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- XXIV Course -**

**Biomass production and biodiversity in herbaceous communities
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1 - Introduction

1.1 Nature from a human perspective: Ecosystem Services

Humans give values to a lot of things that have not practical use. Let's think about art for example. A picture by Picasso has enormous value. You may counter that it has a cultural, intellectual, historical and maybe spiritual value, but you cannot affirm that that's strictly required for the existence of humankind. On the contrary what is culturally attractive and absolutely necessary for men societies to live, is nature itself. In the past decades Holdren & Ehrlich (1974) and Ehrlich & Ehrlich (1981) noticed that ecosystems supported life ensuring:

- purification of air and water
- mitigation of droughts and floods
- generation and preservation of soils and renewal of their fertility
- detoxification and decomposition of wastes
- pollination of crops and natural vegetation
- dispersal of seeds
- cycling and movement of nutrients
- biomass production
- control of the vast majority of potential agricultural pests
- maintenance of biodiversity
- protection of coastal shores from erosion by waves
- protection from the sun's harmful ultraviolet rays
- partial stabilization of climate
- moderation of weather extremes and their impacts
- provision of aesthetic beauty and intellectual stimulation that lift the human spirit

As time goes by, scientific community has recognized the crucial role which natural systems played in underpinning economic activities and anthropocentric wellbeing and has also noticed the increasing pressures being placed upon such systems by humans (Global Environment Facility 1998; Chapin *et al.* 2000; Koziell 2001; Millennium Ecosystem Assessment 2005; Convention on Biological Diversity 2006; Loreau *et al.* 2006). Human needs, indeed, have been and continue to be

Boyd & Banzhaf (2006) expanded on Millennium Ecosystem Assessment definition to propose that Ecosystem Services are “components of nature, directly enjoyed, consumed, or used to yield human well-being”, meaning that services are end-products of nature and not processes. Fisher & Turner (2008) stated that “Ecosystem Services are the aspects of ecosystems utilized (actively or passively) to produce human well-being”. Fig. 1.1.2 summarize and links Ecosystem Services with constituents of human well-being: security, materials necessary for a good life, health and good social relations are supposed as depending on ecosystem supporting, provisioning, regulating and cultural services.

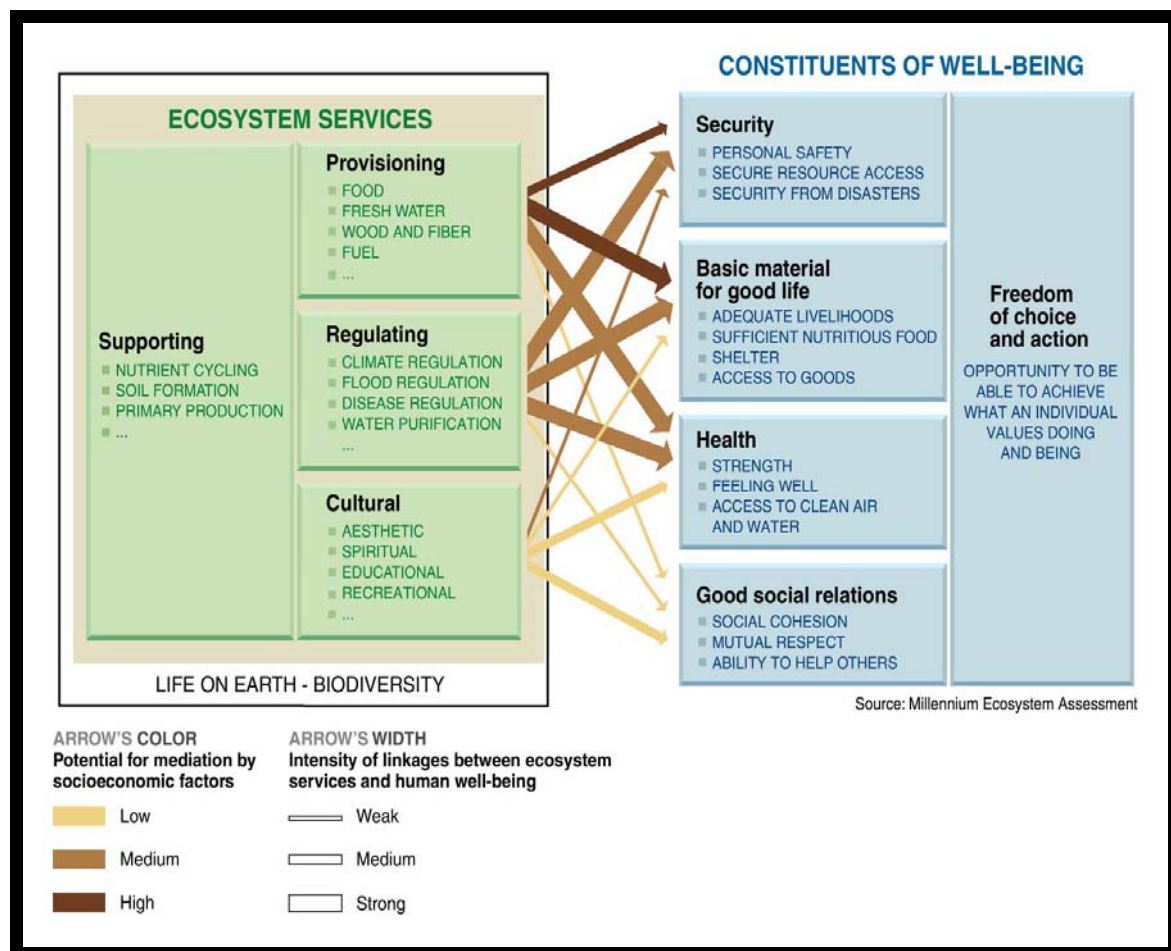


Figure 1.1.2: linkages between Ecosystem Services (on the left) and constituents of human well being (on the right),
Source: Millennium Ecosystem Assessment, 2005.

Many authors have tried to develop a method to account for Ecosystem Services. De Groot *et al.* (2002) presented a conceptual framework and typologies for describing, classifying and valuing ecosystem functions, goods and services in a clear and consistent manner. Fisher & Turner (2008) focused on the quantification of Ecosystem Services and their value to stakeholders and suggested various classification schemes. Cowling *et al.* (2008) recommended mainstreaming the concept in the assessment, planning and management phases of policy-making.

Turner & Daily (2008) proposed that Ecosystem Services research should address the various stages in decision-making, from problem identification to policy evaluation and capacity building. Recently Seppelt *et al.* (2010) have made a quantitative review of Ecosystem Services studies, deriving four facets that characterise the holistic ideal of Ecosystem Services research: biophysical realism of ecosystem data and models, consideration of local trade-offs, recognition of off-site effects and comprehensive but critical involvement of stakeholders within assessment studies.

What is clear is that an ongoing cultural process of objectification of nature's value urges politicians and economists to understand (or maybe we should say "to remember") more and more the leading role of nature on every human activities and share requirement to account for benefits we receive from ecosystems. To emphasize what has been said, we can quote Sukhdev (2008) that has stated that "there are no economies without environments, but there are environments without economies". We may have some difficulty assigning an unambiguous value to Ecosystem Services, but there's no doubt that we have to protect ecosystems to prevent the deterioration of natural components providing us with goods and benefits. Let's focus on two prominent factors influencing services offered by ecosystems: biodiversity and biomass production.

1.2 Biodiversity

1.2.1 Biodiversity: from culture to science and politics

An absolutely remarkable feature in planet earth is the great variety of life forms. Since the dawn of humanity, men felt the need to represent, list and describe this incredible diversity of shapes and colours. Multiplicity of life has played a key role even in men's collective imagination influencing art, mythology and religious scriptures. Think about prehistoric cave paintings for example. Egyptians had many animal shaped gods as Anubis the jackal. The Greeks count a lot of animals in their mythology and, for more, philosopher Aristotle was famous for his interest in zoology, as confirmed by his work "*Historia animalium*", that contains many descriptions of animals with anatomical considerations and comparisons. In the biblical book of Genesis we can read:

" So the Lord God formed from the ground all the wild animals and all the birds of the sky. He brought them to the man to see what he would call them, and the man chose a name for each one. He gave names to all the livestock, all the birds of the sky, and all the wild animals".

If you still have some doubt about the influence that biodiversity had on culture, you may take a look at the paintings below (Fig. 1.2.1.1). These artworks are from Italian painter Giuseppe Arcimboldo (Milano, 1526 - Milano, 1593).



Figure 1.2.1.1: paintings from Italian painters Giuseppe Arcimboldo. On the left "Acqua" (1563-1564, Kunsthistorisches Museum, Wien, Austria); on the right "Aria" (1566, private collection, Basel, Switzerland,).

During the centuries, the variability of living world has gained more and more scientific relevance. Scientists have studied organisms all around the world to put them inside logical and rational schemes according to their characteristic. Of course we can mention the work of Swedish botanist Carl von Linné that created a system of taxonomical classification based on flower elements. Observation of variability had been the basis of Darwin's evolutionary theory too. Nowadays biological diversity is a main concern, not only for scientific community but even for politicians. Although there are many possible definitions for biodiversity, perhaps the most widely-accepted, and the closest to a single legally accepted definition, is that provided in article 2 of the "Convention on Biological Diversity" that took place in 1992 during Rio de Janeiro UN Conferences on the Environment and Development:

"Biological diversity means the variability among living organisms from all sources, including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part;

this includes diversity within species, between species and of ecosystems”.

The contracted term “biodiversity” came from a “National Forum on Biodiversity” held in the USA in 1986, where the term, and concept, were brought into more general use (Wilson 1988).

As it has been said, scientists have collected for many years data and observations all over the world describing over 1.7 million of the world's species of animals, plants and algae; (Tab. 1.2.1.1). Although a lot of work has been done, researchers have yet to describe many species of plants, invertebrates and lichens. In fact, biologists have almost completely identified all the world's species only for mammals, birds and coniferous plants, and that’s why the number of known species increases every year.

Table 1.2.1.1: number of described species according to taxonomical groups (modified from IUCN, 2011).

