from sea level up to 202 m a.s.l. The distribution patterns of these moss banks were analyzed in relation with the main topographic features. They exhibited an unimodal distribution with elevation (Fig. 2A), with a peak in occurrence between 21 and 60 m a.s.l. The non-parametric analyses identified that the median elevation was 52 m a.s.l., and that 75% of the banks occurred below 80 m a.s.l. About 10% of the banks were colonized by the grass *D. antarctica*, mainly below 60 m a.s.l. (Table 1).

An unimodal distribution pattern was also evident with slope (Fig. 2B), with a peak between 10° and 21°, the median at 10°, and 75% of the population was found on slopes ≤ 24°. In terms of aspect (Fig. 2C), more than 50% of the banks were present on N and NW facing areas, a proportion that increased to >70% when W facing banks were included.

Maximum bank depth was measured for 262 of the 310 moss banks. It ranged between 80 and 2100 mm, with a median of 200 mm and a 75th percentile of 400 mm, and exhibited an exponential distribution ($p<0.01$). No relationship was apparent between moss banks thickness and elevation ($p>0.05$).

The impacts of fur seal disturbance were clearly associated with elevation (0-20 m = 78.8% of banks with apparent damage; 21-40 m = 67.9%; 41-60 m = 48.9%; 61-120 m <20%; >121 m = 0%), with the greatest impact close to sea level, and impact almost negligible above 60 m a.s.l. (Table 1).

In terms of the deglaciation age of the surfaces since the Holocene (Smith, 1990) (Figs. 3, 4), 70.3% of moss banks were located on surfaces deglaciated before 7000 y BP, 8% on surfaces deglaciated between 7000 and 5000 y BP, and 14.5% on surfaces deglaciated between 500-350 BP. Only 1.3% occupied surfaces deglaciated since 1960. It is remarkable that moss banks abundance was not related to the extent of the surfaces, but with their deglaciation age (Fig. 4).

Snow cover may be a a proxy both of water supply and of the length of the time the ground is snow-free in summer. Almost a quarter (24.5%) of moss banks received direct water from snow melting, while 9.7% received only a potential indirect water supply, and 65.8% of moss banks did not receive water supply from snow melting at that time of season. Our data, therefore, illustrate that most moss banks were located at sites that are snow-free during the peak of the growing season.

Half of the moss banks were single species stands (32% dominated by *C. aciphyllum* and 18% by *P. strictum*, respectively), while 50% included both species. Both single species and mixed stands were found over the entire island (Fig. 5). A monospecific *C. aciphyllum* bank provided the highest elevation record (202 m a.s.l.), followed by mixed stands (189 m a.s.l.), while the maximum elevation of pure stands of *P. strictum* was only 107 m a.s.l. (Fig. 6A). Both *C. aciphyllum* and *P. strictum* banks exhibited an unimodal distribution pattern with elevation, with a peak at 41-60 m a.s.l. for the former, and 21-40 a.s.l. m for the latter. Conversely, the mixed stands were characterized by a bimodal pattern with a main peak at 21-40 m a.s.l. and secondary peak at 81-100 m a.s.l.. Despite their different patterns, all stand types had both a similar median (at about 30 m a.s.l., accounting for 50% of the population) and 75th quartile (between 72 and 83 m a.s.l.). The distribution with elevation among the single species and the mixed stands did not show any statistically significant difference (t-test, $p > 0.05$). All bank types exhibited an unimodal distribution with respect to slope (Fig. 6B), with no statistically significant differences detected.

Finally, there was a similar partitioning across the bank types among the eight aspect sectors, with a prevalence for records in the NW, N and W sectors (Fig. 6C), and a lack of statistically significant differences between patterns. However, a broad comparison of the eastern vs. the western sides of Signy Island revealed that the number of moss banks was comparable (166 and 144, respectively), as was their distribution pattern with elevation, with an unimodal distribution pattern with a peak between 21 and 60 m a.s.l. in both parts of the island.

Banks dominated by *P. strictum* showed the least evidence of disturbance by fur seals (26.7% of banks), while the levels of disturbance were greater and similar in those dominated by *C. aciphyllum* (52%) and the mixed stands (44.8%). The amount of fur seal disturbance was linked with elevation, illustrated by the undisturbed moss banks having a higher median elevation than those with disturbance (71 m a.s.l. vs. 40 m a.s.l. for *C. aciphyllum*; 63 m a.s.l. vs. 32 m a.s.l. for *P. strictum*; 64 m a.s.l. vs. 37 m a.s.l. for the mixed stands).

The quantitative relation with snow cover differed between species. *C. aciphyllum* showed the highest proportion of banks having direct interaction with snow cover (37.7%, vs 22.4% of the mixed banks and 7.1% of *P. strictum*). In constrast, *P. strictum* showed the highest proportion of banks with no direct interaction with snow cover (84% vs 69.3% for the mixed stands and 51.1% for *C. aciphyllum*), while for all species the potential for indirect interaction was limited (12.2% for *C. aciphyllum*, 8.9% for *P. strictum* and 8.3% for the mixed banks).

DISCUSSION

The unimodal distribution pattern (“humped”), with a peak at intermediate values that was typically shown by moss banks in this study with respect to elevation and slope (Figure 3A, B), is similar to that which has been reported in the distribution of species richness with elevation in mountain areas (e.g. Rahbek, 1997; Grytnes & Vetaas, 2002). This kind of pattern has been interpreted as the result of a combination of different factors including hard boundaries (i.e. the existence of ecophysiological limits and/or some degree of resistance to dispersal, Colwell & Lees, 2000), monotonic trends in species richness, and incomplete sampling (Grytnes & Vetaas, 2002).

Given the exhaustive sampling achieved in the current study, the patterns obtained here are unlikely to be sampling artefacts. This implies that moss bank distribution is controlled by specific limiting factors at their distribution range boundaries (upper and lower) both for elevation and slope.

There was a very clear impact of fur seal disturbance at the lower elevation boundaries of moss bank occurrence. Our data indicate that the highest impact of fur seal disturbance occurs between 0 and 20 m, and is still intense up to 60 m, and confirm the importance of biotic disturbance as an effective environmental factor involved in determining the extent of moss banks, as also proposed by Fenton & Smith (1982). It has recently been demonstrated that the distribution patterns of the higher plants *D. antarctica* and *C. quitensis* are also influenced by fur seal disturbance, although their impact is only strongly apparent up to 20 m a.s.l. (Cannone *et al.*, 2016), and with only limited damage apparent above that altitude band. Mosses are clearly more vulnerable to this form of biotic disturbance than both higher plants, and epilithic lichens (Smith, 1988; Favero-Longo *et al.*, 2011). Our data document and confirm the original predictions of Smith (1988) and, more recently, Royles & Griffiths (2015), that increases in fur seal populations may have negative consequences on moss banks. An analogous example of the limiting impact of biotic disturbance on plants has been reported in the sub-Antarctic, where a tangential consequence of predation of seabirds by introduced feral cats resulted in a contraction of the lower distribution limits of coprophilous vascular plant species (le Roux & McGeoch, 2008).

At the upper boundary of moss bank distribution, species ranges could be limited by physiological tolerances (which define their fundamental niche), as well as by biotic interactions and dispersal barriers (which further constrain the fundamental niche to the realized niche) (Tingley *et al.*, 2014). Although the maximum elevation recorded for an individual moss bank was 202 m (Fig. 2A, B, 6A), overall bank distribution patterns with elevation showed a clear altitudinal threshold, with a sharp decrease in numbers above 120 m. We hypothesize that one or more disturbance factors limit the occurrence and development of moss banks above this elevation threshold. One such driver could be air temperature, with lapse rates being almost linear with elevation (1.1°C/100 m on Signy Island, data not shown). However, the relatively small difference in elevation between upper and lower distribution boundaries (202 m), corresponds to ~ 2.2°C temperature difference, which does not appear to be potentially enough to explain the observed patterns.

Fenton & Smith (1982) proposed wind as a limiting factor for moss bank distribution (describing its action as "environmental harshness"). Wind speed typically increases with elevation, and therefore also its erosive impact. Erosion could be effective both in damaging existing banks and in limiting the initial establishment of new moss growth, which is more vulnerable in the early years after establishment (Collins, 1976). Exposure to higher wind speeds may also keep bank surfaces clear of snow and hence directly exposed to both abrasion and freezing winter temperatures well below zero (Collins, 1976). On sub-Antarctic Macquarie Island, wind disturbance has been recognized as the main environmental determinant of vegetation cover, showing an elevation threshold at 200 m a.s.l. (Adamson *et al.*, 1993), similar to the maximum elevation observed for moss banks on Signy Island. The mean annual wind speed measured at Macquarie Island is 9.3 m s^{-1} and gale force winds have been recorded, on average, on 180 d yr^{-1} (Adamson *et al.*, 1993). The mean annual wind speed recorded at Signy Island at 80 m a.s.l. is much lower than that at Macquarie Island, ranging between 3.6 and 4.5 m s^{-1}, with the daily maximum speed not exceeding 20 m s^{-1} (Guglielmin *et al.*, 2012). Nevertheless, at Jane Col (150 m a.s.l.) the mean annual wind speed is considerably higher, ranging between 5.5 and 6.7 m s^{-1}, with daily maxima exceeding 24 m s^{-1} on several days each year. Based on these data, we feel that it is reasonable to hypothesize that increasing wind speed between 80 and 150 m a.s.l. could be one of the limiting factors leading the apparent threshold of 120 m a.s.l. at which occurs the sharp decrease of moss banks development.

Within terms of slope topography, as areas with more gentle slopes (0°-10°) are more accessible to fur seals, the frequency of moss banks in such areas is lower than those with slopes between 11° and 30°. Conversely, at slopes > 40° the establishment and development of moss banks becomes more difficult, limiting their abundance. Fenton & Smith (1982) also proposed that slope was an important environmental factor driving the extent of moss banks.

Although Fenton & Smith (1982) did not identify aspect amongst the main environmental factors influencing moss bank distribution in their survey, we detected a clear bias towards northern and western slopes, with around 50% of moss banks located on N and NW slopes, increasing to 70% when the W slopes were included. These aspect sectors provide microclimatic conditions more favorable to moss bank growth. In a comparison of the ground surface temperatures (GST) of two areas of barren ground located in the same site (CALM grid) on Signy Island, in the same conditions of elevation and slope but with opposite aspect (N vs. S), Guglielmin *et al.* (2012) detected significant differences in both GST and of the thawing degree days (TDD), with the N facing area being warmer than the S facing, especially during the summer (≥30% for GST and ≥40% for TDD).

The age of surfaces (the length of time the surface has been available for colonization) is an important factor driving both the extent of ice-free areas suitable for vegetation establishment, and the patterns of plant colonization and succession and soil development. Based on the reconstruction of the main stages of Holocene glacial evolution on Signy Island provided by Smith (1990), we can propose a relationship between moss bank abundance and the deglaciation age of the surfaces and with the potential of moss banks to colonize recently deglaciated terrain. The retreat of the island's ice cap has been particularly pronounced in the last 20 years, with a mean loss of ice thickness of around 1 m y^{-1}, providing extensive new ice-free areas available for colonization (Favero-Longo *et al.*, 2012). Despite this availability of recently deglaciated ground (almost 40% of the entire island) these areas currently remain devoid of moss bank forming species, suggesting that they exhibit a preference for surfaces with the oldest deglaciation age (before 7000 y BP) and for those deglaciated for at least several centuries (Figs. 3, 4), such as during the Medieval Warm Period (see also Guglielmin *et al.*, 2016). The relationship identified here between moss bank abundance and surface age is consistent with the role of the community dominated by *Polytrichum strictum* - *Chorisodontium aciphyllum* as a climax stage, developing on the oldest terrains, but only where local-scale environmental features are more favourable (Favero-Longo *et al.*, 2012). This also suggests that it is unlikely that moss banks could develop rapidly on areas that have become ice-free over a small number of decades, where there is greater probability of colonization by saxicolous lichens and scattered mosses (e.g. *Andreaea*, *Sanionia*). As the proportion of recently ice-free area is greater above 120 m a.s.l., this could be one of the most important factors underlying the current elevation threshold on moss bank distribution. Other factors such as soil chemistry and surface stability of recently ice-free areas may also be compatible only with the establishment of pioneer species, and not of the climax community dominated by *P. strictum* and *C. aciphyllum*, but this remains uninvestigated.

The form of the relationship between moss banks and snow distribution on the island at peak season could be considered a proxy of a) direct water supply, b) length of the time the ground is snow-free in summer. Our data indicate that only c. 25% of moss banks receive direct water supply from snow melting during the peak of the growing season, consistent with the semi-ombrotrophic nature of moss banks (Fenton & Smith, 1982; Royles *et al.*, 2012). The greater direct association of *C. aciphyllum* with snow cover is also consistent with its ecological requirements for wetter (but not waterlogged) conditions, when *C. aciphyllum* becomes the dominant moss rather than *P. strictum* (Fenton & Smith, 1982). These data also indicate that the development of moss banks dominated by *C. aciphyllum* may also occur in sites characterized by a longer permanence of snow cover, differently from those dominated by *P. strictum*. Our data confirm the hypotheses of Fenton & Smith (1982) on the role played by water supply and the length of the time the ground is snow-free in summer as important factors influencing moss bank distribution.

The last factor we considered was the potential occurrence of an asymmetrical distribution of moss banks between the eastern and western sides of the island. Such asymmetry might be predicted due to differential influence of the prevailing westerly winds, leading to greater abrasion and erosion of bank on the more exposed western side of the island. However, contrasting with observations at the sub-Antarctic locations, Macquarie Island and Marion Island (e.g. Adamson et al. 1993, Selkirk and Saffigna 1999, Haussmann et al. 2009), at Signy Island we did not detect any significant differences in moss bank distribution between the eastern and western sides of the island.