Taxonomical groups	Number of described species
Vertebrates	
Mammals	5490
Birds	9998
Reptiles	9084
Amphibians	6433
Fishes	31300
Subtotal	62305
Invertebrates	
Insects	1000000
Molluscs	85000
Crustaceans	47000
Corals	2175
Arachnids	102248
Velvet Worms	165
Horseshoe Crabs	4
Others	68658
Subtotal	1305250
Plants	
Mosses	16236
Ferns and Allies	12000
Gymnosperms	1021
Flowering Plants	281821
Green Algae	4053
Red Algae	6081
Subtotal	321212
Fungi and Protists	
Lichens	17000
Mushrooms	31496
Brown Algae	3067
Subtotal	51563
TOTAL	1740330

According to Duraiappah *et al.* (2005), Hooper *et al.* (2005) Balvanera *et al.* (2006), Diaz *et al.* (2006) and Worm *et al.* (2006) there is clear evidence that biodiversity has positive effects on the provision and maintenance of Ecosystem Services and that further biodiversity loss can only be expected to compromise service delivery and that extinctions critical for ecosystem functioning, be they global or local, are quite certain to reduce societal options for adaptation responses. For more, Isbell *et al.* (2011) stated that high plant diversity is needed to maintain Ecosystem Services and that, although species may appear functionally redundant when one function is considered under one set of environmental conditions, many species are needed to maintain multiple functions at multiple times and places in a changing world.

1.2.2 Political actions for biodiversity

As Politicians and Heads of State all around the World have recognized that biological diversity is a valuable resource for humankind, actions for its preservation were taken. Awareness led in 1979 to the Convention on the Conservation of European Wildlife and Natural Habitats adopted at Bern on 19 September. It's main focus was to promote cooperation between Nations in order to prevent exploitation of wild flora, fauna and natural habitats. It also committed single States to contemplate in their policies measures for biological diversity conservation. In that same year, another important act was issued: Council Directive 79/409/EEC also known as Directive for Conservation of Wild Birds. In 1982 Council Decision 82/461/EEC (Bonn convention), had the purpose to protect migratory species worldwide. In 1992, the Community and all the Member States at the United Nations Conference on Environment and Development in Rio de Janeiro signed the Convention on Biological Diversity (CBD). This convention purpose was to anticipate, prevent and attack the causes of significant reduction or loss of biological diversity at source, because of its intrinsic value and because of its ecological, genetic, social, economic, scientific, educational, cultural, recreational and aesthetic value. That was a great year for nature! European Union, indeed, with Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, tried to ensure biodiversity by conserving natural habitats and wild fauna and flora in the territory of the Member States. An ecological network of special protected areas, known as "Natura 2000", has been set up for this purpose. Other activities involving monitoring and surveillance, reintroduction of native species, introduction of non-native species, research and education were contemplated. In 1996 another important European regulation ensured the control of trade of endangered species of wild fauna and flora, by establishing conditions for their importation, exportation or re-exportation and on their movement within the European Union (EU), in accordance with CITES (Convention on International Trade in

Endangered Species of Wild Fauna and Flora). Ten years after the Rio convention, at the Johannesburg World Summit on Sustainable Development in 2002 (the "Rio + 10" summit), the Heads of State agreed on the need to significantly reduce the loss of biological diversity by 2010. Furthermore, in 2006, the Commission has produced an Action Plan aimed at conserving biodiversity and preventing biodiversity loss within the European Union (EU) and internationally, halting the loss of biodiversity. Considering this actions, it's clear that Humankind has understood that nature conservation has no political boundaries and that protection of flora and fauna worldwide needs protection of habitats. Unluckily, Global Biodiversity Outlook 3, a document prepared by the Secretariat of the Convention on Biological Diversity, stated that the target agreed by the world's Governments in 2002, "to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on Earth", has not been met (Secretariat of the Convention on Biological Diversity, 2010). Anyway, it seems that politicians really do care about nature and its health!

1.3 Biomass production

1.3.1 Of biomass and men

Living creatures seek for resources and transform them for their own needs as maintaining organism functionality and increasing body mass. Vegetal ability to use solar energy and inorganic compounds to increase their structures made them the main biomass producers into the ecosystems, forming an essential element for most of the food webs. Humankind sustenance too depends (directly or indirectly) on plants providing food, materials and energy. Even urban areas organization well reflected this men dependence on nature. In the past, indeed, human agglomeration centres were usually surrounded and sustained by larger forest and agricultural systems, necessary to satisfy villages' hunger for food and materials. Nowadays, instead, cities seem to rise everywhere, almost independently from the livelihoods offered by the neighboring areas, supplied with primary goods coming from natural and agricultural systems all over the world. A new trade network has indeed linked distant countries with flows of goods, often with little respect for environmental sustainability and forgetting to count the costs of this global market for both nature and society. For more, this trading reaches only wealthy populations who can economically afford to participate and cope with prices variability, excluding about one billion of undernourished people (FAO 2010); (Fig. 1.3.1.1). All in all, it seems that human development has broken down geographical barriers only, not affecting economic ones. If an ethical effort is required to defeat world hunger, men must also remember and deepen the comprehension of

their dependency relationship with nature and its products (specifically with biomass production), calibrating their needs on the present and future carrying capacity of ecosystems which currently seems to be put to the test.

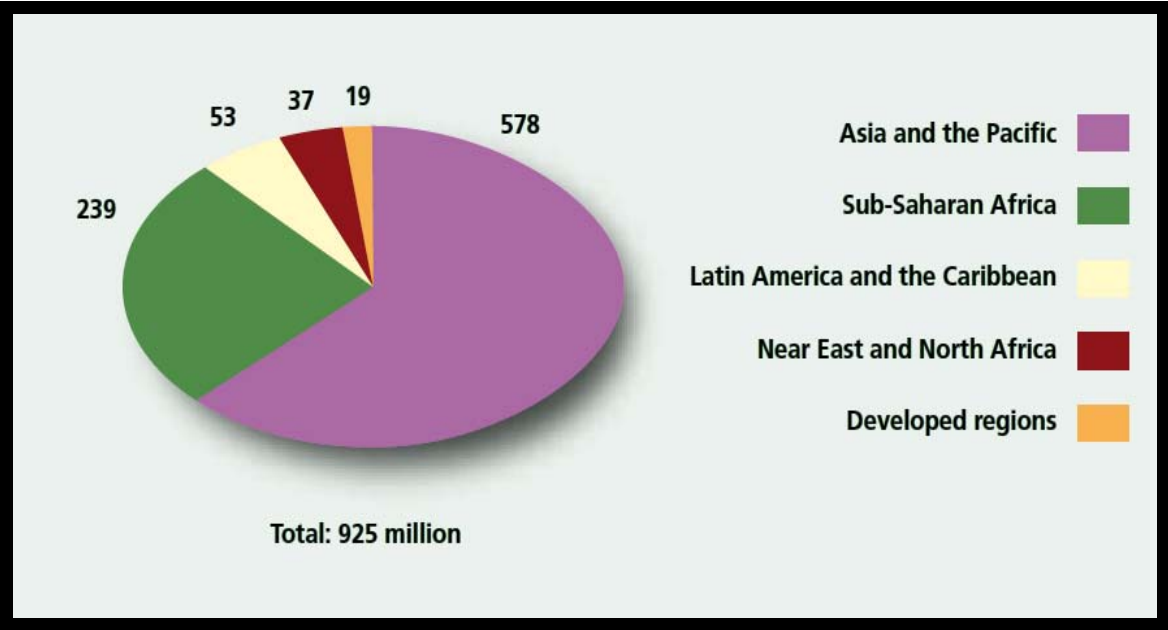


Figure 1.3.1.1: number of undernourished people in 2010, by region (millions). Source: FAO, 2010.

Maps below (Fig. 1.3.1.2, 1.3.1.3 and 1.3.1.4) show the truth of this assertions: nowadays, widespread forest and agricultural lands barely meet the needs of world’s slightly extended but devouring urban areas, leaving, on the contrary, entire countries undernourished.

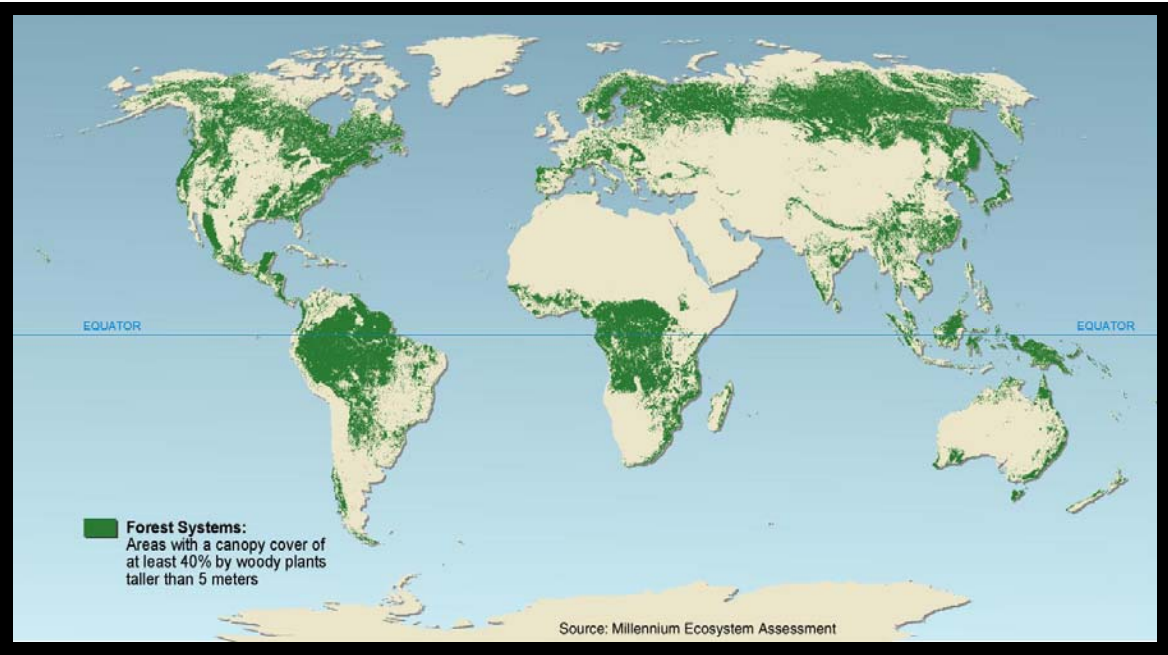


Figure 1.3.1.2: forest systems of the world. Source: Millennium Ecosystem Assessment, 2005.