CONCLUSIONS

We identified the main ecological requirements of moss banks in relation to the investigated environmental factors including topography (elevation, slope, aspect), biotic disturbance, deglaciation age of the surfaces, and snow cover (as a proxy of both the possibility of direct or indirect water supply as well as of the time the ground is snow-free in summer).

Moss banks abundance and distribution is the result of the interaction of multiple abiotic and biotic factors, some relating to recent processes (fur seal disturbance), others relying on long-term landscape evolution (deglaciation age of the surfaces) interacting with topographical characteristics. Concerning biotic disturbance, moss banks show the highest vulnerability from fur seals disturbance than higher plants and lichens.

These findings allow a better understanding of the environmental value of this almost unique feature of maritime Antarctic vegetation and provide quantitative knowledge on their ecology.

ACKNOWLEDGMENTS

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Table 1. Abundance of moss banks, their composition and relationship with selected biotic factors in 2011 at Signy Island. Legend: n = total number; 1 = moss banks damaged by fur seals; 2 = moss banks not damaged by fur seals; CA = moss banks dominated by *Chorisodontium aciphyllum*; PS = moss banks dominated by *Polytrichum strictum*; MIX = mixed banks of the two moss species; DA = moss banks in which the grass *Deschampsia antarctica* is present; noDA = moss banks without *D. antarctica*.

	n	**1**	**2**	**CA**	**PS**	**MIX**	**DA**	**noDA**
Total	310	136	174	98	56	156	28	282
<60 m	184	116	68	56	31	97	21	163
> 60m	126	20	106	42	25	59	7	119

Figure captions

Figure 1. Map of the distribution of moss banks in 2011. Legend: grey line = 60 m contour; thin grey line= 120 m contour; pale grey area= glacier boundary in 2011; black areas = moss banks present in 2011.

Figure 2. Partitioning of the moss bank distribution in relation to topographic features: A) elevation (m); B) slope (°); C) aspect range (eight sectors, see Methods). Distribution with respect to the topographic features (elevation, slope, aspect) was evaluated in terms of: a) the % of population (bars), b) the absolute number of moss banks (squares).

Figure 3. Map of moss bank distribution in relation with the deglaciation age of surfaces according to Smith (1990). Deglaciation age legend: gray star = since 1960; grey rhombus = 250-20 BP; white square = 350-250 BP; white circle = 500-350 BP; white star = 650-500 BP; black square = 800-650 BP; black rhombus = 7000-5000 BP; grey circle = deglaciated before 7000 BP.

Figure 4. Partitioning of the percentage of moss banks (black columns) occurring on surfaces of different deglaciation age (grey columns).

Figure 5. Map of the distribution of moss banks relating to their species composition: pure banks of *C. aciphyllum* (grey triangle); pure banks of *P. strictum* (black rhumbus); mixed banks containing both species (grey stars).

Figure 6. Partitioning of the different moss bank forming species (pure banks of *C. aciphyllum* - CA; pure banks of *P. strictum* - PS; mixed banks of both species – MIX) across

topographic features: A) elevation (m); B) slope (°); C) aspect range. Distribution with respect to these topographic features was evaluated in terms of: a) the % of population (bars), b) the absolute number of moss banks (squares). Legend: white columns/bars = *C. aciphyllum*; pale grey columns/bars = *P. strictum*; dark grey columns/bars = mixed banks.

Figure 1

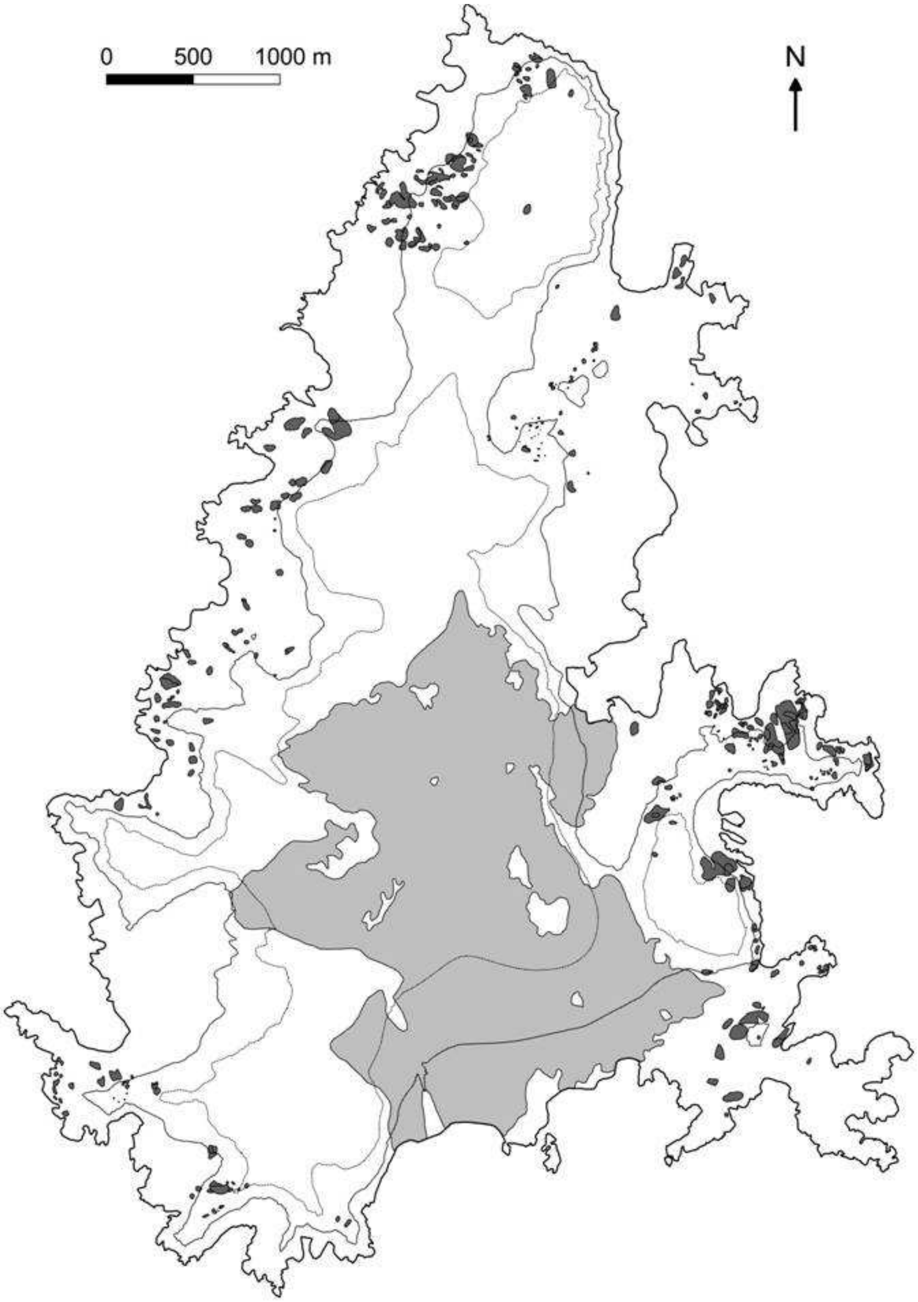


Figure 2

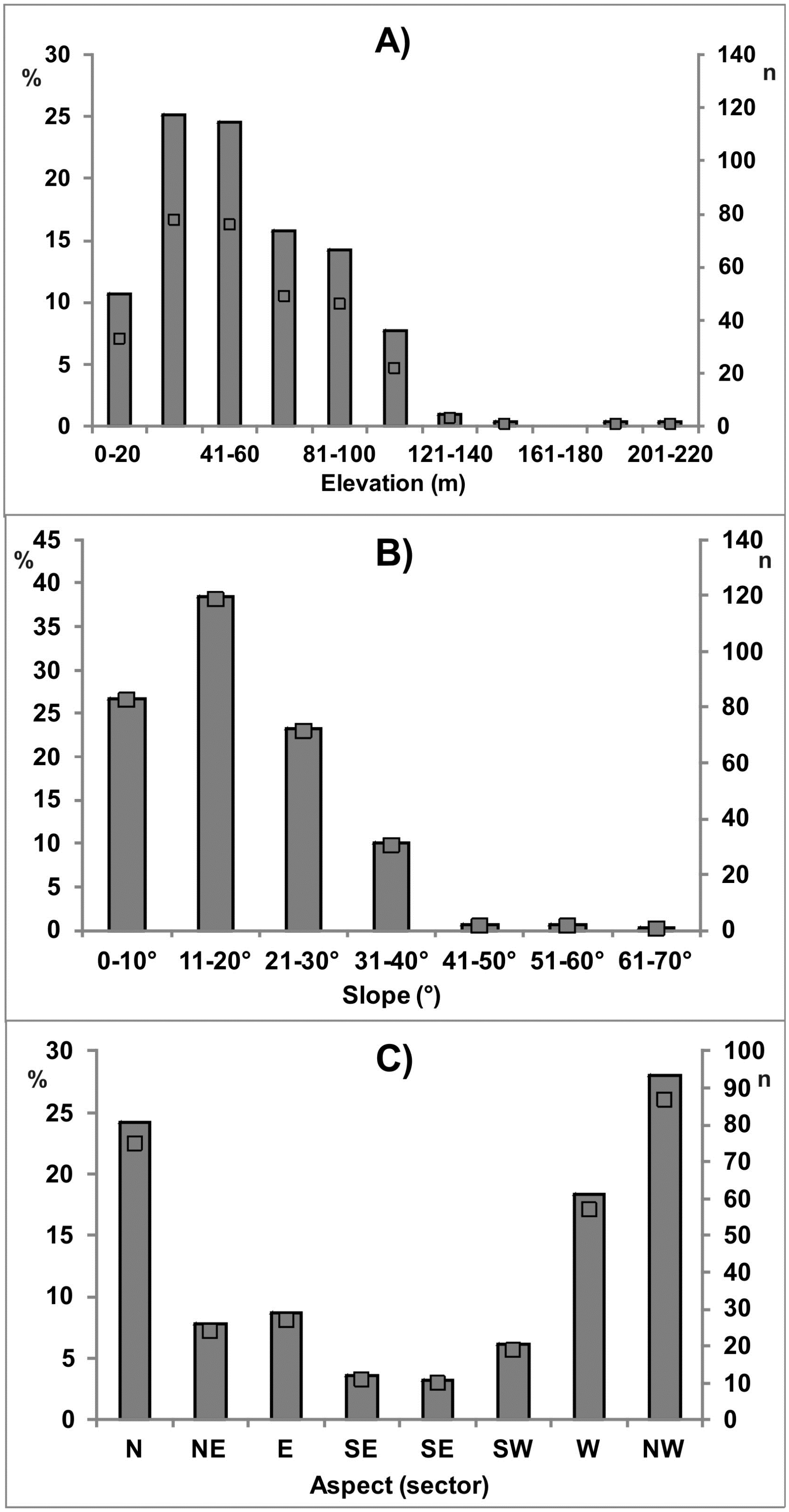

A)
%
30
25
20
15
10
5
0
n
140
120
100
80
60
40
20
0
0-20
41-60
81-100
121-140
161-180
201-220
Elevation (m)
B)
%
45
40
35
30
25
20
15
10
5
0
n
140
120
100
80
60
40
20
0
0-10°
11-20°
21-30°
31-40°
41-50°
51-60°
61-70°
Slope (°)
C)
%
30
25
20
15
10
5
0
n
100
90
80
70
60
50
40
30
20
10
0
N
NE
E
SE
SE
SW
W
NW
Aspect (sector)

Figure 3

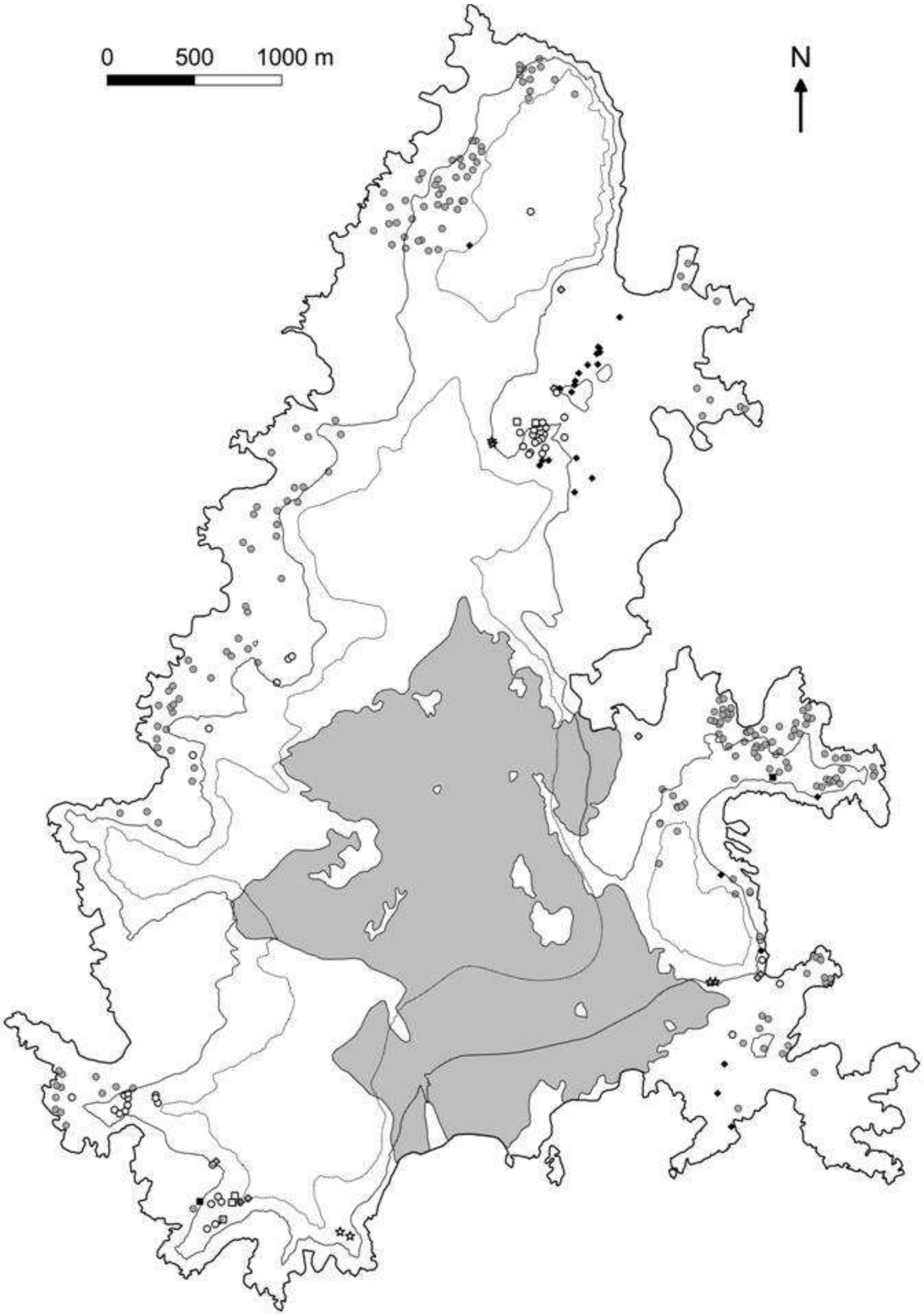


Figure 4

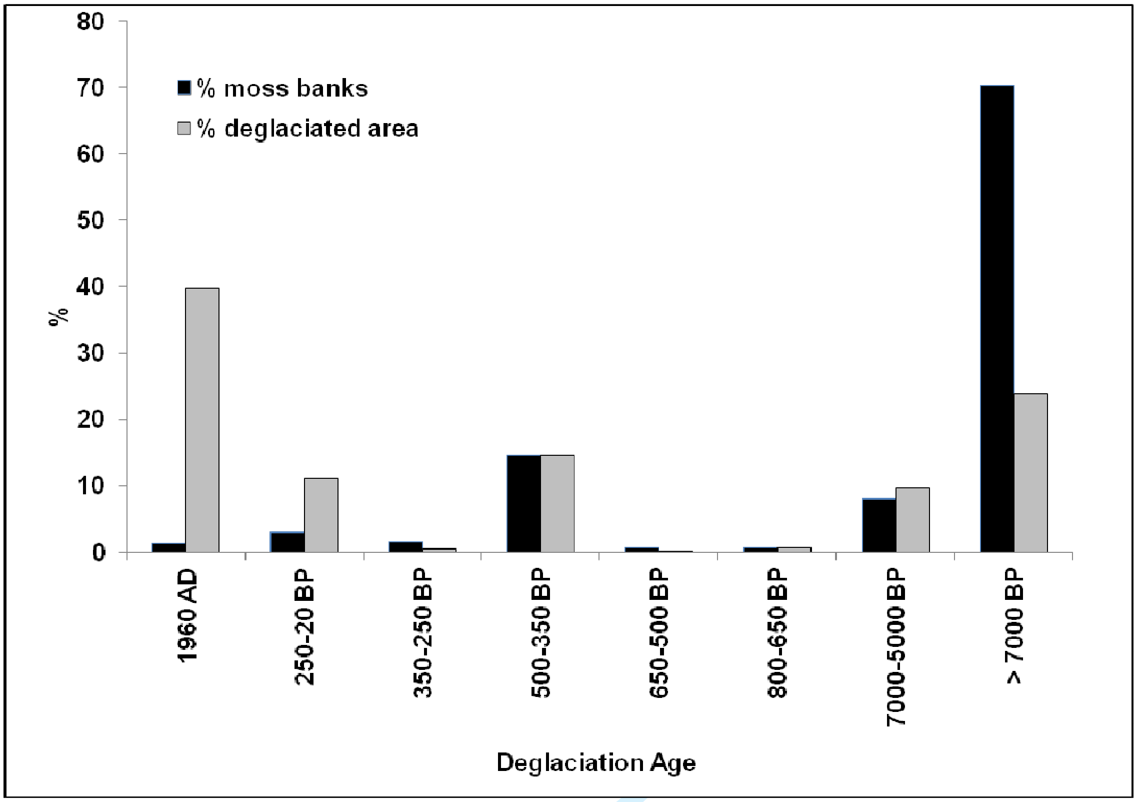
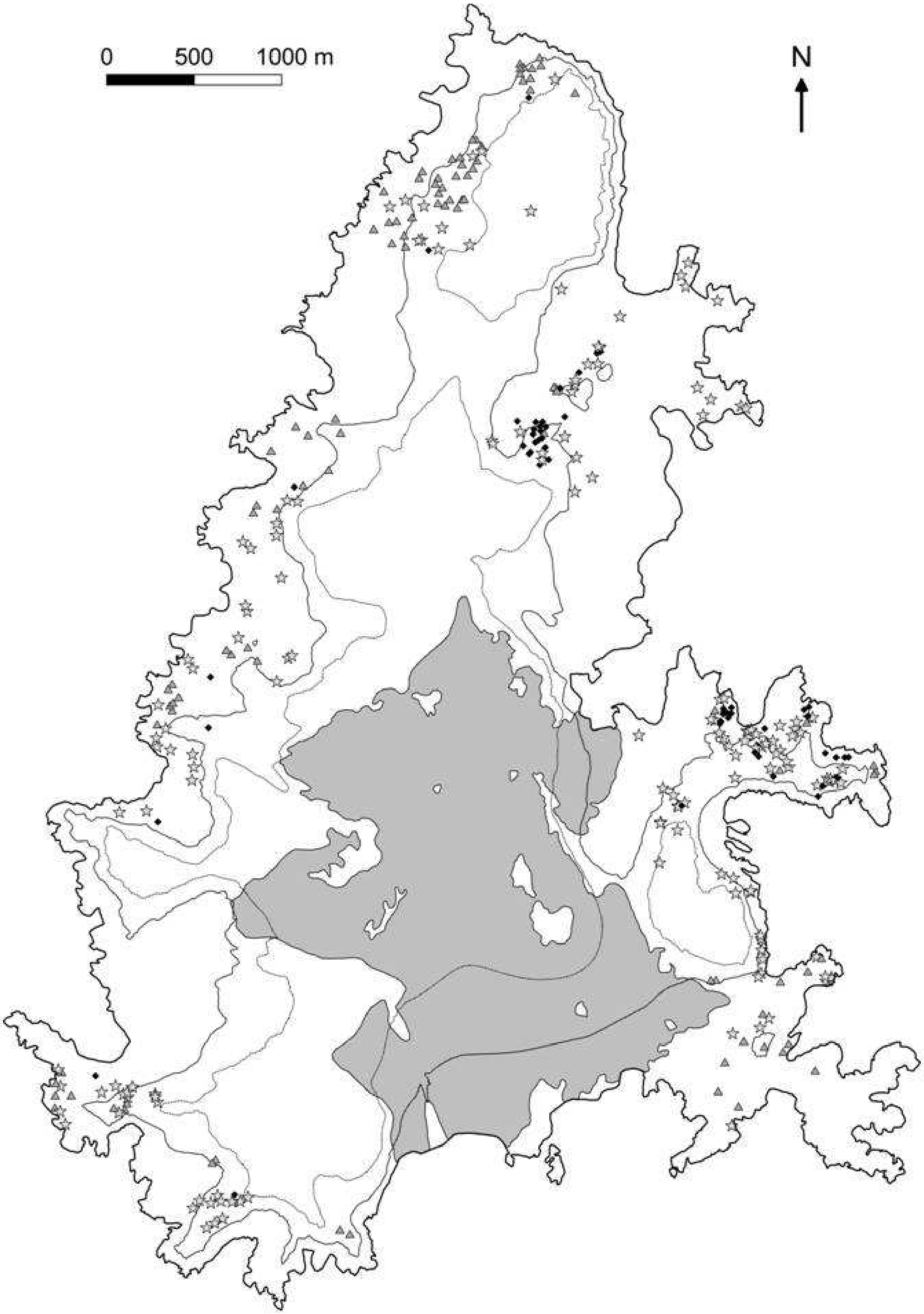
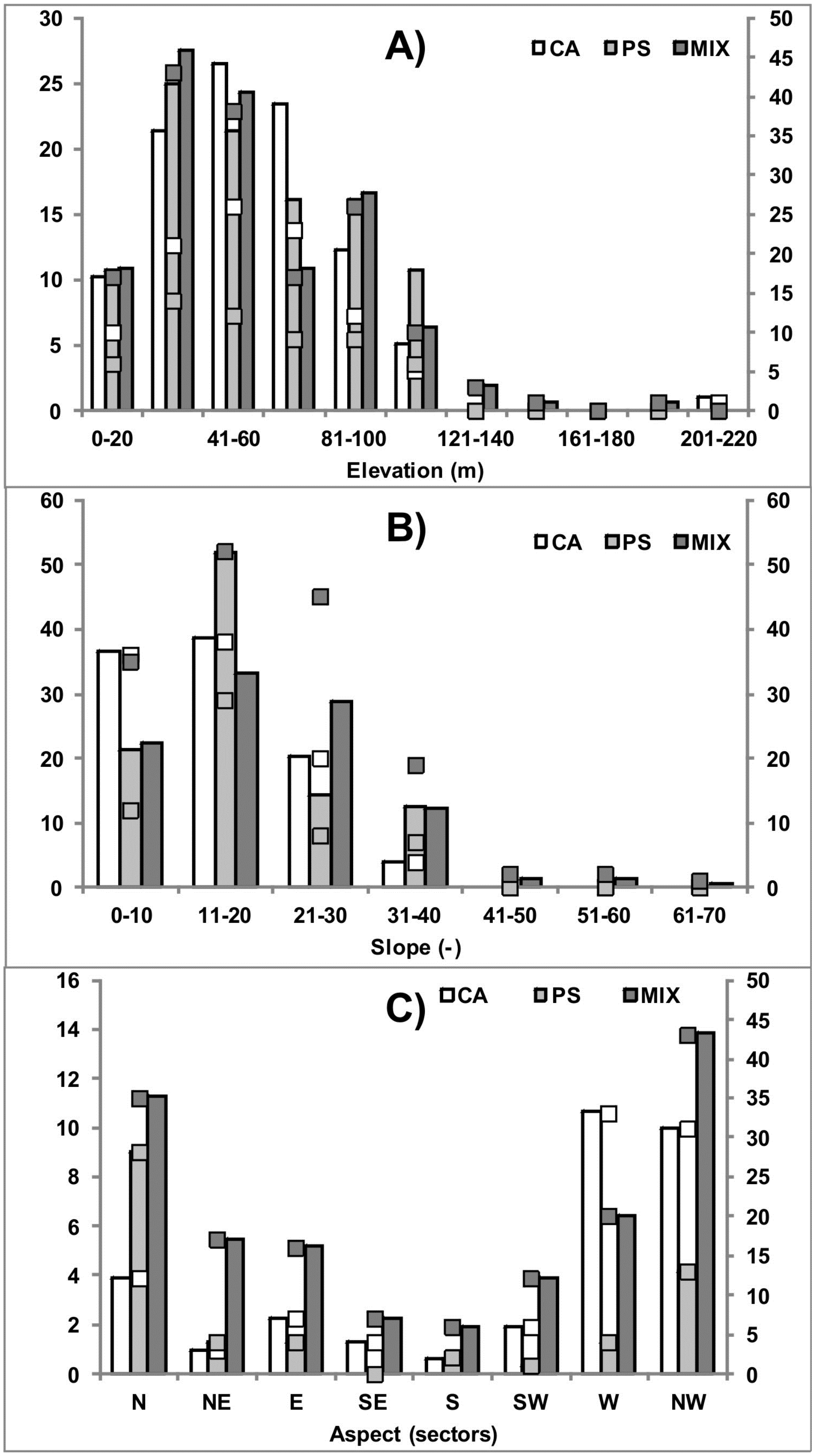

80
70
60
50
40
30
20
10
0
%
■ % moss banks
■ % deglaciated area
1960 AD
250-20 BP
350-250 BP
500-350 BP
650-500 BP
800-650 BP
7000-5000 BP
> 7000 BP
Deglaciation Age

Figure 5



545

546 Figure 6



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V.4.B. Range filling as a strategy of polar mosses in response to climate change

In Antarctica, mosses are crucial in regulating permafrost stability by buffering surface temperature (e.g. Cannone et al., 2006; Guglielmin et al., 2008; 2012).

Despite the dominance of mosses in terrestrial vegetation in Antarctica, few long-term monitoring studies are available (e.g. Royles et al., 2012; Guglielmin et al., 2014). Field manipulation experiments stressed the importance of water availability in a warming climate such as in maritime Antarctica (e.g. Bokhorst et al., 2013)

The spatial distribution of these bank forming mosses on Signy Island was mapped in detail in the 1970s (Fenton & Smith, 1982) providing a strong and regionally unique baseline. In 2011 we re-surveyed moss bank abundance and distribution adopting the methods of Fenton & Smith (1982), in order to quantify their ecological requirements and provide a baseline for the assessment of past and future changes (Cannone et al, 2016b submitted).

In the following paper (Cannone et al., 2016c submitted), based on comparison of the 1970s and 2011 surveys we show, after around 40 y of intense regional climate and environmental change, changes in moss bank distribution and abundance, and use these data to infer the major physical and biological drivers of these changes.

Range filling as a strategy of polar mosses in response to climate change

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Running Title: Responses of polar mosses to climate change

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Abstract

Background and Aims. Mosses are dominant components and play an important role in key processes of high latitude ecosystems and is mandatory to understand how climatic change (CC) will affect them in polar areas. Indeed, their responses are still debated in the Arctic, and few studies are available for Antarctica. Here we assess long-term and large-scale moss responses to CC and identify the underlying ecological processes through a case study located at Signy Island (maritime Antarctic), a paradigmatic example of polar ecosystems which experienced intense climate change over the last decades.