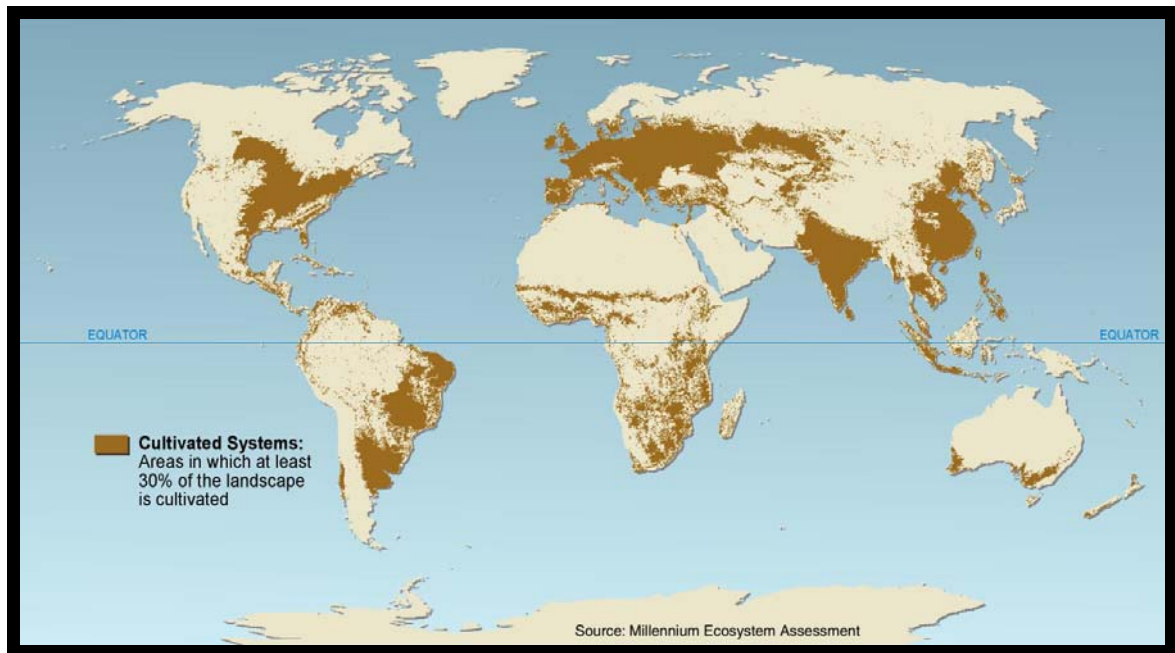


Figure 1.3.1.3: cultivated systems of the world. Source: Millennium Ecosystem Assessment, 2005.

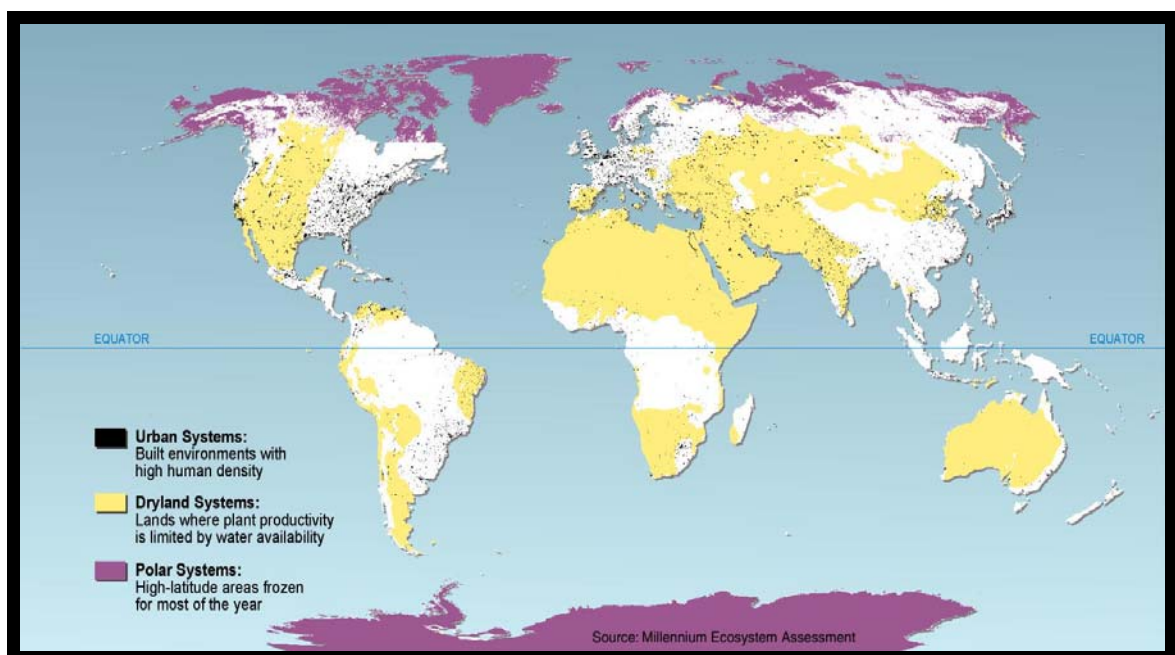


Figure 1.3.1.4: urban, dryland and polar systems of the world. Source: Millennium Ecosystem Assessment, 2005.

After centuries of exploitation of vegetal products, biomass is now gaining attention even in industry as a valuable and renewable energy source. In fact, many countries are developing new technologies that enable them to obtain good performances from engines powered with biomass in place of fossil fuels. Anyway, convenience of using lands to produce biomass for energy production instead of food is an ongoing debate.

According to plant productivity, there's at least one more benefit to consider: sequestration of CO₂ from atmosphere. This service could be included in "climate

regulation" Ecosystem Services that refer in particular to the role of ecosystems in managing levels of green-house gases (GHGs) in the atmosphere. This is a prominent benefit that earth receive, as current climate change is largely driven by the increase of GHGs and many ecosystems may take several centuries (vegetation) or even possibly millennia (where soil formation is involved) before responses to a changed climate are played out (Lischke *et al.* 2002). Since the dawn of the industrial era, indeed, the atmospheric concentrations of several radiatively active gases have been increasing as a result of human activities (Ramanathan 1988), specifically use of fossil fuels as well as changes in land-use, leading to an increase in global temperatures; (Fig. 1.3.1.5).

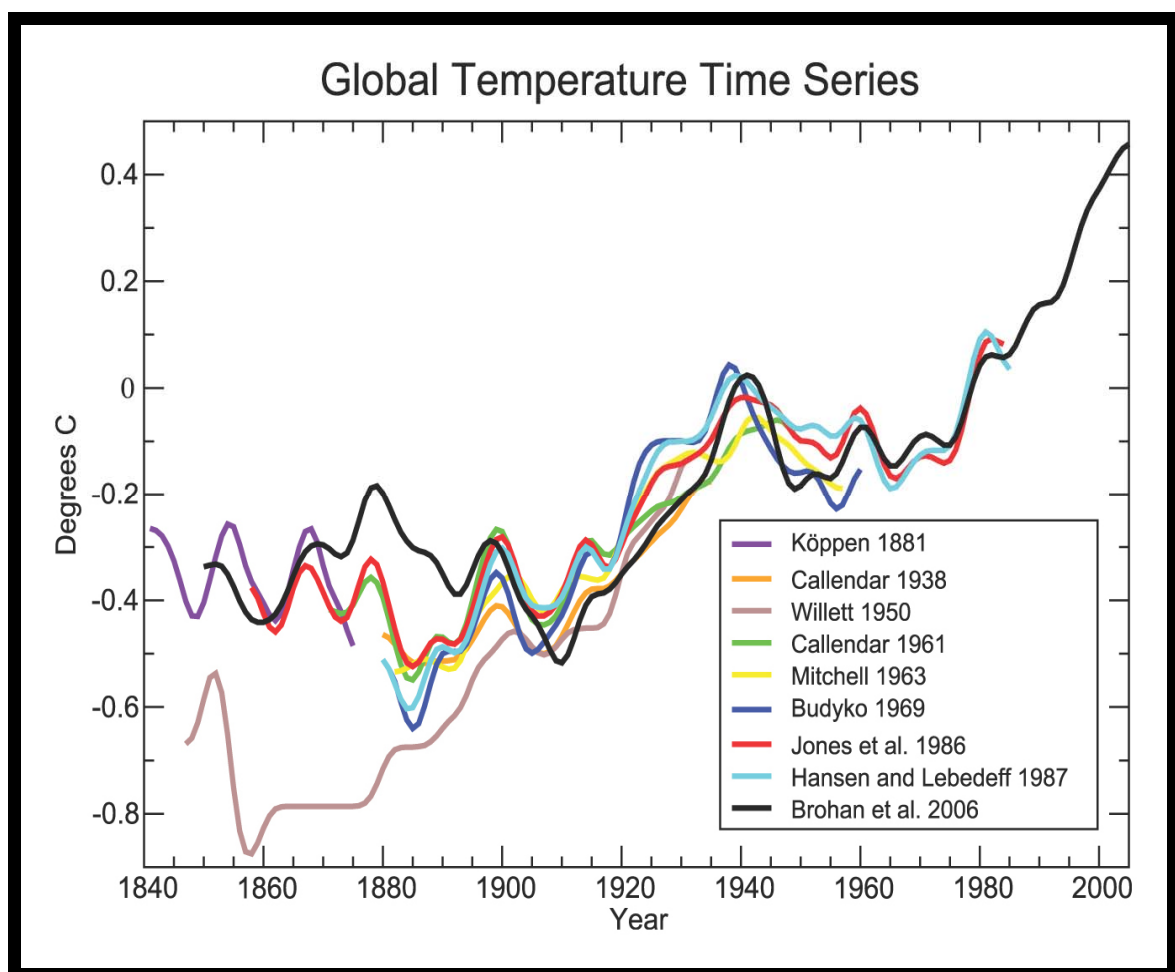


Figure 1.3.1.5: global temperature trends from 1840 to 2000 according to data from different authors (Köppen 1881; Callendar 1938; Willett 1950; Callendar 1961; Mitchell 1963; Budyko 1969; Jones *et al.* 1986a; Jones *et al.* 1986b Hansen & Lebedeff 1987; Brohan *et al.* 2006). Source: IPCC, 2007.

Carbon dioxide (CO₂) is absorbed by vegetation as well by phytoplankton and water, leading to storage in the oceans, biomass and soils. Schimel *et al.* (2001) stated that terrestrial and marine ecosystems currently absorb roughly half of anthropogenic CO₂ emissions. IPCC Fourth Assessment Report (IPCC 2007) summarize the importance of natural ecosystems in the carbon cycle quantifying their CO₂ uptake according to data

from different authors (Sarmiento & Gruber 2006; Sabine *et al.* 2004; Houghton 2003); (Fig 1.3.1.6).