Methods. The study is based on a resurvey allowing comparison of new (2011) and historical (1970s) data. We analyze quantitative changes of moss distribution and abundance.

Key Results. Moss changes are the result of the interaction of multiple biotic (fur seal disturbance) and abiotic (climate change) factors producing a heterogeneity of responses across an elevation gradient. Below the elevation threshold of 60 m mosses decreased due to fur seal disturbance; between 60 and 120 m they increased due to a range filling process in response to the ameliorated climatic conditions; above 120 m there was no change, as well as no suggestion of any range shift towards higher elevations.

Conclusions. Our data I) emphasize the similarity of the ecological processes occurring in Antarctica with those of geographically remote Arctic and alpine locations; II) highlight the role of range filling as an effective ecological process adopted by mosses; III) underline that their ecological requirements are vital to understanding their changes, with special reference to the lack of upward migration at higher elevations. The changes described at this location, a paradigm of biological environmental change in Antarctic terrestrial ecosystems provide important insights into future vegetation responses to CC in the polar and alpine regions generally.

Keywords: Climate change; Mosses; Long-term changes; Polar regions; Range-Filling; Biotic Disturbance; Ecological Processes.

INTRODUCTION

Mosses are ubiquitous components of plant communities in high latitude ecosystems, becoming dominant in terms of diversity and biomass in the High Arctic (Meltofte, 2013) and, particularly, in the Antarctic (Longton, 1988; Wasley *et al*., 2006a; Ochyra *et al*., 2008; Convey, 2013; Pointing *et al*., 2015). The importance of mosses in key ecosystem processes relating to nutrient, carbon and water cycling, permafrost formation and thaw, and peat (carbon) accumulation is well demonstrated, especially in high latitude ecosystems where they can contribute 30-50% of primary production (Turetsky *et al*., 2010, 2012; Jorgenson *et al*., 2010).

High latitude permafrost environments constitute approximately 25% of the Earth's terrestrial surface (French, 2007) and play a key role in the global carbon cycle, as they store a large amount of the global carbon pool (≥400 Pg; Davidson and Janssens, 2006). In these environments mosses are crucial in regulating permafrost stability by buffering the soil surface temperature (Cannone *et al*., 2006; Guglielmin *et al*., 2008, 2012, Cannone and Guglielmin, 2009; Soudzilovskaia *et al*., 2013), which is negatively related to the thickness of organic soil layers (Cannone *et al*., 2006; Harden *et al*., 2006; Romanovsky *et al*., 2007; Guglielmin *et al*., 2008, 2012). The fate of the carbon stored in permafrost environments is still uncertain, although it is well appreciated that its release may trigger significant climate feedbacks (Schuur *et al*., 2008). It is, therefore, vital to understand how current trends of climatic change will impact this key sensitive component of high latitude terrestrial ecosystems.

Moss responses to recent climate change in High Arctic tundra are inconsistent and debated. Some reports suggest that the abundance of mosses has increased over recent decades

(Hudson and Henry, 2009), while others point to them remaining relatively stable (Prach *et al*., 2010). Despite the dominance of mosses in the terrestrial vegetation of the Antarctic (Ochyra *et al*., 2008), few long-term monitoring studies of moss communities are available (Melick and Seppelt, 1997; Brabyn *et al*., 2006; Wall *et al*., 2011; Clarke *et al*., 2012; Royles *et al*., 2012, Guglielmin *et al*., 2014), as most studies to date have focused on vascular plant species (e.g. Smith, 1994; Parnikoza *et al*., 2009; Vera, 2011; Cannone *et al*., 2016). In the absence of detailed studies, there remains large uncertainty about moss response to contemporary environmental change. Hence it is difficult to predict with any confidence their future contribution to polar biodiversity, or the fate of entire ecosystems.

In field manipulation experiments performed in Arctic tundra, mosses have shown contrasting responses to warming (van Wijk *et al*., 2004; Walker *et al*., 2006; Lang *et al*., 2009; Turetsky *et al*., 2010). These divergences appear to depend partly on moisture availability (Elmendorf *et al*., 2012a, b; Lang *et al*., 2012) with, in most cases, positive responses where increases in available moisture are involved (Turetsky *et al*., 2010). Changes in water availability have a direct impact on growth in xeric and mesic moss species, which can spend considerable periods desiccated and inactive, while growth in hygric mosses (such as the genus *Sphagnum*, typically found in continuously moist or wet locations) shows a clearer direct response to increasing temperatures (Gunnarsson, 2005; Lang *et al*., 2009). The importance of water availability in a warming climate is particularly acute in Antarctica, where both field manipulation experiments (Convey *et al*., 2002; Bokhorst *et al*., 2011, 2013) and ecophysiological observations (Convey *et al*., 2003) have been interpreted as demonstrating that warming can also be linked with increased overall stress through reduced relative humidity and soil moisture.

Signy Island (South Orkney Islands, maritime Antarctic) has been recognized as a paradigmatic example of polar cryptogam-dominated terrestrial ecosystems, illustrating the diversity of changes which may affect the structure and dynamics of Antarctic ecosystems in general (Smith, 1990). Moreover, the South Orkney Islands lie within the region of the Antarctic experiencing the most rapid warming of air temperatures (+2±1°C) over the past 50 y, together with an increase in precipitation (Turner *et al*., 2009; Royles *et al*., 2012). This warming has been the fastest anywhere in the Southern Hemisphere and, with two regions of the Northern Hemisphere, equal fastest globally. In response to recent climate warming at Signy Island, the two native Antarctic vascular plant species (*Deschampsia antarctica* and *Colobanthus quitensis*) have exhibited significant changes since the 1960s (Cannone *et al*., 2016).

A characteristic feature of maritime Antarctic vegetation that is particularly well represented on Signy Island is the development of deep (1-3 m depth) moss banks (Collins, 1976; Fenton and Smith, 1982; Roads *et al*., 2014), the formation of some dating back over 5000 years (Fenton, 1980). These are composed of the tall turf-forming mosses *Polytrichum strictum* Brid. and *Chorisodontium aciphyllum* (Hook.f. and Wilson) Broth, and are characterised by low humification and a lack of water saturation, receiving moisture supply mainly from precipitation (semi-ombrotrophic) (Fenton and Smith, 1982; Royles *et al*., 2012). In these systems true peat is not accumulated in anaerobic waterlogged conditions, but rather moss preservation is strictly linked to the occurrence of permafrost. Indeed, once the moss becomes perennially frozen it remains virtually unaltered (Fenton, 1980), with a very high level of morphological preservation and even remaining viable for at least 1600 years (Roads *et al*., 2014).

The spatial distribution of these bank forming mosses on Signy Island was mapped in detail in the 1970s (Fenton and Smith, 1982) providing a strong and regionally unique baseline. In 2011 we re-surveyed moss bank abundance and distribution adopting the methods of Fenton and Smith (1982), in order to quantify their ecological requirements and provide a baseline for the assessment of past and future changes (N. Cannone et al., Insubria University, Italy, unpubl. res.).

Strongly negative impacts of fur seal disturbance have recently been reported to affect the development and maintenance of populations of the two native vascular plant species, *D. antarctica* and *C. quitensis*, on Signy Island, with the greatest impact being restricted to elevations between sea level and 20 m a.s.l. (Cannone *et al*., 2016). Smith (1988) and, more recently, Royles and Griffiths (2015) predicted that the steep increase in fur seal numbers over the last three decades may have negative consequences for the establishment of bank forming mosses and the maintenance of existing moss banks. The occurrence of fur seals has been identified by N. Cannone et al. (Insubria University, Italy, unpubl. res.) as one of the factors defining the lower boundary of contemporary moss bank distribution with elevation on the island.

Here, based on comparison of the 1970s and 2011 surveys we show, after around 40 y of intense regional climate change, changes in moss bank distribution and abundance, and use these data to infer the major physical and biological drivers of these changes. We aimed to assess whether since the 1970s I) multiple abiotic and biotic factors exerted different impacts on mosses across the elevation gradient provided by Signy Island, II) identify the processes responsible for the observed moss changes and relate them to their main environmental drivers. We hypothesized that moss responses would change across the elevation gradient in response to the prevailing action of different abiotic and biotic environmental factors (mainly climate change and fur seal disturbance) and that, without biotic disturbance, the moss response to the ameliorated climatic conditions would be promoted by a range-filling process, underlying the similarity of the ecological processes occurring in high latitude polar areas with those observed at high elevation areas at mid-latitudes in response to climate change.

MATERIALS AND METHODS

Study Area

The Antarctic Peninsula and Scotia Arc (including the biological region of the maritime Antarctic) has been one of the three fastest warming regions of the planet over the last 50 y (Convey *et al*., 2009; Turner *et al*., 2009, 2014). Signy Island (60°43'S, 45°38'W; South Orkney Islands) is characterised by a cold oceanic climate, with mean annual air temperature of −3.5 °C and annual precipitation of 400 mm, primarily as summer rain (Smith, 1990; Royles *et al*., 2012). Signy is also characterised by prevailing westerly winds linked to the Southern Annular Mode (SAM, Zazulie *et al*., 2010). The speed of these westerly winds has increased by 15-20% since the late 1970s (Korhonen *et al*., 2010; Turner and Marshall, 2011). Total annual precipitation also increased over the same period (Royles *et al*., 2012; Cannone *et al*., 2016). Signy Island possesses a rapidly shrinking ice cap (losing >1 m/year in thickness over the last 20 y), currently covering approximately half of the island's area (Favero-Longo *et al*., 2012). Permafrost is continuous, with an active layer thickness ranging between 40 cm and more than 3 m (Guglielmin *et al*., 2008, 2012), and that is currently deepening by *c*. 1 cm/year in response to changing air temperature (Cannone *et al*., 2006). The island's terrestrial habitats and its vegetation are well characterised, and are widely regarded as representative of the entire maritime Antarctic region, as well as of cryptogam-dominated fellfield habitats across the polar regions (Smith, 1972, 1984, 1990; Longton, 1988). The contemporary abundance and distribution patterns of moss banks have been recently re-surveyed across the whole island in 2011 (N. Cannone et al., Insubria University, Italy, unpubl. res.).

As well as the physical environmental changes noted above, important biological changes have also taken place recently, in particular through a large increase in the numbers of resting and moulting fur seals (*Arctocephalus gazella* Peters 1875) utilising the island since the late 1970s (Waluda *et al*., 2010). This factor is not thought to have influenced the island's terrestrial ecosystems previously in the current interglacial period (Hodgson *et al*., 1998). Fur seal activity can negatively impact vegetation, producing considerable visible damage by trampling/crushing (Smith, 1988), as well as though nitrogen release in faeces/urine (Favero-Longo *et al*., 2011). In 1985 a fence was installed between sea level and 20 m a.s.l. in the Backslope area (close to the research station), protecting an area of 21.5 ha by excluding fur seals from a specific and spatially restricted area of vegetation on the island (Fig. 1 Supplementary Materials).

Methods

In order to describe changes in climate between the two surveys, we used air temperature data provided by the Orcadas AWS (Orcadas Automatic Weather Station, Laurie Island (60° 43'S; 44° 31' W)), which is located c. 50 km from Signy Island. This AWS is the nearest long-term World Meteorological Observatory monitoring station close to the study area, and its data record is very strongly correlated with that of Signy Island between 1947 and 1995 (when a year-round meteorological station was operated on the island), and provides the longest and most complete climate dataset available in Antarctica (Convey *et al*., 2009; Royles *et al*., 2012). Using daily air temperature data, we calculated mean daily and yearly minimum, maximum and range (maximum – minimum), and other indices including thawing degree days (TDD, the cumulative sum of the mean daily temperatures above 0°C), freezing degree days (FDD, the cumulative sum of the mean daily temperatures below 0°C), growing season length (following Hudson and Henry, 2009), and number of potential freeze-thaw cycles (following Guglielmin *et al*., 2012). We used the daily total precipitation data, that included liquid (rain) as well as solid (snow) precipitation (the latter as water equivalent; Gomez A., pers. comm.), to calculate indices including the number of days with different threshold amounts of precipitation (P) (P=0=dry days; P<1 mm; 1≤P<5; P≥5; P≥10; P≥20; P≥30; P≥40; P≥50 mm), the maximum daily precipitation event (mm), the mean daily precipitation and finally the mean and maximum length of dry and wet spells (following le Roux and McGeoch, 2008a). In order to identify differences in wind speed with elevation we used the maximum daily wind speed recorded at two automatic weather stations located respectively at 80 and 150 m a.s.l. on Signy Island.

For assessment of changes in moss bank abundance and spatial distribution over time we compared the data of the two detailed surveys carried out during the 1970s (Fenton and Smith, 1982) and in 2011 (N. Cannone et al., Insubria University, Italy, unpubl. res.) across the entire island. These surveys provide complete and robust baseline datasets representing the full distribution of moss banks over the entire island in the 1970s and 2011, giving the unique opportunity in the Antarctic for the assessment of changes in their distribution over time.

The detailed map provided by Fenton and Smith (1982) was geo-referenced and re-drawn using ArcGIS 9.2 in order to make it comparable with the data recorded in 2011, which were mapped using the same software. The 2011 survey provided additional data relating to the dominant moss species (*C. aciphyllum* or *P. strictum*), and presence/absence of fur seal disturbance. To assess changes over time, we compared the two sets of detailed maps and classified the moss areas identified into the following categories: new, extinct, persistent. "New" were those observed in 2011 but not in the 1970s survey. "Extinct" were those mapped in 1970s but not present in 2011, with loss of (almost) the entire area of living moss and underlying moss-peat (generally associated with fur seal activity) (Fig. 2 Supplementary Material). The "persistent" category refers to moss banks present in both surveys in the same location.

To assess any changes with respect to elevation and slope, we used a non-parametric statistical approach based on the maximum and minimum elevations, median, 25% and 75% quartiles, providing a description of the core of the moss distribution (Maggini *et al*., 2011). We performed these analyses using the entire datasets (1970s vs. 2011). In addition, we carried out separate analyses a) on the moss banks located above the elevation threshold of 60 m, representing the maximum elevation at which the fur seal damage is still recognizable (N. Cannone et al., Insubria University, Italy, unpubl. res.), and b) comparing the eastern and the western sides of the island above 60 m. Differences in distribution with respect to elevation, slope and aspect were tested using the Wilcoxon test. These analyses were performed using Statistica®.

RESULTS

Climate

Over the period 1970-2008, in addition to the increase of 1°C in mean annual and summer air temperatures reported in previous studies (Royles *et al*., 2012; Cannone *et al*., 2016), important significant changes in thermal indices included increases in growing season length (+27 days, $p<0.01$), mean daily maximum temperature (+1.3°C, $p<0.01$), and summer thawing degree days (TDD_DJF = +76 degree days, $p<0.01$) (Fig. 1A-C). These data also underline that the air temperature warming detected was mainly concentrated during the summer months and the beginning of autumn (March). The other thermal indices calculated (potential freeze-thaw cycles, FDD) did not show any statistically significant trend since the 1970s (data not shown).

Total precipitation is known to have increased significantly, especially in summer (Royles *et al*., 2012; Cannone *et al*., 2016), and again the current analyses reveal further detail. Extreme precipitation events increased considerably, as indicated by the increase of more than threefold in the maximum daily precipitation (Fig. 1D; +36mm, $p<0.01$). The temporal distribution of extreme events also changed. The number of days with precipitation exceeding 5 and 10 mm per day increased significantly ($P\geq5$mm, + 22 d, $p<0.01$; $P\geq10$ mm, + 7 d, $p<0.01$) (Fig. 1E). During the same period, the number of days with $P<1$ mm per day significantly decreased (Fig. 1F; - 16 d, $p<0.01$) while the duration of the dry or wet spells did not change significantly (data not shown). The remaining precipitation indices did not show any significant trends (data not shown).

Comparing the data available at Signy from two stations located at different elevations (80 vs 150 m a.s.l), mean and maximum wind speed were up to 30% greater at higher than the lower station (Figure 3 Supplementary Material).

Moss bank changes since the 1970s across their overall elevation range

Various features of the bank forming mosses have changed over the last 40 y (Fig. 2). Of the 323 moss banks mapped in the 1970s, c. 30% had become extinct by 2011 (Table 1). Newly developed moss banks accounted for c. 21% of the total recorded in 2011 (Table 1). Between the two surveys the total number of moss banks had decreased by 4%, although their pattern of change varied with elevation (Table 1): below 60 m moss banks decreased (-25%), while above this elevation their number increased (+63.6%). Two-thirds of the new moss banks mapped were located above 60 m, while almost all cases of extinction (c. 93%) were below this elevation threshold. Extinct and new moss banks exhibited statistically significant differences in their distribution patterns with elevation ($p<0.01$, Wilcoxon test), with the largest extinction occurring below 40 m and the largest new colonization between 60 and 80 m (Fig. 3B).

These changes were evaluated with respect to topographic features (elevation, slope, aspect) (a) in terms of the percentage (%) of the entire population, and (b) the absolute numbers of moss banks. There was a statistically significant change in distribution of moss banks with respect to elevation ($p<0.01$, Wilcoxon test), although the minimum and maximum elevations recorded did not change (Fig. 3A). Between the two surveys, the contribution of moss banks located below 60 m to the entire population decreased from c. 75% to c. 60%. Across the elevation gradient the most important changes of distribution identified were a clear decrease below 60 m (with maximum loss between 0 and 40 m) and a concomitant increase between 61 and 120 m (with a maximum increase between 81 and 100 m), with no significant changes above 120 m (Fig. 3A). Changes in distribution were statistically significant with respect to slope ($p < 0.05$, Wilcoxon test), with a decrease on the flattest areas (<10°) and an increase between 21° and 30°. No statistically significant changes were detected with respect to aspect (p = 0.93, Wilcoxon test) (Figs. 3C, D).

As an artefactual consequence of the large numbers of moss banks destroyed by fur seal activity at altitudes below 60 m, the overall contemporary distribution appeared to perform a "lean uplope" (*sensu* Breshears *et al*., 2008) as, since the 1970s, across the entire elevation range the core distribution increased in elevation by 10-22 m (25% quartile = +10 m; median = +15 m; 75% quartile = +22 m) but within the same overall elevation range (Fig. 4 Supplementary Materials). The impacts of fur seal disturbance were clearly associated with elevation (0-20 m = 78.8%; 21-40 m = 67.9%; 41-60 m = 48.9%; 61-120 m <20%; >121 m = 0%), being highest from sea level up to 20 m, and almost negligible above the threshold of 60 m, where moss banks not damaged by fur seals were five times more abundant than damaged areas (Table 1). As a direct demonstration of the impact of fur seals, the number of moss banks identified in the area protected by the seal fence in the Backslope area (Fig. 1 Supplementary Material) almost doubled between the 1970s and 2011.

Distribution patterns and changes above the 60 m elevation threshold

Further analyses were performed focusing only on the moss banks located above 60 m, to attempt to identify patterns and drivers of change in areas subject to much lower and negligible levels of fur seal disturbance. Comparing the two surveys, since the 1970s the overall elevation range as well as medians and quartiles did not show any change of distribution with elevation above the 60 m threshold (Fig. 4A). However, since the 1970s the number of moss banks between 60 and 120 m increased considerably (61-80 m = +63%; 81-100 m = +70%; 101-120 m = +57%) and these changes were statistically significant ($p<0.01$, Wilcoxon test) (Fig. 3A, 4A). In contrast, above 120 m a.s.l., changes were negligible and not statistically significant (p = 0.8, Wilcoxon test). The highest elevation of new moss banks was limited to 140 m (Fig. 4A).

The distribution of moss banks with slope did not change above the 60 m threshold comparing the two surveys (p>0.05, Wilcoxon test) (Fig. 4B). The slope range of the majority (75%) of new moss banks was restricted, developing preferentially on gentle slopes of up to 20°, with more limited numbers on slopes of up to 40°. There was a statistically significant difference in moss bank occurrence with aspect above 60 m a.s.l. between the two surveys (p = 0.011, Wilcoxon test), with an increase on N facing slopes and a concomitant decrease on NW and W slopes, this being particularly clear in the distribution of the new moss banks observed in 2011 (Fig. 4C).

Eastern vs western sides of the island

Since the 1970s the total number of moss banks has decreased on the eastern and increased on the western sides of the island, although with different patterns with elevation (Table 1, Fig. 5 A, B). Below 60 m the decrease on both sides of the island (Table 1) was, as described above, due to fur seal disturbance. Above the 60 m threshold there was a statistically significant increase in moss bank numbers on both sides of the island (p<0.01, Wilcoxon test) (Table 1, Fig. 5 A, B), which was much more pronounced on the western side (+250% vs. +13.5%). The western increase was mainly concentrated at elevations between 41 and 120 m a.s.l. (Fig. 5B). Despite these changes, the overall distribution range with elevation did not change substantially between surveys, with only a slight increase in maximum elevation and 75% percentile on the western side (Fig. 5C).

There were no significant changes with respect to slope between the two surveys on either side of the island (p>0.05, Wilcoxon test) (Fig. 5D). Minor and non-significant (p>0.05) changes with aspect were observed on the eastern side of the island, with stronger changes on the western side (p = 0.01, Wilcoxon test), where there was a large increase in the numbers of moss banks on facing N, NW and NE facing slopes (Fig. 5E, F).

DISCUSSION

Moss bank changes since the 1970s: interaction of multiple drivers

Since the 1970s moss banks on Signy Island have exhibited changes in abundance and in distribution patterns, especially with elevation above or below a threshold altitude of 60 m a.s.l., driven by the recent steep increase in fur seals on the island and their direct physical impacts. Further asymmetrical changes were apparent between the two sides of the island (E vs W), especially between 60 and 120 m a.s.l. Our data indicate that the observed changes are the result of the interaction of multiple biotic and abiotic factors, together resulting in a heterogeneity of responses across the elevational gradient of the island.

Both in the 1970s and the 2011 surveys, moss banks on the island exhibited an unimodal distribution with elevation (Figure 3A). This type of distribution has been interpreted as the result of a combination of different factors including hard boundaries or/and incomplete sampling (Grytnes and Vetaas, 2002). Given the exhaustive sampling achieved in both surveys on Signy Island, the patterns obtained are unlikely to be a sampling artefact, implying that moss bank distribution with elevation is controlled by the occurrence of limiting factors at both altitudinal boundaries (upper and lower).

Effect of biotic disturbance

At the lower altitudinal boundary (between sea level and 60 m a.s.l.), decreases in moss bank abundance along with considerable local loss of banks present in the 1970s were mainly the result of the negative impact of fur seal disturbance. This effectively masked any direct effect of physical environmental change. A similar impact has been observed on Signy Island in distributional changes of the higher plants *D. antarctica* and *C. quitensis* between the 1960s and 2009 (Cannone *et al*., 2016). The moss banks surveyed here exhibited thresholds at different elevations to those of the two native vascular plants, with fur seal disturbance affecting moss banks up 60 m a.s.l., consistent with previous observations of higher sensitivity of mosses to vertebrate trampling (Smith, 1988; Favero Longo *et al*., 2011). An analogous example has been reported in the sub-Antarctic, where predation of native seabirds by introduced feral cats resulted in a contraction of the lower distribution limits of coprophilous vascular plant species (le Roux and McGeoch, 2008b).

Similar responses to biotic disturbance has also been recorded in the Arctic in studies on vascular plants (Van Bogaert *et al*., 2009; Callaghan *et al*., 2013). In particular, in the Swedish sub-Arctic, van Bogaert *et al*. (2009, 2010) reported that aspen did not increase in lowland areas due to moose browsing, while at the tree-line aspen colonization was not affected by animal disturbance but rather by summer temperature. Removal of the biotic factor, achieved in the current study by the pre-existing fur seal exclusion area on Signy Island, indicates that in the absence of this factor moss bank expansion would also occur at lower elevations. In addition, as about one third of new moss banks were still observed below 60 m despite the overall amount of fur seal disturbance on the island, implying a continuing role for other physical environmental factors rather than biotic disturbance.

Climate change as a potential driver of moss bank change

Since the 1970s Signy Island has experienced pronounced climatic changes, as revealed in our detailed analyses and in the available literature (Convey *et al*., 2009; Turner *et al*., 2009, 2014; Royles *et al*., 2012; Cannone *et al*., 2016). These changes in climate, in particular air warming, growing season lengthening and increase of total precipitation (especially during the summer) are factors likely to underlie the observed moss bank increases on Signy Island.

Air warming could induce an increase in bryophyte productivity in Antarctica as, in most cases, bryophytes are functioning at temperatures below their optima for net photosynthesis, which is above 20°C for both *C. aciphyllum* and *P. strictum* (Davey and Rothery, 1997). At Signy Island in the last 40 y the documented air warming has also increased the energy supply through increased thawing degree days (+76 degree days, only in summer). Moreover, growing season length, a factor recognized as limiting for the development of moss banks (Gimmingham and Smith, 1971), extended considerably over the study period, by almost one month (+27 days in the period 1970-2011). Consistent with this prediction, Royles *et al*. (2012), in a study of peat accumulation in moss banks over time at Signy Island using stable isotope data, reported an increase since c. 1950 in the annual growth rate of *C. aciphyllum*, related to a lengthening of the terrestrial growing season. They also reported, over the same time period, a decrease of $\Delta^{13}C$, which would be expected with the observed warmer and wetter summers. Further, recent manipulation experiments carried out in maritime Antarctica on several moss species (including *Polytrichastrum alpinum,* a species belonging to the same family as *Polytrichum strictum*) led to greater moss cover, reduced physiological and cellular stress, increased investment in primary productivity and increased reproductive success under warming conditions (Shortlidge *et al*., 2016 in press).

Precipitation has also increased in the South Orkney Islands since the 1970s, especially during the summer (Royles *et al*., 2012; Cannone *et al*., 2016). The importance of water availability for the growth of bryophytes is widely recognized (e.g. Davey, 1997; Smith, 1984; Kennedy, 1993; Wasley *et al*., 2006a, b; Schlensog *et al*., 2013). It has been hypothesized that precipitation increase will promote the development of bryophytes, although this would be a long-term process due to their typically low growth rates (Davey and Rothery, 1997). Changes in water availability (e.g. due to air temperature or wind speed changes) can significantly affect moss growth (Clarke *et al*., 2012) through effects on photosynthetic performance (Royles and Griffiths, 2015). Given the semi-ombrotrophic nature of bank-forming mosses, we suggest that increased water availability associated with the documented precipitation increase as well as the longer summer period of positive (thawing) temperatures, would also contribute to the increased numbers of moss banks documented. A further confirmation of the semi-ombrotrophic nature of moss banks and of their dependency on precipitation for their water supply is the observation that only c. 25% of the moss banks examined here received direct water supply from snow melting (N. Cannone et al., Insubria University, Italy, unpubl. res.).

Range filling or upward migration?

Globally warming temperatures have led ecologists to predict that vegetation gradients will “march up the hill” as climate envelopes shift with elevation (Walther *et al*., 2002; Breshears *et al*., 2008), with observations of a range of vascular plants providing support for this prediction (e.g. Walther *et al*., 2005; Pauli *et al*., 2007; Cannone *et al*., 2007; Lenoir *et al*., 2008; Kelly and Goulden, 2008). In the southern polar regions similar responses have been detected on sub-Antarctic Marion Island, where vascular plants have increased their maximum elevation by around 70±30 m in response to a warming of +1.2°C over a 40 y period (1966-2006) (le Roux and McGeoch, 2008b). However, in the maritime or continental Antarctic no analogous evidence is available for either vascular plants or mosses. Since the 1970s, Signy Island moss banks have exhibited a large increase in numbers between 60 and 120 m a.s.l., but no substantial change between 120 and 200 m and a lack of upward migration above their previously highest recorded elevation (200 m).