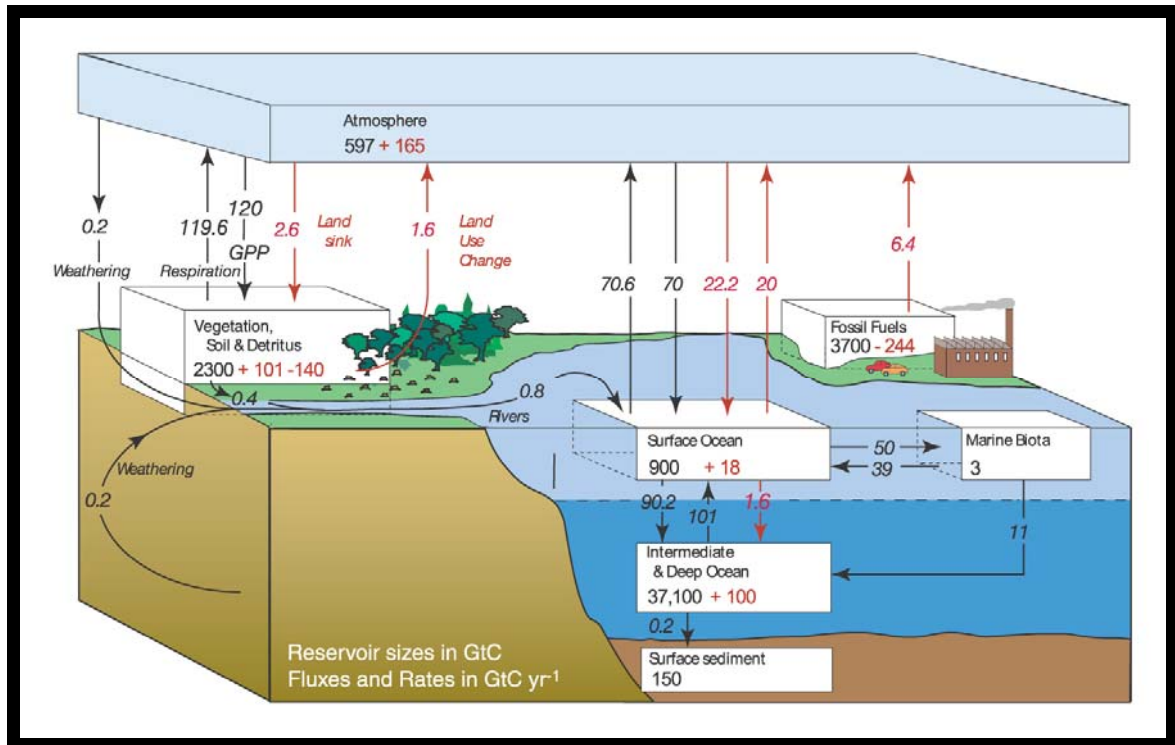


Figure 1.3.1.6: the global carbon cycle as summarized by IPCC (2007) with data taken from many authors (Sarmiento & Gruber 2006; Sabine *et al.* 2004; Houghton 2003). Fluxes are in GtC yr⁻¹: pre-industrial natural fluxes in black and anthropogenic fluxes in red. GPP is annual gross (terrestrial) primary production. Sources: IPCC, 2007.

The additional burden of CO₂ added to the atmosphere by human activities (often referred to as “anthropogenic CO₂”) consist of two fractions: CO₂ from fossil fuel burning (newly released from hundreds of millions of years of geological storage) and CO₂ from deforestation and agricultural development (which has been stored for decades to centuries). Thus, on the one hand it’s important to limit the usage of fossil fuels, and on the other hand to stop or compensate for carbon sinks lost with deforestation. Of course, all carbon stored in vegetal organisms would be still available soon or later. In fact, the use of vegetation sinks is often described in terms of ‘buying time’ or playing a ‘bridging role’ (Noble & Scholes 2001; Lecocq & Chomitz 2001). This generally refers to the expectation that future anthropogenic CO₂ emissions could be greatly curtailed through the use of cleaner technologies, and that carbon sinks can be useful in bridging the gap until these new technologies become available. Even if some authors suggested that a more specific analysis needs to be carried out to define whether, or under what conditions, vegetation, indeed, play a useful role in minimizing climate-change impacts (Kirschbaum 2003), there could be strong temptation to maximize productivity searching for the most productive vegetal species and diffuse them worldwide as much as possible. But times we’re living in require a more

conscious approach to environmental management, considering the complexity of Ecosystem Services, trying to maximise and preserve all of them, including biodiversity.

1.3.2 Political actions to promote the use of biomass

The use of renewable energy sources is becoming increasingly necessary, if we want to achieve the changes required to address the impacts of global warming. In the first years of the new millennium politicians have positively welcomed biomass as a valid and renewable alternative to fossil fuels. European commission Biomass Action Plan (Commission of the European Communities 2005) defines as biomass all organic plant and animal products used to produce energy. The Plan stated that an increase in the utilization of biomass as a renewable resource could bring more diversification in Europe's energy supply as well as reduction in greenhouse gas emissions. Further benefits could be new employment opportunities and potential lowering of the price of oil as a result of lower demand. The Commission identified three sectors in which biomass use should be prior, namely heat production, electricity production and transport. In terms of agriculture, the reform of the Common Agricultural Policy (CAP) introduced a special "aid for energy crops". It must be noticed that albeit increased production of biomass for energy has the potential to offset substantial use of fossil fuels, it also risks sacrificing natural areas to managed monocultures, contaminating waterways with agricultural pollutants, threatening food supplies or farm lifestyles through competition for land and increasing net emissions of carbon to the atmosphere, as a consequence of increased deforestation or energy-demanding manufacturing technologies (Field *et al.* 2008). For more, many biomass utilizations are actually not effective enough: e.g. the entire global harvest of corn (700 million tons, USDA 2007) converted to ethanol with current technology would yield enough transportation fuels to supply only 6% of the global gasoline and diesel demand (BP 2007). Furthermore, the fossil energy required to produce this amount of ethanol would represent 80–90% of the energy stored in the ethanol (Farrell *et al.* 2006, Hill *et al.* 2006). For this reasons, politicians are actually addressing more efforts to promote research on biomass utilization as a clean and effective energy source.

1.4 An ecological dilemma: searching for the missing link between biomass and biodiversity.

Many authors have investigated the mechanism whereby biodiversity varies between habitats differing in productivity as it is a 'missing link' between ecological and evolutionary theory with vital implications for biodiversity conservation, management

and ecosystem services. Studies have focused on both natural and experimental communities, often with contrasting results. Authors studying natural communities, in fact, stated that a unimodal, 'humped-back' relationship, with biodiversity greatest at intermediate productivities, is evident when plant (Grime 1973, Al-Mufti *et al.* 1977, Moore & Keddy 1989, Guo & Berry 1998, Molino & Sabatier 2001, Olde Venterink *et al.* 2001, Allcock & Hik 2003, Cornwell & Grubb 2003, Bhattarai *et al.* 2004, Espinar 2006), animal (Aronson & Precht 1995, Chown & Gaston 1999, Cornell & Karlson 2000, Fock 2009) and microbial (Grime & Pierce 2012) communities are compared across productivities. Adler *et al.* (2011), on the contrary, have studied natural plant communities worldwide concluding that only a "weak and variable" relationship between biomass and biodiversity exists. A recent meta-analysis from Cardinale *et al.* (2011) using experimental plant cultures and specifically excluding observations from wild systems, found out a linear relationship between biomass and biodiversity.

In the next chapters results from a research concerning with this ecological dilemma are reported: chapter two focuses (with a functional and evolutionary perspective) on mechanisms that lead to changes in species richness in natural and semi-natural habitats of different productivity; chapter three shows results in terms of biomass and biodiversity from experimental sowings of pasture communities differing in seed rain and substrate nitrogen content; chapter four proposes a new method to estimate herbaceous biomass non destructively; chapter five presents an attempt to empirically assess Ecosystem Services using data of plant functional traits, biomass production and floristic features.

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2 - Diversity in evolutionary strategies and trait values favours species richness in habitats of moderate biomass production

2.1 Introduction

The relationship between biodiversity and productivity is a subject of both great import and great controversy in contemporary ecology. Most general theory has been developed based on empirical evidence from plant assemblages, for the simple reason that plants are sessile and form extensive communities which are easily studied in their entirety (Harper 1977). Controversy has arisen in part from the contrast between the biodiversity/productivity relationships observed in natural plant communities and those recorded in experimental studies in which groups of species are raised together from seed. For example, the most recent meta-analysis of diversity/productivity relationships (Cardinale *et al.* 2011) focussed on experimental plant cultures and specifically excluded observations from wild systems, but also stated that this approach provided insufficient evidence to address the question of how realistically experimental results reflect ecosystems in nature. Indeed, experimental cultures constructed by sowing seeds of a small number of species on bare substrate do not reflect the selection pressures operating when seeds fall amongst established vegetation, which is an altogether different environment in which to survive.

Studies of biodiversity/productivity relationships in nature often rely on large but incomplete datasets that do not cover the entire productivity range, and continue to fuel controversy. For example, Adler *et al.* (2011) concluded that relationships between diversity and productivity are “weak and variable”, but more than 90 per cent of their sampling points had low biomasses of less than 500 g m⁻², and the highest value was only 1534 g m⁻²: in stark contrast to data previously published by members of this research group (Grace *et al.* 2007) showing the full biomass range up to 4000 g m⁻² in species-poor wetland communities. A reliance on data mainly from vegetation of “low stature” (Adler *et al.* 2011) has drawn the criticism that an insufficient productivity range was studied, alongside a range of other methodological shortcomings such as the specific exclusion of high biomass/low diversity communities from parts of the analysis (Grime & Pierce 2012, Fridley *et al.* 2012).

When wild communities are compared across a broad productivity range a humped-back or unimodal relationship between the maximum potential biodiversity (usually measured as species/taxonomic richness) and the amount of above ground biomass is the most common type of relationship (Mittelbach *et al.* 2001). Indeed, when wild communities are compared over broad productivity ranges, rather than within communities over restricted productivity ranges (Guo & Berry 1998), the

humped-back curve is a global phenomenon, with ambiguous or linear relationships in greater evidence when this distinction is not made (Grime & Pierce 2012). Originally observed by Grime (1973) and Al-Mufti *et al.* (1977), humped-back curves have now been recorded throughout Europe (Cornwell & Grubb 2003) and for a range of plant communities including Australian *Eucalyptus* woodlands (Allcock & Hik 2003), Himalayan mountain grassland (Bhattarai *et al.* 2004), Mediterranean wetlands (Espinar 2006), tropical rainforests (Connell 1978, Molino & Sabatier 2001), and wetland and meadow communities (Moore & Keddy 1989, Olde Venterink *et al.* 2001).

The humped-back model (HBM) suggests that no potential exists for high biodiversities in habitats with either extremely high or low biomass production, whilst biodiversity may reach the greatest values at intermediate productivities, although this potential is not always achieved. Indeed, when biomass is collected in years that deviate markedly from climatic norms a humped-back relationship may not be evident, but reappears when conditions return to those more typical and favourable for the growth of local vegetation (Laughlin & Moore 2009). As such, the model describes an upper limit to biodiversity-productivity relationships, or a 'filled' (Olde Venterink *et al.* 2001) or 'saturated' (Houseman & Gross 2006) unimodal curve. As a maximum potential relationship, the humped-back curve suggests that biodiversity may potentially reach the greatest values at intermediate productivities, although this potential is not always achieved, but that there is no potential for high biodiversities at extremes of biomass production.

Crucially, and central to the present study, although the existence of this phenomenon in nature is now well supported, the mechanism by which it arises remains enigmatic. The main implication of the humped-back model is that in extreme environments (even extremely productive and abiotically benign environments) organisms exhibit a high degree of adaptive/evolutionary specialisation in order to survive. In contrast, the greatest diversities potentially represent a wider variety of evolutionary strategies occupying the relatively heterogeneous fine-scale niches that are exposed by the exclusion of large monopolists at intermediate levels of disturbance or stress (Grime & Pierce 2012). The hypothesis of adaptive specialisation at productivity extremes applies as much to high productivity environments as it does to abiotically harsh environments because organisms specialised for resource acquisition are more likely to monopolise resources and exclude other species (Grime 2001).

The hypothesis that diversity in suites of life-history traits is a principal constituent of the mechanism underpinning the humped-back curve could be confirmed by empirical findings that diversity in evolutionary strategies, and indeed functional trait values, is most extensive at intermediate productivities. Navas & Violle (2009) provide

a hint that this may be the case: they examined *functional diversity* (i.e. diversity in trait values) in a single trait, plant height, along a productivity gradient, and found that diversity in this trait was greatest at intermediate productivities. From hereon this shall be referred to as 'trait diversity'.

Thus the present study aims to investigate the hypothesis that, for herbaceous communities characteristic of a range of bioclimatic zones in Europe, a humped-back diversity/biomass curve exists for which greater biodiversity is associated with greater diversity in a range of morpho-functional trait values and in the overall adaptive strategies that emerge from these suites of traits. Variability in the values of a range of traits and strategy variation were determined within a wide variety of natural herbaceous plant communities characteristic of lowland, mid-elevation and high-elevation Europe. This was supplemented by measurements of above-ground peak biomass production for each community, to provide a definitive test of the hypothesis that humped-back biodiversity/productivity relationships are an emergent property of diversity in suites of functional traits, or evolutionary strategies.

2.2 Methods

2.2.1 Data collection

We recorded taxonomic identities and quantified species relative abundance, peak above ground dry matter (i.e. standing crop plus litter harvested at the annual maximum of biomass production at each site; Grime 1973; Al-Mufti *et al.* 1977) and adaptive trait values (listed below) for 39 natural and semi-natural herbaceous communities selected to represent a diverse range of seasonal, elevational and ecological conditions typical of continental Europe. We worked with plant communities for the simple logistical reason that 'plants stand still and wait to be counted' (Harper 1977). This allowed inclusion of a wide range of communities at contrasting productivities, with geographic locations spanning the Po Plain of Lombardy to the high Alpine zone of Northern Italy (see Figure 2.2.1.1 and Table 2.2.1.1, including geographic locations and elevations recorded using a Garmin eTrex Summit GPS receiver (with an electronic barometer), alongside details of the particular plant communities investigated at each site). Vegetation was assigned a physiognomic description based on comparison of the dominant species with those of vegetation types recorded in Mucina *et al.* (1993a,b), Grabherr & Mucina (1993) and Aeschimann *et al.* (2004); (Table 2.2.1.1).

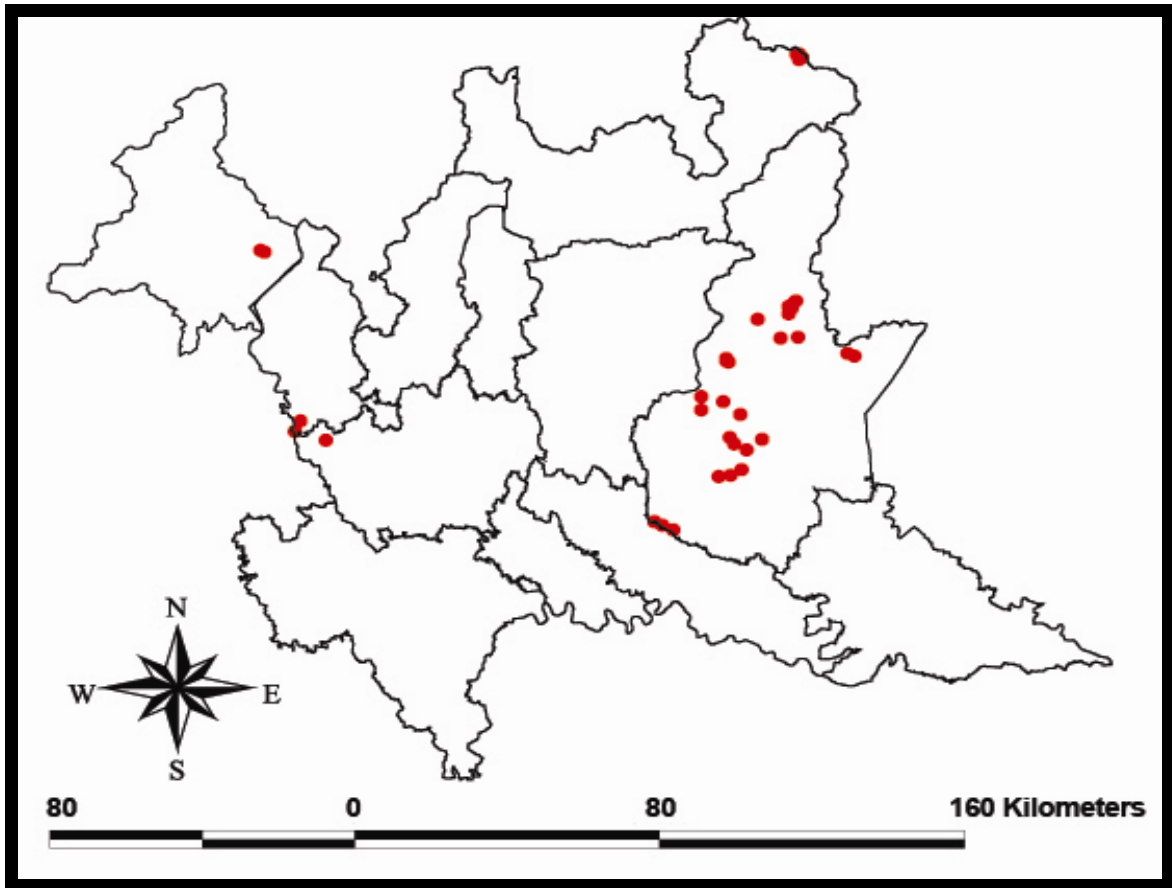


Fig. 2.2.1.1: geographic distribution of investigated herbaceous plant communities.

Table 2.2.1.1: locations and physiognomic descriptions of the plant communities sampled. Nomenclature follows Conti *et al.* (2005).

Survey no.	Survey Date	North Coordinate	East coordinate	Elevation (m a.s.l.)	Slope (°)	Aspect (°)	Physiognomic description
1	7/5/2009	45°32'9.1"	10°11'12"	130	0	0	Abandoned grassland dominated by <i>Poa pratensis</i> L.
2	14/5/2009	45°27'44.7"	10°7'55.2"	92	0	0	Wasteland dominated by <i>Ranunculus sardous</i> Crantz
3	25/6/2009	45°45'48.8"	10°34'20.1"	1050	5	195	Verge dominated by <i>Pteridium aquilinum</i> (L.) Kuhn subsp. <i>Aquilinum</i>
4	4/7/2009	45°53'10.3"	10°22'31.6"	1770	0	0	Nitrophilous meadow dominated by <i>Poa annua</i> L.
5	12/7/2009	45°48'18.2"	10°20'48.7"	1000	5	220	Margins dominated by <i>Stachys sylvatica</i> L.
6	21/7/2009	46°31'09.8"	10°25'46.7"	2646	20	279	Discontinuous grassland dominated by <i>Luzula alpinopilosa</i> (Chaix) Breistr. subsp. <i>Alpinopilosa</i>
7	22/7/2009	46°31'54.7"	10°25'16.5"	2608	25	285	Dwarf shrub vegetation dominated by <i>Kalmia procumbens</i> (L.) Gift, Kron & Stevens ex Galasso, Banfi & F. Conti
8	23/7/2009	46°31'05"	10°25'47.1"	2600	12	330	Grassland dominated by <i>Carex curvula</i> All.
9	23/7/2009	46°31'26.6"	10°26'16.5"	2673	10	5	Dwarf shrub vegetation dominated by <i>Salix herbacea</i> L.
10	1/10/2009	45°51'15.5"	10°16'17.1"	1733	5	60	Peaty slopes dominated by <i>Eriophorum angustifolium</i> Honck.
11	1/10/2009	45°51'14.6"	10°16'17.5"	1742	5	70	Peatland dominated by <i>Trichophorum cespitosum</i> (L.) Hartm.