The increase in numbers observed between 60 and 120 m a.s.l. could be explained by a range filling process within the existing elevation range. Range filling is the result of the progressive occupation of the available ecological niches within the existing distribution range, while range shifts occur at range margins through colonization and establishment events at the maximum elevation and/or extinctions at the minimum elevation (Lenoir and Svenning, 2015). The range filling process has been documented as a species response to climate change in alpine tundra (Cannone and Pignatti, 2014), as well as in sub-Antarctic island vegetation (e.g. Chown *et al*., 2012), but never in Antarctica.

At Signy Island, the observed moss banks changes were more concentrated at the core rather than the edge of their distribution, with increases being particularly notable at elevations where the banks were already well represented in the 1970s (e.g. Fig. 4A, B). The range filling process is even more evident when considering elevation, slope and aspect range of the new moss banks observed in 2011 (Figs. 3B, 4A, B, C). The range filling occurred with maximum intensity on the western side of the island where, between 60 and 120 m a.s.l., there was an increase in numbers of banks of c. +250%, contrasting with only +13% on the eastern side in the same elevation range. A possible explanation of these asymmetrical range filling patterns could be a stronger increase in precipitation on the western side of the island, facing the prevailing westerly winds. Indeed, despite the absence of local wind data for Signy

Island, recently Garreaud *et al*. (2013) documented that in southern Patagonia an increase in westerly winds led to precipitation increase on the windward slopes along with a simultaneous decrease on the leeward side.

The ecological requirements of moss banks could explain the lack of upward migration at higher elevations on Signy Island. Both *P. strictum* and *C. aciphyllum* are species characteristic of the climax community that develops on the oldest terrains, and then only where local-scale environmental features are more favorable (Favero Longo *et al*., 2012). Therefore, despite the retreat of the island's ice cap, that has been particularly pronounced in the last several decades and provided large new ice-free areas potentially available for colonization, these have largely remained devoid of new moss bank growth. Given that the proportion of recently ice-free area is greater above 120 m (> 40% of the total ice-free area), the paucity of the oldest deglaciated terrains at these elevations could be one of the most important factors underlying this threshold.

In conclusion, the observed changes in moss bank abundance and spatial distribution on Signy Island over the last c. 40 y result from the interaction of multiple drivers producing a heterogeneity of responses across an elevational gradient. Some of these relate to recent processes (contemporary climate change and the large recent increase in fur seal disturbance), and others to long-term landscape evolution (deglaciation age), with all interacting with the species' ecological requirements. The dynamic patterns and changes described at this location, a paradigm of biological environmental change in Antarctic terrestrial ecosystems (Smith, 1990), over only a 40 y period provide important insights into future vegetation responses to climatic changes in the polar regions generally.

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Table 1. Moss bank numbers in the two surveys (1970s, 2011) at Signy Island and their changes, analyzing the total dataset (total), moss banks extinct since 1970s (extinct), moss banks new in 2011 (new), and persistent moss banks occurring in both surveys (persistent). Legend: All = all moss banks within each category; East = eastern side of the island; West = western side of the island; 1 = area damaged by fur seals; 2 = area not damaged by fur seals.

	1970			**2011**					**1970-2011**		
	All	**East**	**West**	**All**	**1**	**2**	**East**	**West**	**All (%)**	**East (%)**	**West (%)**
Total	323	170	153	310	136	174	144	166	-4	-15.3	+8.4
<60 m	246	110	136	184	116	68	76	108	-25	-30.9	-20.6
> 60m	77	60	17	126	20	106	68	58	+63.6	+13.3	+241
Extinct since 1970	96								-100		
< 60 m	90								-100		
> 60 m	6								-100		
New in 2011				66	7	59			IN		
< 60 m				21	7	14			IN		
> 60 m				45	0	45			IN		
Persistent	244			244	136	108			0		
< 60 m				138	94	44			0		
> 60 m				106	42	64			0		

Figure captions

Figure 1. Climate changes at Orcadas recorded in the period 1970-2010: A) growing season length (days); B) mean daily maximum temperature (°C), C) thawing degree days during the summer (TDD-DJF, °C); D) maximum daily precipitation (mm); E) number of days with precipitation $\geq$ 5 mm (back circle) and $\geq$ 10 mm (grey circle); F) number of days with precipitation < 1mm.

Figure 2. Location and dynamics of bank-forming mosses banks at Signy Island between the 1970s and 2011 surveys, relating to A) extinct (red); B) new (green); C) persistent (grey). Legend: bold line indicates 60 m elevation; blue line = fur seal exclusion fence; pale blue area = glacier extent in 2011.

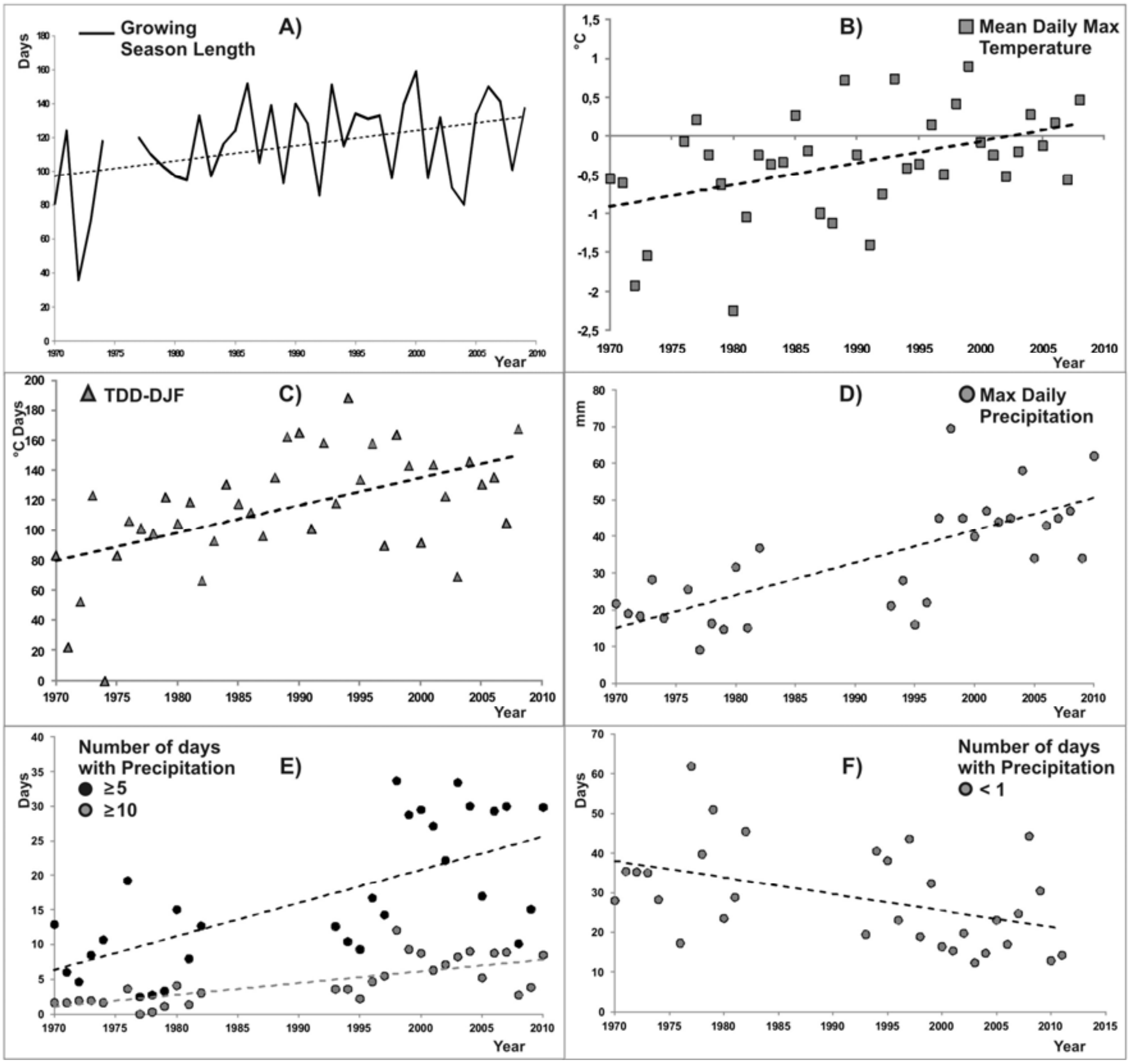
Figure 3. Partitioning of the 1970s and 2011 moss banks across topographic features: A) elevation; B) elevation range of only extinct versus new; C) aspect; D) slope. The changes were evaluated: a) considering the % of population (bars), b) the absolute number of moss banks (squares). * = statistically significant differences between 1970s and 2011 ($p<0.05$).

Figure 4. Comparison, above the elevation threshold of 60 m, of the entire 1970s dataset, the entire 2011 dataset and only the new moss banks observed in 2011, relating to their distribution patterns with: A) elevation (m); B) slope (°); C) aspect.

Figure 5. Partitioning of the 1970s and 2011 moss banks across topographic features comparing the eastern and western sides of the island: A) elevation of 1970s mosses (white = east; grey = west); B) elevation of 2011 mosses (white = east; grey = west); C) distribution

with elevation only in areas without fur seal disturbance (above 60 m) (white = 1970s; grey = 2011); D) distribution with slope (°) (white = 1970s; grey = 2011); E) aspect range in 1970s (white = east; grey = west); F) aspect range in 2011 (white = east; grey = west).

Figure 1



A)
Growing Season Length
Days
0
20
40
60
80
100
120
140
160
180
1970
1975
1980
1985
1990
1995
2000
2005
2010
Year
B)
Mean Daily Max Temperature
°C
1,5
1
0,5
0
-0,5
-1
-1,5
-2
-2,5
1970
1975
1980
1985
1990
1995
2000
2005
2010
Year
C)
TDD-DJF
°C Days
0
20
40
60
80
100
120
140
160
180
200
1970
1975
1980
1985
1990
1995
2000
2005
2010
Year
D)
Max Daily Precipitation
mm
0
10
20
30
40
50
60
70
80
1970
1975
1980
1985
1990
1995
2000
2005
2010
Year
E)
Number of days with Precipitation
≥5
≥10
Days
0
5
10
15
20
25
30
35
40
1970
1975
1980
1985
1990
1995
2000
2005
2010
Year
F)
Number of days with Precipitation
< 1
Days
0
10
20
30
40
50
60
70
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
Year