12	1/10/2009	45°51'14.5"	10°16'17.1"	1742	5	70	Peatland dominated by <i>Carex panicea</i> L.
13	10/4/2010	45°39'28.9"	10° 4'35.1"	504	5	205	Wasteland dominated by <i>Capsella grandiflora</i> (Fauché & Chaub.) Boiss.
14	26/4/2010	45°33'06.1"	10°10'18.4"	148	0	0	Understorey dominated by <i>Ranunculus ficaria</i> L. and <i>Anemone nemorosa</i> L.
15	6/5/2010	45°19'01.5"	9°58'32.6"	52	0	0	Wasteland dominated by <i>Stellaria media</i> (L.) Vill.
16	24/5/2010	45°31'11.8"	10°13'40.1"	130	0	0	Wasteland dominated by <i>Avena fatua</i> L.
17	28/5/2010	45°19'39.5"	9°56'26"	44	0	0	Wasteland dominated by <i>Saxifraga tridactylites</i> L.
18	1/6/2010	45°20'11.4"	9°54'40.8"	39	0	0	River margin dominated by <i>Elymus athericus</i> (Link) Kerguëlen
19	9/6/2010	45°35'56.6"	8°43'27.2"	207	0	0	Meadow dominated by <i>Filago minima</i> (Sm.) Pers.
20	29/6/2010	45°32'45.6"	10°16'45.7"	790	20	150	Meadow dominated by <i>Bromus erectus</i> Huds.
21	5/7/2010	45°54'00.2"	10°24'12.4"	2010	15	185	Pasture grassland dominated by <i>Horminum pyrenaicum</i> L.
22	5/7/2010	45°53'46"	10°23'51.9"	2020	30	250	Pasture grassland dominated by <i>Carex sempervirens</i> Vill.
23	9/7/2010	45°44'48.8"	10°09'56.6"	1571	0	0	Seasonal livestock enclosure dominated by <i>Rumex alpinus</i> L.
24	12/7/2010	45°38'41.4"	10°09'00.3"	720	15	198	Meadow dominated by <i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. & C. Presl
25	15/7/2010	45°44'45.2"	10°10'14.7"	1492	30	235	Grassland dominated by <i>Festuca paniculata</i> (L.) Schinz & Thell. subsp. <i>Paniculata</i>
26	19/7/2010	45°37'25.1"	10°04'36.1"	190	0	0	Wasteland dominated by <i>Sorghum halepense</i> (L.) Pers.
27	22/7/2010	45°44'56"	10°09'44.6"	1621	10	190	Meadow dominated by <i>Phleum alpinum</i> L.
28	4/8/2010	45°52'01.1"	10°22'39.5"	2150	5	300	Pasture dominated by <i>Nardus stricta</i> L.
29	4/8/2010	45°52'46.3"	10°23'17.1"	1890	25	266	Stream margin dominated by <i>Senecio alpinus</i> (L.) Scop.
30	6/8/2010	45°45'18.7"	10° 9'50.12"	1780	20	260	Pasture dominated by <i>Geum montanum</i> L.
31	18/8/2010	45°48'22.8"	10°24'26.1"	1726	15	74	Grassland dominated by <i>Sesleria caerulea</i> (L.) Ard.
32	31/8/2010	45°27'20"	10°10'18.1"	97	0	0	Wasteland dominated by <i>Setaria viridis</i> (L.) P. Beauv.
33	15/9/2010	46°01'52.7"	8°36'62.4"	1018	10	100	<i>Pteridium aquilinum</i> (L.) Kuhn subsp. <i>aquilinum</i> stand
34	15/9/2010	46°02'11.2"	8°35'19.4"	1380	30	165	Abandoned oldfield meadow dominated by <i>Molinia caerulea</i> (L.) Moench subsp. <i>arundinacea</i> (Schrank) K. Richt.
35	29/9/2010	45°28'03.1"	10°12'25.7"	95	0	0	Wasteland dominated by <i>Abutilon theophrasti</i> Medik.
36	11/10/2010	45°36'34.3"	10°12'25.3"	211	0	0	Wasteland dominated by <i>Helianthus tuberosus</i> L.
37	13/10/2010	45°32'57.9"	8°48'40.7"	180	0	0	Wasteland dominated by <i>Artemisia verlotiorum</i> Lamotte
38	13/10/2010	45°34'15.1"	8°42'22.2"	192	0	0	Margin dominated by <i>Solidago canadensis</i> L.
39	28/10/2010	45°45'20.8"	10°35'47.5"	602	1	272	Stream margin dominated by <i>Fallopia japonica</i> (Houtt.) Ronse Decr.

For each community a standard quadrat size of 16 m² was employed during floristic surveys and point analysis (Fig. 2.2.1.2), during which counts of species in contact with a needle inserted at 75 points on a grid within the survey area provided a measure of species relative abundance (e.g. Pierce *et al.* 2007a; Cerabolini *et al.* 2010a).



Figure 2.2.1.2: standard quadrat size of 16 m² employed during floristic surveys and point analysis.

Simpson's reciprocal diversity index was calculated, as described previously (Pierce *et al.* 2007a; see also Simpson 1949), using these data. Sampling and subsequent analysis of functional traits were carried out for species touched by the needle during point analysis four or more times. Traits were measured from six replicate individuals, avoiding damaged or diseased plants. Canopy height (CH) and lateral spread (LS) were measured directly in the field, and leaves were collected from these plants and taken to the laboratory for the measurement of leaf fresh weight (LFW; i.e. saturated or turgid fresh weight), leaf dry weight (LDW) and leaf area (LA), using standard methods (Hodgson *et al.* 1999; Cornelissen *et al.* 2003). Leaf dry matter content (LDMC) and specific leaf area (SLA) were then calculated (Pierce *et al.* 2007a). Phenological traits, measured as the month of flowering onset for each species (flowering start, FS) and the duration of flowering, in months, (flowering period, FP) were used alongside leaf and whole-plant traits to calculate adaptive strategies, using

CSR classification (Hodgson *et al.* 1999) as detailed and justified previously (Caccianiga *et al.* 2006; Pierce *et al.* 2007a, b) and as applied to over a thousand plant species *in situ* in a range of habitats throughout Europe (Simonová & Lososová 2008; Massant *et al.* 2009; Cerabolini *et al.* 2010a, b; Kiliç *et al.* 2010; Navas *et al.* 2010). Note that 19 tertiary CSR strategy categories are recognised by Hodgson *et al.* (1999), and the trait “number of CSR strategies” in the present study reflects the categorisation of species between these 19 strategies.

Biomass was sampled at the peak of biomass production, between April and October, during 2009 to 2010. Dates as early as April were necessary for communities of therophytes on disturbed ground at low elevations that peaked extremely early, but these communities were nonetheless sampled at peak biomass and the fruiting phase of the majority of species within the community. Biomass was sampled according to Al-Mufti *et al.* (1977): i.e. standing crop plus litter was harvested using a battery-powered clipper and scissors from three 0.25 m² sub-plots, with data combined to calculate the mean dry weight per m² at each site. Dry weight was measured following drying in a forced-air oven at 95°C for eight hours.

2.2.2 Ordination and statistical techniques

Principal components analysis (PCA) was conducted using MSVP 3.13o software (Kovach Computing Services, Anglesey, Wales). Correlations between multivariate analysis axes and factors/trait scores were tested using Spearman rank correlation (Systat 12, SPSS Inc., Chicago, IL, USA) following ranking of data within the species × traits matrix. The critical values of the Spearman rank correlation coefficient (ρ) previously calculated by Zar (1972) were consulted to determine significance at the $p \leq 0.001$, $p \leq 0.01$, and $p \leq 0.05$ levels.

Peak curves were fitted to scatter plots using the Lorentzian 3-parameter option of SigmaPlot v10 (Systat Software Inc., Chicago, IL, USA). The humped-back model suggests that the curve should be an upper limit to biodiversity (i.e. the humped-back curve should be filled underneath, rather than an average fitted through the dataset), and thus fitting a curve to all the data present will not accurately fit the upper boundary, although it may determine the presence of a peak. Thus, for each plot an additional curve was fitted to maxima along the biomass gradient, these maximal data points defined as the three highest values present within each 500 g m⁻² interval class of dry matter (i.e. within 0-500 g m⁻², 500-1000 g m⁻², 1000-1500 g m⁻², etc.). Trait diversity was calculated as the variance (the sum of squared deviations from the mean) of trait values within each community.

2.3 Results

Species richness, Simpson's reciprocal diversity index, and the number of evolutionary strategies (CSR strategies) all exhibited statistically significant unimodal relationships with peak above ground dry matter ($R^2 = 0.831, 0.778, 0.921$, respectively, $P \leq 0.006$; Fig. 2.3.1a,b,c). Indeed, the greatest species richness (41-42 species per 16 m^{-2} plot) was apparent at low to intermediate biomass (480-910 g m^{-2} of peak above ground dry matter) and diminished towards both the lowest and highest biomasses (i.e. 5 species at 101 g m^{-2} , and 1 species at 2880 g m^{-2} , respectively; Fig. 2.3.1a).

The first two axes of a principal components analysis (Fig. 2.3.2) accounted for over 53.9 % of the variability in the data, and demonstrated a principal component (PCA1) that was significantly positively correlated, at the $P \leq 0.001$ level, with species richness ($\rho = 0.918$, $n = 39$), the number of tertiary CSR strategies ($\rho = 0.888$), Simpson's reciprocal diversity index ($1/D$) ($\rho = 0.833$), and diversity in all traits apart from canopy height and leaf dry weight (i.e. leaf dry matter content diversity, lateral spread diversity, flowering start diversity, lateral spread diversity, specific leaf area diversity and flowering period diversity, and the degree of S-selection). Factors correlated negatively with PCA1 (at the $P \leq 0.01$ level or above) included peak biomass ($\rho = -0.397$), canopy height ($\rho = -0.692$), leaf dry weight ($\rho = -0.497$), specific leaf area ($\rho = -0.320$) and the degree of C-selection ($\rho = -0.645$), with relatively similar trait values apparent (i.e. diversity in these traits was not correlated negatively with PCA1; Fig. 2.3.2).

PCA2 (Fig. 2.3.2) was significantly and positively correlated at the $P \leq 0.001$ level with the degree of R-selection, flowering period, specific leaf area and flowering period diversity, and negatively correlated with lateral spread, leaf dry matter content, peak biomass, flowering start, C-selection and leaf dry weight.

When Spearman rank correlation coefficients were calculated between species richness and all other variables (Table 2.3.1) the factor most highly and positively correlated with species richness was the number of CSR strategies within the community ($\rho = 0.920$). Diversity in all the plant traits measured apart from canopy height was highly and positively correlated with species richness, although absolute values were not (Table 2.3.1). The plant traits most negatively correlated with richness were the size-related traits canopy height and leaf dry weight ($\rho = -0.528$ and -0.318 , respectively) and the degree of C-selection (Table 2.3.1).

Diversity in LDMC, LS and FS (i.e. the three trait diversities shown by the PCA and Spearman rank correlation to be most highly correlated with species richness; Fig. 2.3.2; Table 2.3.1) reached the greatest values at intermediate biomasses of between

500 to 1000 g m⁻² (Fig. 2.3.3), mirroring the humped-back biodiversity/biomass curves shown in Fig. 2.3.1. Canopy height exhibited a significant positive linear correlation with biomass production; (Fig. 2.3.4).