Figure 2

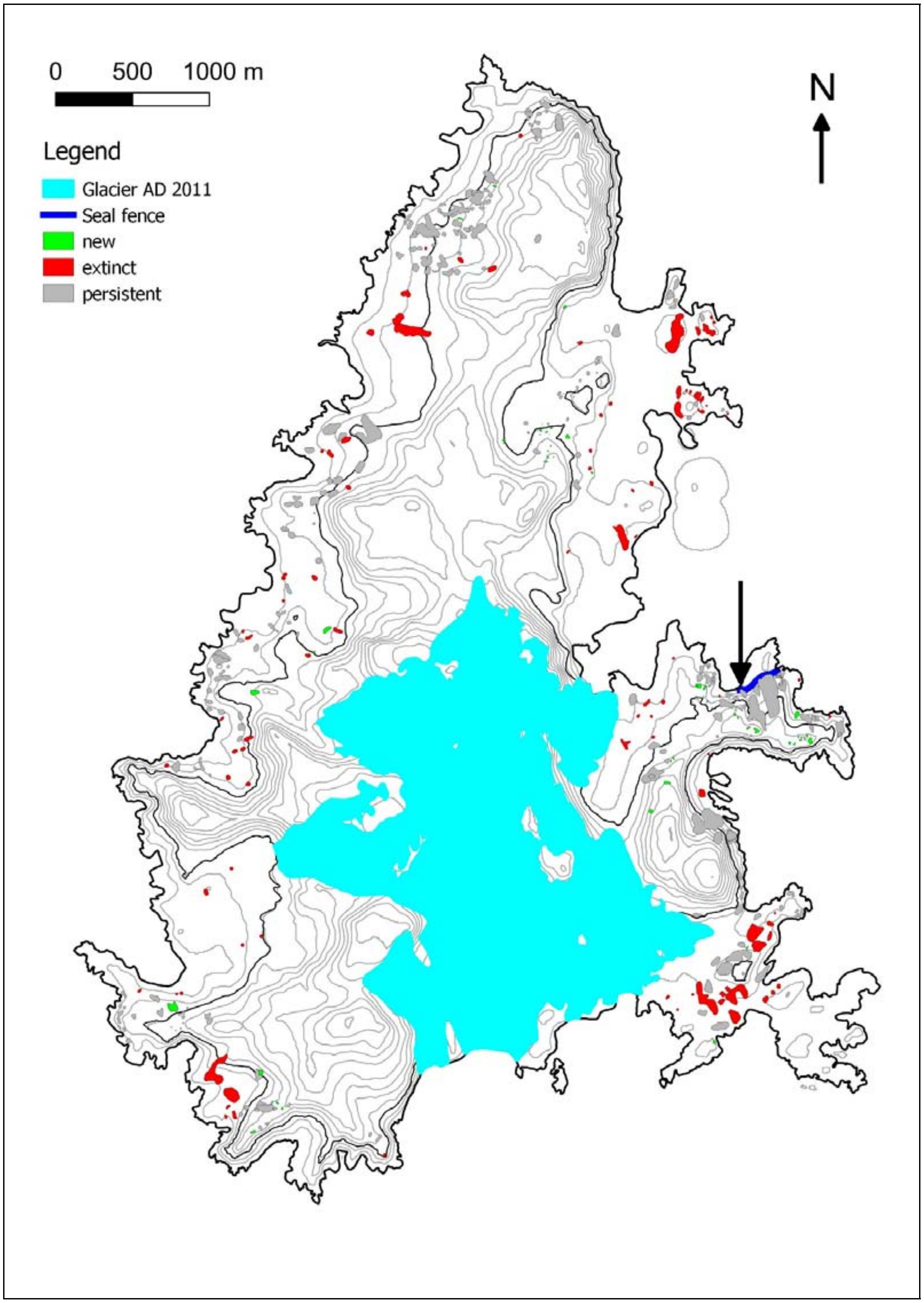

0
500
1000 m
N
Legend
Glacier AD 2011
Seal fence
new
extinct
persistent

Figure 3

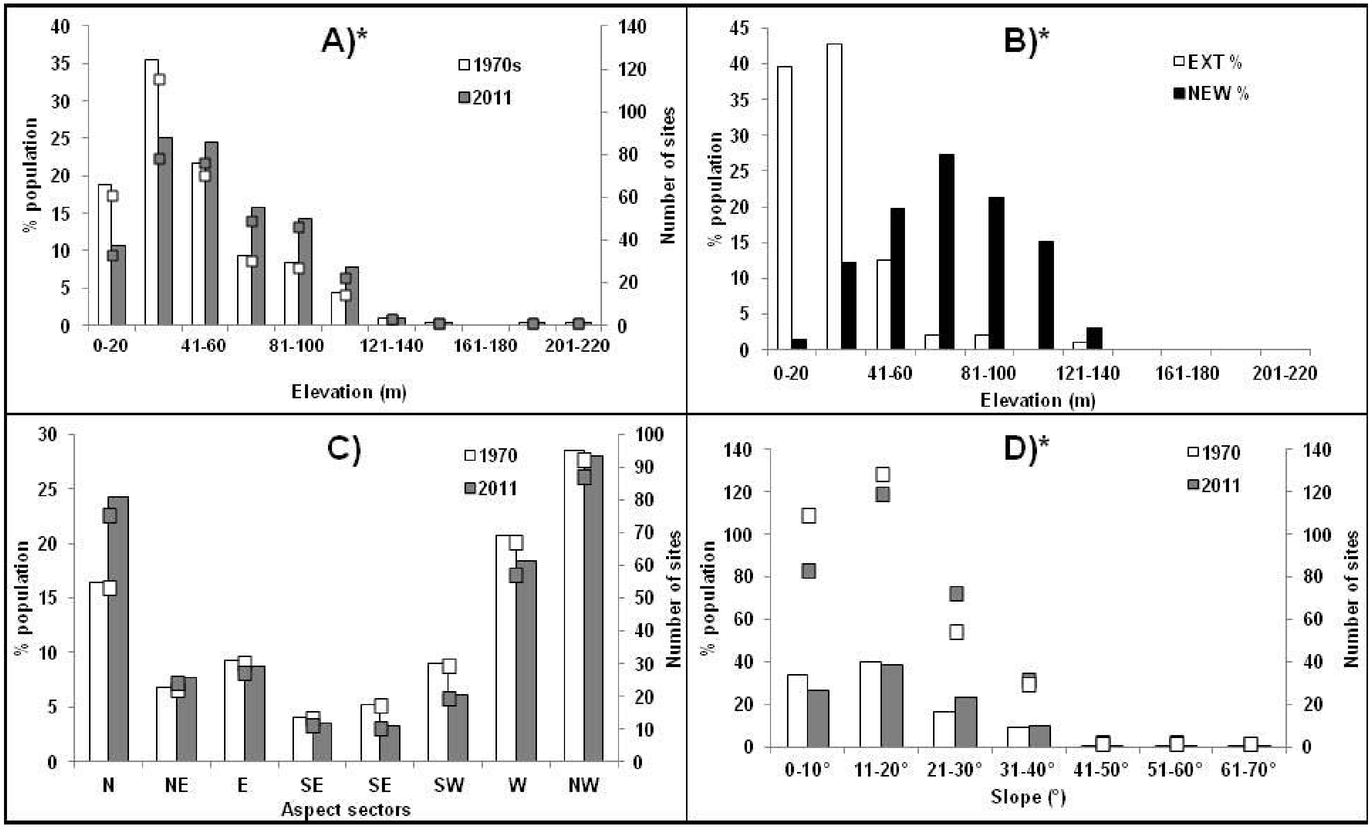

A)*
1970s
2011
% population
Number of sites
0
5
10
15
20
25
30
35
40
0
20
40
60
80
100
120
140
0-20
41-60
81-100
121-140
161-180
201-220
Elevation (m)
B)*
EXT %
NEW %
% population
0
5
10
15
20
25
30
35
40
45
0-20
41-60
81-100
121-140
161-180
201-220
Elevation (m)
C)
1970
2011
% population
Number of sites
0
5
10
15
20
25
30
0
10
20
30
40
50
60
70
80
90
100
N
NE
E
SE
SE
SW
W
NW
Aspect sectors
D)*
1970
2011
% population
Number of sites
0
20
40
60
80
100
120
140
0-10°
11-20°
21-30°
31-40°
41-50°
51-60°
61-70°
Slope (°)

Figure 4

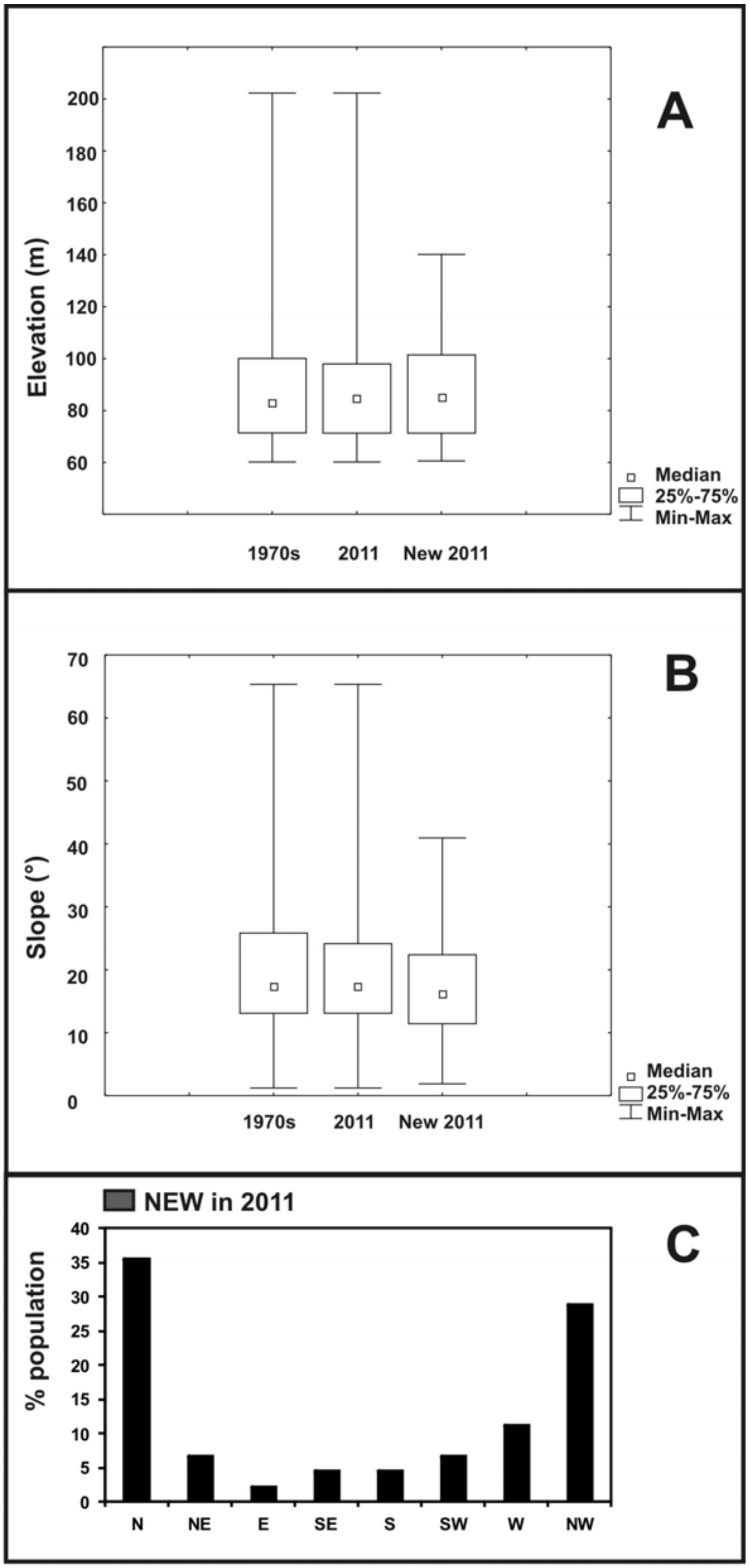
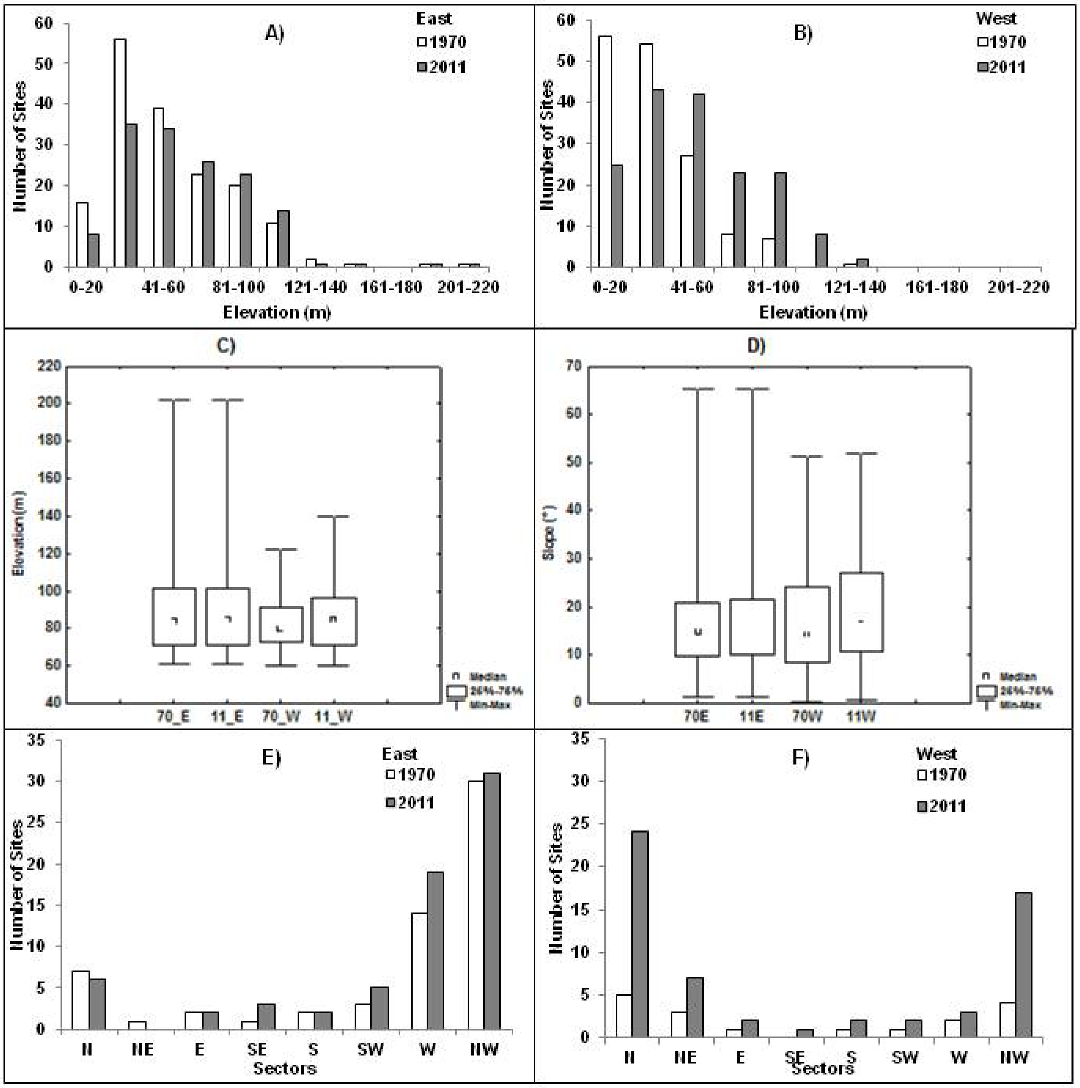

A
Elevation (m)
200
180
160
140
120
100
80
60
Median
25%-75%
Min-Max
1970s
2011
New 2011
B
Slope (°)
70
60
50
40
30
20
10
0
Median
25%-75%
Min-Max
1970s
2011
New 2011
C
▆ NEW in 2011
% population
40
35
30
25
20
15
10
5
0
N
NE
E
SE
S
SW
W
NW

Figure 5


A)
East
1970
2011
Number of Sites
60
50
40
30
20
10
0
0-20
41-60
81-100
121-140
161-180
201-220
Elevation (m)
B)
West
1970
2011
Number of Sites
Elevation (m)
C)
Elevation (m)
220
200
180
160
140
120
100
80
60
40
70_E
11_E
70_W
11_W
Median
25%-75%
Min-Max
D)
Slope (°)
70E
11E
70W
11W
E)
East
1970
2011
Number of Sites
35
30
25
20
15
10
5
0
N
NE
E
SE
S
SW
W
NW
Sectors
F)
West
1970
2011
Number of Sites
Sectors

SUPPLEMENTARY MATERIAL

Figure 1 Supplementary Materials. The exclusion fence installed in 1985 at Signy Island close to the research station to prevent fur seal damage to vegetation.

Figure 2 Supplementary Materials. Extinct moss bank characterized by removal of the entire bank of living and preserved moss. This is an example where severe surface disturbance by seals has led to the complete loss of moss banks.