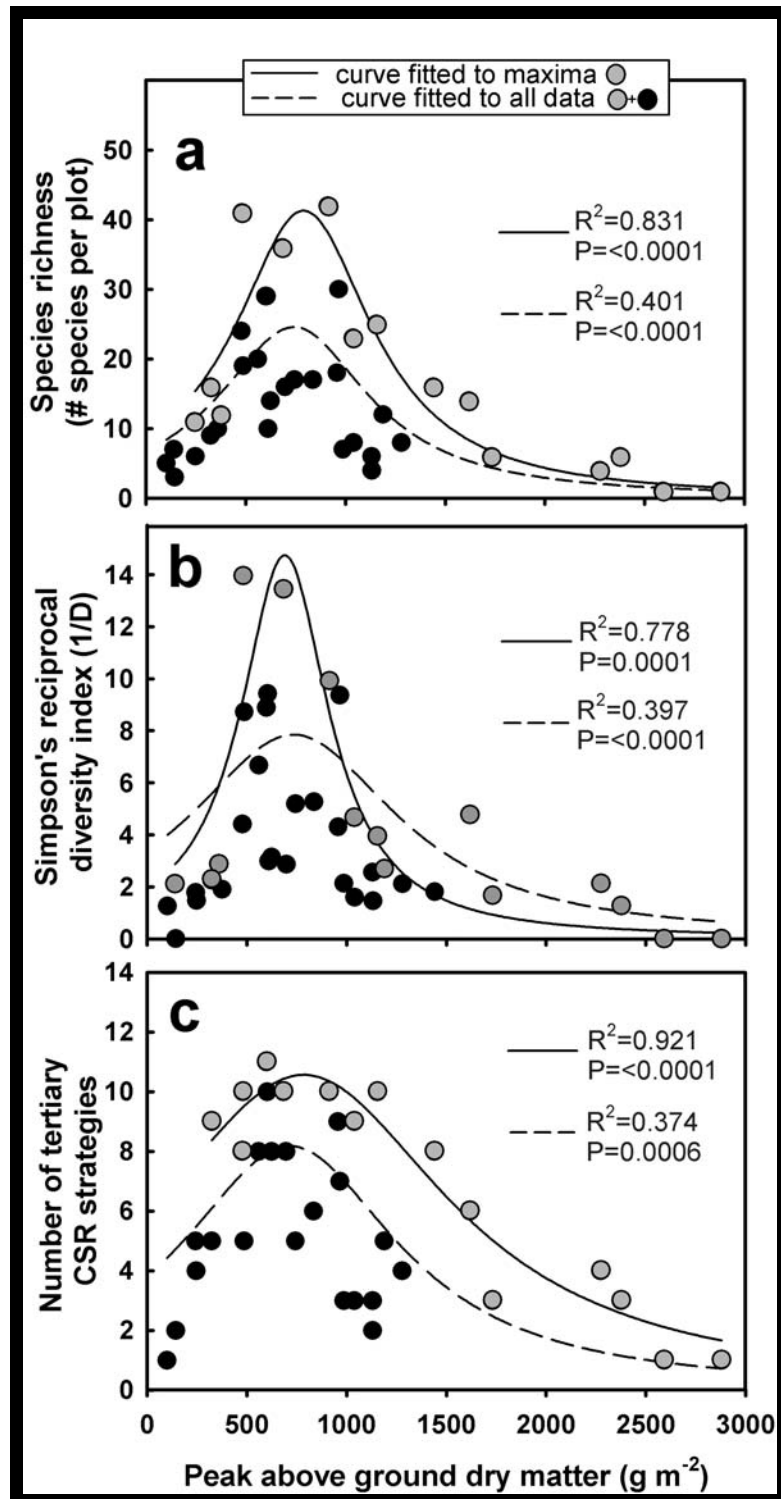


Fig 2.3.1: changes in biodiversity along the gradient of peak above ground dry matter (standing crop + litter) for 39 herbaceous plant communities: a). species richness (number of species per 16 m² plot), b). Simpson's reciprocal diversity index (1/D), c). adaptive strategies (number of tertiary CSR plant strategies per 16 m² plot). Curves are fitted either to all data (black and grey points), or to maxima only (grey points): the latter defined as the three highest values within each 500 g m⁻² interval along the gradient of peak above ground dry matter.

Table 2.3.1: Spearman's correlation coefficients (ρ) between species richness and other measures of biodiversity (Simpson's reciprocal diversity index, the number of tertiary CSR strategies, and trait diversities), for 39 herbaceous plant communities (i.e. $n = 39$). *** denotes a significant correlation at the $p \leq 0.001$ level, ** $p \leq 0.01$, * $p \leq 0.05$, and n.s. denotes no significant correlation. Correlation coefficients are ranked from the most highly positive correlation to the most negative correlation with species richness.

	Species richness	
Number of CSR strategies	0.920	***
Simpson's reciprocal diversity index (1/D)	0.902	***
Leaf Dry Matter Content diversity	0.848	***
Lateral Spread diversity	0.756	***
Flowering Start diversity	0.722	***
Specific Leaf Area diversity	0.704	***
Degree of S-selection	0.539	***
Flowering Period diversity	0.487	***
Leaf Dry Weight diversity	0.393	**
Leaf Dry Matter Content	0.142	n.s.
Canopy Height diversity	0.110	n.s.
Flowering Start	0.070	n.s.
Lateral Spread	-0.056	n.s.
Degree of R-selection	-0.057	n.s.
Specific Leaf Area	-0.180	n.s.
Peak Above Ground Dry Matter (biomass)	-0.191	n.s.
Flowering Period	-0.196	n.s.
Leaf Dry Weight	-0.318	*
Degree of C-selection	-0.448	**
Canopy Height	-0.528	***

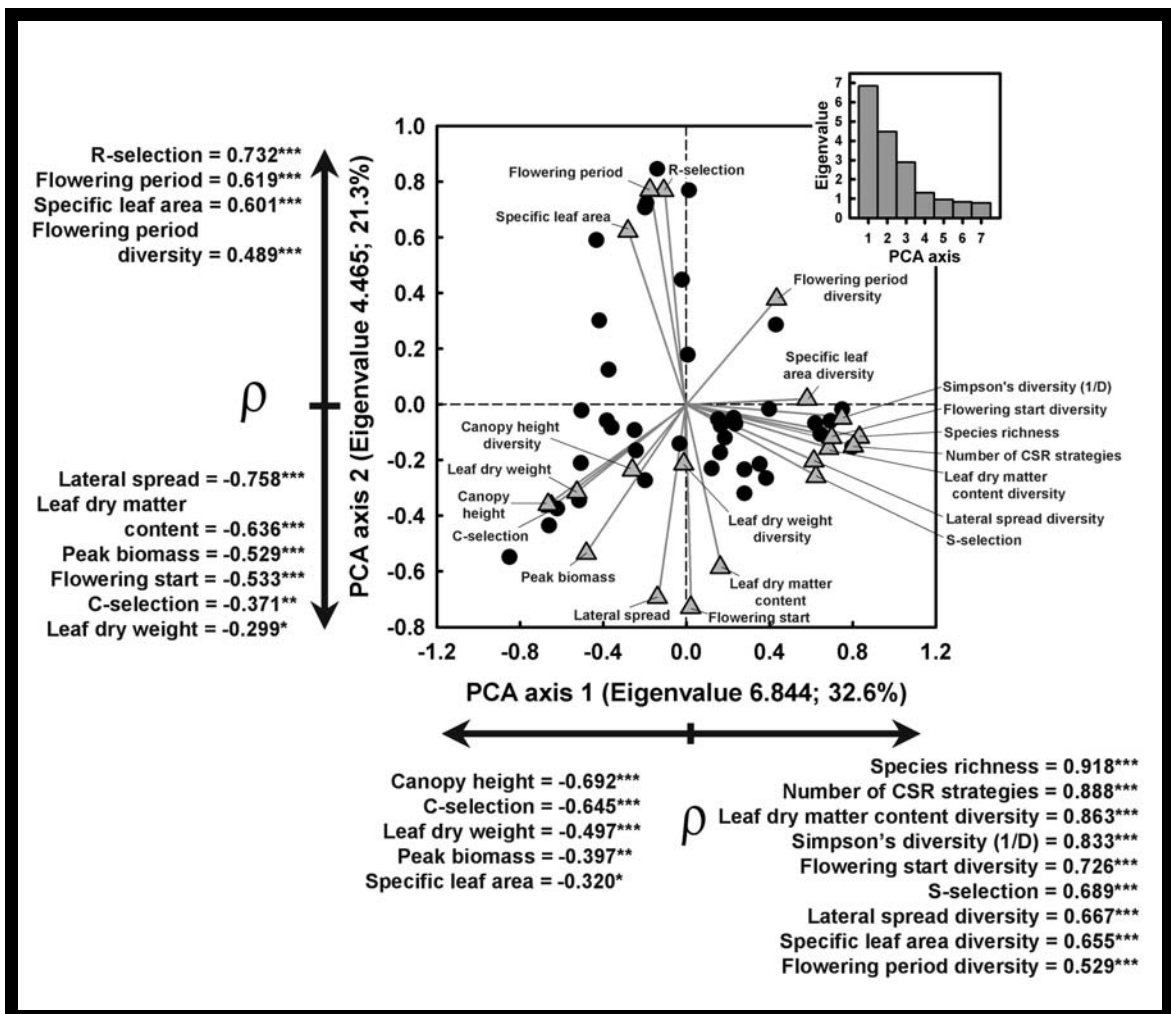


Fig. 2.3.2: principal components analysis (PCA) showing the main axes of variability in the adaptive traits of herbaceous plant species from 39 communities in relation to peak biomass (peak above ground dry matter) and different measures of biodiversity (species richness, trait functional diversity and extent). Significant correlations between the main axes of trait

variability (PCA1 and PCA2) and variables are shown, as determined by Spearman's correlation coefficient (ρ) where *** denotes a significant correlation at the $p \leq 0.001$ level, ** $p \leq 0.01$, * $p \leq 0.05$, and factors are presented ranked in descending order of their respective correlation coefficient values. Inset, top right, shows the Eigenvalues of all PCA axes, including those beyond PCA2.