Figure 3 Supplementary Materials. Example of the wind speed increase with altitude at Signy Island. The daily mean wind speed at CALM site (80 m asl) is almost always lower than at Jane Col (150 m asl) and on some days this difference exceeds 10 ms^{-1}. Jane Col: black dotted line and square; CALM site: grey line and circle.

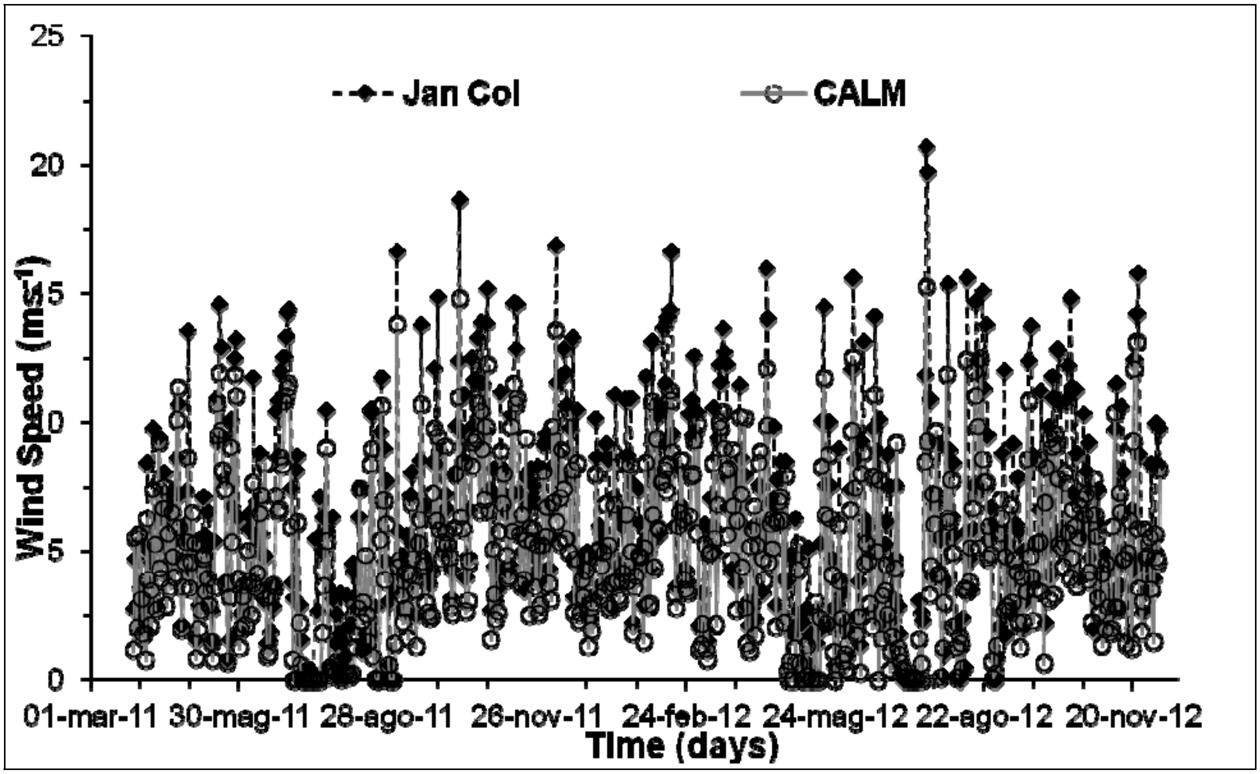
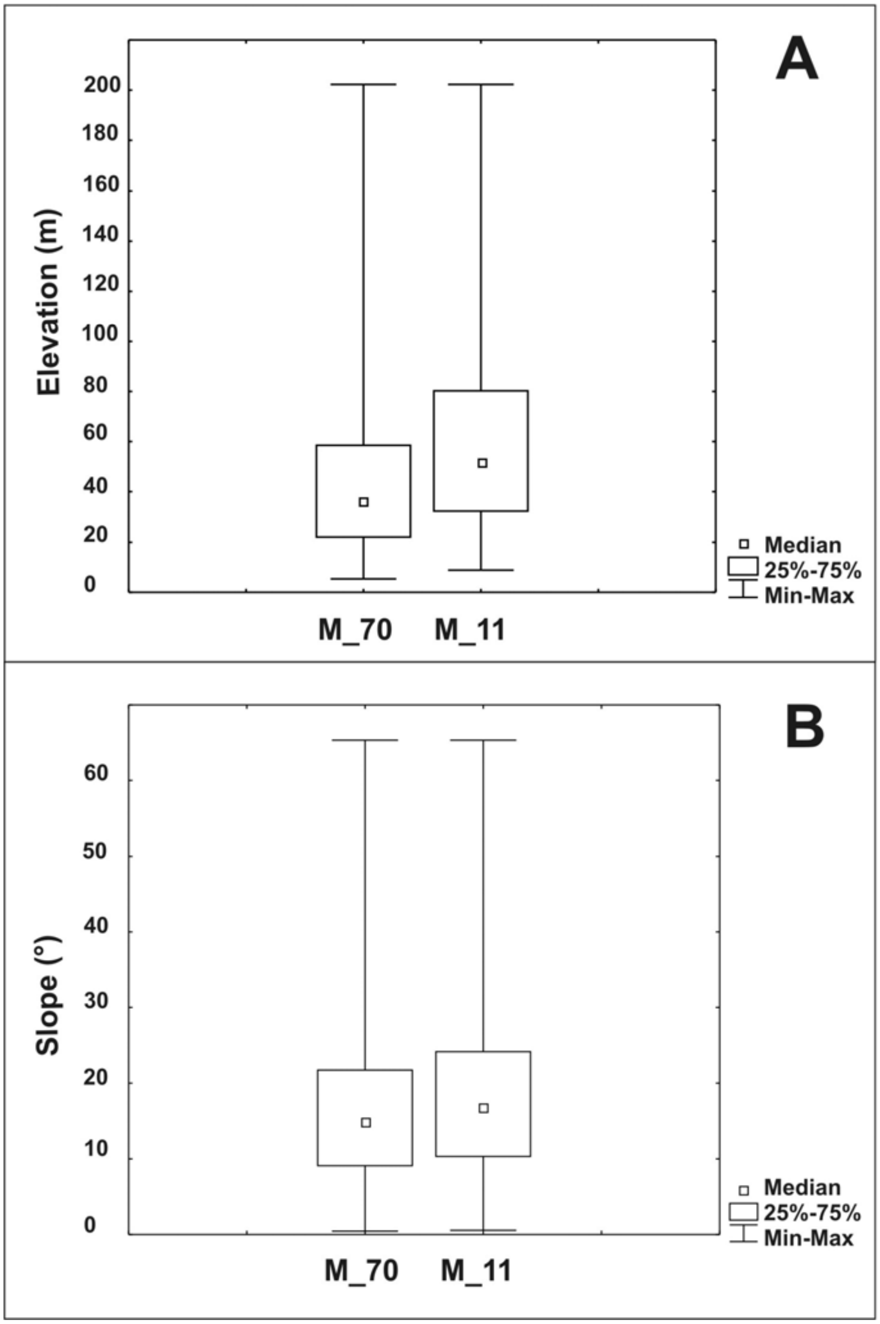


Figure 4 Supplementary Materials. Changes of spatial distribution (minimum; 25% percentile; median; 75% percentile; maximum) of moss banks across their entire elevation range, relating to A) elevation; B) slope.



VI. CONCLUSIONS AND FINAL REMARKS

In conclusion, we assessed the impacts of climate change on terrestrial ecosystems among three case studies in regions geographically, climatically and evolutionary remote and distinct: European Alps, Continental Antarctica and Maritime Antarctica. These three areas were analyzed in order to assess the spatial variability of climate change and its impacts, in regions of the world subject to different environmental and anthropogenic pressures. Moreover, trends in air warming were different in these regions, which allowed us to evaluate the variability of the global change phenomena.

Continental Antarctica provides a unique opportunity to assess the natural dynamics and responses of cryptogams without the disturbance effect due to the competition with vascular plants or biotic disturbances, and with the complete absence of any anthropogenic impact.
Despite the lack of air warming in Continental Antarctica, our data emphasize that ecosystem changes occurred rapidly, as they are already detectable in only 10 years. Here, the active layer is thickening at a rate comparable to areas in which air warming is occurring, emphasizing the role of solar radiation and snow cover. Continental Antarctica is thus experiencing climatic and environmental changes different from Maritime Antarctica. The active layer thickening resulted in a soil drying, with consequential changes in moss and lichen colonization following the species-specific water requirements.
The manipulation experiments that we started in this area, could thus help to verify these observations, and allow to disentangle which are the main drivers of vegetation colonization and stabilization, in order to create models on the evolution of Antarctic terrestrial ecosystems under different future climate change scenario, which could enforce the management strategies of these peculiar environments.

The work done at Signy Island, Maritime Antarctica, allowed us to determine the main ecological requirements of moss banks in relation to the environmental factors, which included topography, biotic disturbance, deglaciation age of the surface and snow cover distribution (in terms of water supply).
Moss banks showed a large vulnerability from fur seals disturbance, than higher plants and lichens. The observed changes in moss banks abundance and spatial distribution since 1970s result from the interaction of multiple drivers, producing heterogeneous responses along the elevation gradient. At lower elevation, we observed a large impact from the fur seals population expansion observed in the last decades, while effects of the recent climate warming coupled with the surface age of deglaciation were important factors determining the moss banks distribution.
The analysis of this unique feature of the Maritime Antarctica (moss banks), provided thus important insights into future vegetation responses to climatic changes, that can be focused on the specific case of Antarctica, but also exportable to other moss-dominated ecosystems of polar latitudes.

In the Alps, the results from the long-term monitoring of phenology, snow and ground surface temperature, and the implementation with the manipulation experiments, allowed us to identify and quantify the main drivers influencing the phenological stages and plant growth, as well as ground surface temperatures.

The alpine system is characterized by a large topographic and climate variability, and thus it would need data on the local scale to be longer than the data analyzed in this PhD (10 years), to get a more robust signal of climate related impacts. However, some statistically significant trends concerning phenological stage were already detectable over the 10 years study, thus indicating a strong responsiveness to climate of phenology of alpine tundra plants. In particular, the greatest advances were observed for the greening stages, confirming the high sensitivity of spring phenology to changes in snow cover. In any case, our dataset was characterized by a large inter-annual variability of climate parameters, which could allow us to determine with large accuracy the ranges of photoperiod among which plants are able to cope with the variability of climate. This constitutes a novelty element, since little is known about quantitative information of plasticity of phenology of alpine plants.

The environmental factors driving the phenological responses vary according to the phenological stage and the selected growth form. Thanks also to the manipulation experiments, we could observe how phenology is influenced not only by temperature and precipitation regimes, but also by other drivers such as soil water and nutrient availability.

It is of relevant interest the main effect of the photoperiod on determining the start of phenological stages from flowering, to seed development, seed ripening, and leaf senescence. The photoperiodic limitation plausibly constitute a conservative strategy of the selected species, which in literature has been particularly emphasized for the phenology of the reproductive stages (e.g., flowering) but has been neglected concerning other phenological stages of alpine plants (e.g., leaf senescence), providing thus a novelty element that should be taken into account to evaluate and model the degree of plasticity of such ecosystems under modelled future climate change scenario.

Moreover, our findings were largely in agreement with observation from long-term (>50 years) studies of alpine plant communities evolution. Indeed, we found grasses and shrubs to be highly sensitive and more plastic species that could be favored by climate warming. An increasing trend of evergreen shrubs height was observed, in agreement with the observed expansion of shrubs in all the Alps, which allowed us to explain that this expansion is related to the climate amelioration, since land use changes are negligible in our study area.

As a consequence of changes in vegetation distribution, the ground surface temperature of alpine soils will be affected with unexpected responses. We identified the pioneer species (*Cerastium uniflorum*) as ground-cooler plants that can lead to permafrost presence, which should be considered in the ground surface temperature modelling in the Alps. In Polar regions, the cooling of vegetated soils is a well-known phenomenon, but comparatively neglected in the Alps. However, we detected that shrubs vegetated soils, could enhance soil temperatures more than the IPCC scenarios, with evident positive feedbacks on the carbon emission from these soils.

More detailed analyses will be provided in specific papers that are under preparation. However, we think that the results from this monitoring could be of high relevance to define models at local scale, as well as providing important insights that should be considered also at regional and global scales. All the data that we collected at the Foscagno valley could be used for the adaptation strategies and management plans, which have to be implemented for sites of community importance of Nature 2000 network, to which the Foscagno valley belongs.

Future perspectives

Several points of these experiments and data elaboration could improve our knowledge on the plasticity of alpine plants. For example, our general understanding of phenological responses to climate change is based almost solely on the first days of observation on which an event is observed, but for further extending our analyses it will be interesting to consider all the distribution curve of each phenological stage, in order to assess how communities respond as a whole.

We observed the responses only among the selected growth forms, but it would be relevant in the future to analyze in detail the species-specific responses, for each phenological stage, in order to identify “winner” and “looser” species in a climate change scenario, depending on their plasticity and conservative/adaptive strategies. Similarly, the comparison of the same species between different communities could help to quantify the degree of species plasticity.

A more detailed climatic analysis could also improve our knowledge about plants behavior. For example, the changes of monthly minimum air temperature, was demonstrated to influence the long-term evolution of grasslands in high elevation central Appennines (central Italy) (Giarrizzo et al., 2016).

The analysis of the changes in distribution of species and communities among the permanent plots of the long-term monitoring project could also allow to verify our statements and definitively quantify the potentiality of the alpine plant phenology, particularly in terms of loss of biodiversity and ecosystems services.

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“*It is astonishing how soon and unexpectedly flowers appear, when the fields are scarcely tinged with green. Yesterday, for instance, you observed only the radical leaves of some plants; to-day you pluck a flower*”. Henry David Thoreau, 1962

VIII. REFERENCES

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