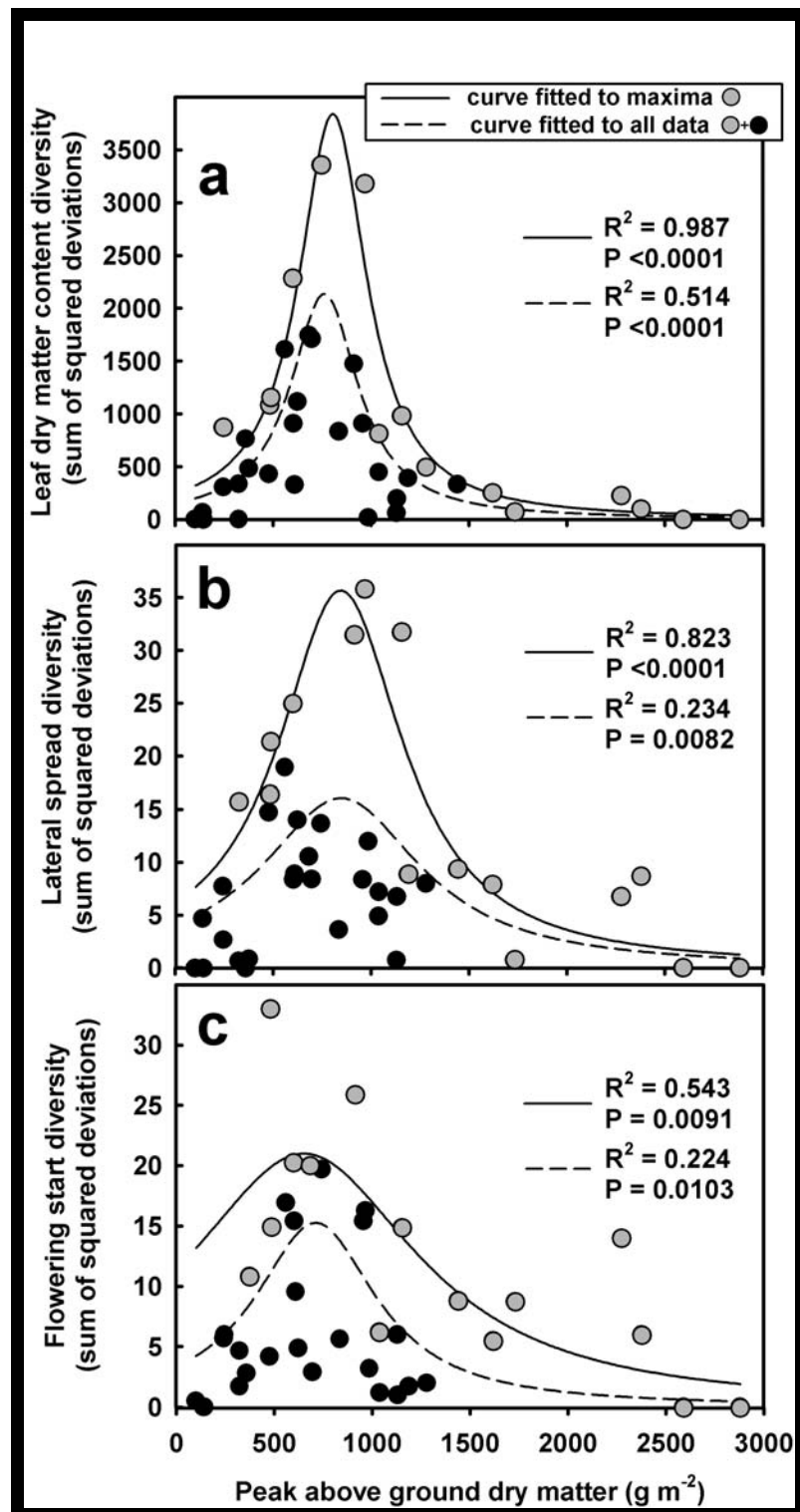


Figure 2.3.3: diversity in leaf dry matter content, lateral spread and flowering start within communities along a gradient of peak above ground dry matter. Curves are fitted either to all data (black and grey points), or to maxima only (grey points): the latter defined as the three highest values within each 500 g m^{-2} interval along the gradient of peak above ground dry matter.

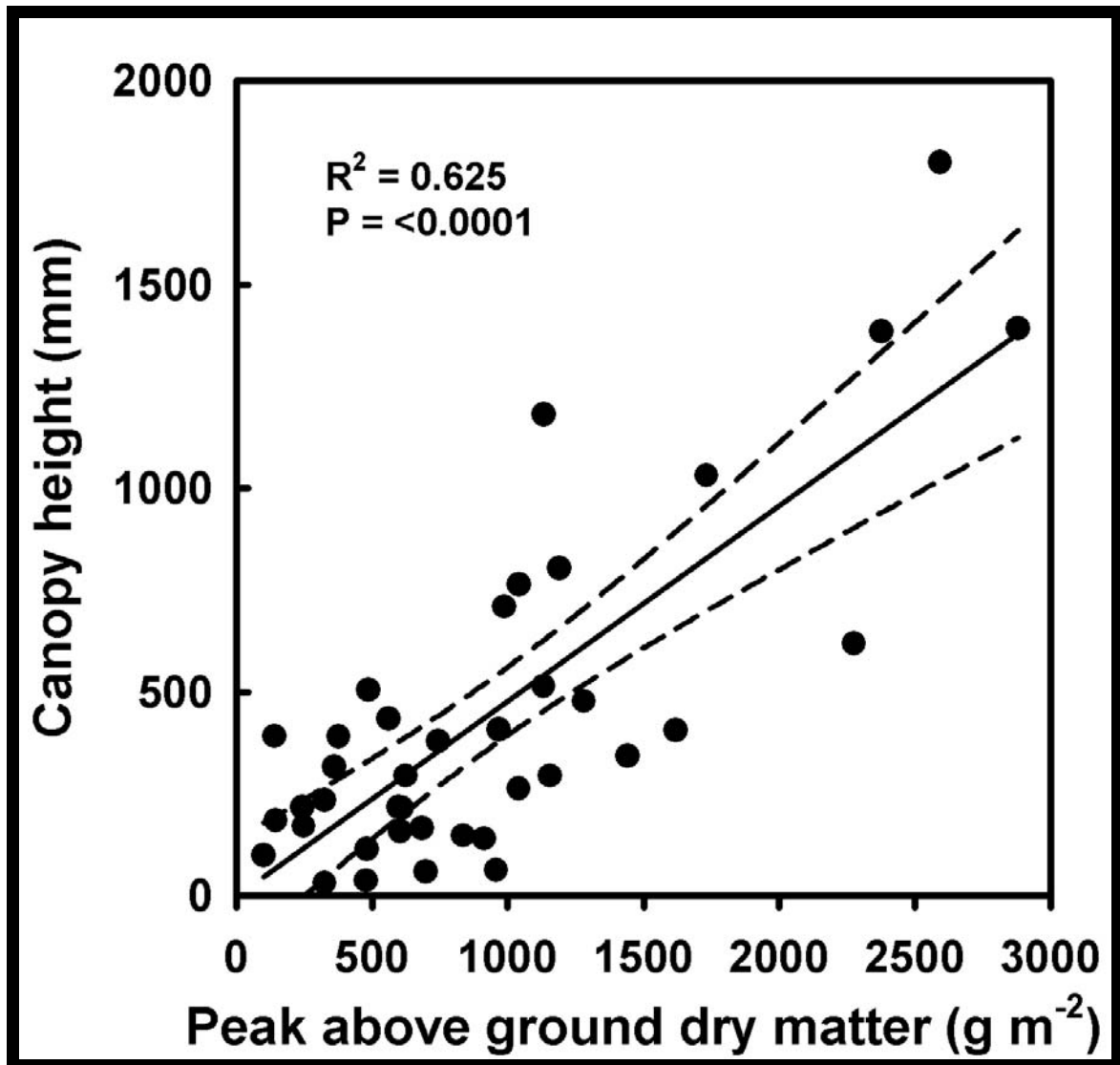


Figure 2.3.4: the relationship between canopy height and peak above ground dry matter for 39 herbaceous plant communities.

2.4 Discussion

Our finding that species richness peaked at just over 500 g m⁻² of biomass precisely matches the peak found by Al-Mufti *et al.* (1977) and other authors (e.g. Rapson *et al.* 1997), and the extent of values, ranging up to almost 3000 g m⁻², was slightly greater (although not the highest ever recorded; Grace *et al.* 2007). Thus we can have a high degree of confidence that the humped-back curve recorded in our study encompasses a full range of productivities and mirrors curves found to date in other parts of Europe and in North America. Crucially, previous studies have not adequately investigated the character of species, in terms of functional traits, functional diversity and adaptive strategies, along this gradient. Our results demonstrate, first and foremost, a highly significant positive correlation between species richness and the number of CSR strategies in the community (Table 2.3.1), and that the factors most antagonistic to

species richness, and closely associated with biomass production, are large size and competitive ability (the degree of C-selection). This strongly supports the hypothesis that the humped-back curve arises due to the extreme adaptive specialisation required for survival at productivity extremes, and greater variability in both trait values and evolutionary strategies at intermediate productivities. Thus evolutionary divergence in the manner in which resources are partitioned between life-history traits implicated in competitive ability, stress-tolerance and regeneration is central to biodiversity creation, *sensu* Grime & Pierce (2012).

As canopy height was positively correlated with biomass production (Fig. 2.3.4) maximisation of productivity and the character of the taxa present appear to be associated in a relatively straightforward manner with size and competitive ability. Within communities, taxonomic diversity depends more on diversity in resource economics and regeneration traits, particularly for relatively S-selected species in the communities under study here (Fig. 2.3.2; Table 2.3.1).

These results for plant communities are likely to be of much wider relevance. A humped-back relationship is also apparent for coral diversity (Connell 1978, Aronson & Precht 1995, Cornell & Karlson 2000), the diversity of Procellariiform birds in response to ocean surface productivity (Chown & Gaston 1999); it describes changes in the diversity of bathypelagic (deep-sea) fishes along productivity gradients encompassing entire oceans (Fock 2009) and even the relationship between soil microbial diversity and soil fertility (reviewed by Grime & Pierce 2012). Large size achieved early in development is a widespread trait of animals for which maximisation of the ability to gather resources in productive habitats is crucial to survival, such as whale sharks, rorquals, and the common hippopotamus (reviewed by Grime & Pierce 2012), in a similar manner to the large size (canopy height and leaf mass) that allows plants to maximise resource acquisition and compete effectively in high productivity/low diversity habitats. This is in contrast to S-selected organisms that may attain large size but for which size is neither an immediate advantage nor essential to survival, and is accrued gradually over longer life spans in unproductive habitats (Grime & Pierce 2012). Size traits, when combined with economics traits, delimit an adaptive space within which organisms with highly contrasting growth forms can be ordinated and compared in terms of CSR strategies (Pierce *et al.* 2012).

CSR strategies are also applicable to organisms other than plants. Grime & Pierce (2012) reviewed the life-history traits of organisms throughout the tree of life and concluded that a universal trade-off in resource investment has resulted in three main directions of adaptive specialisation for all organisms, favouring either resource acquisition in consistently productive niches, maintenance of metabolic performance in variable and unproductive niches, or rapid completion of the lifecycle and regeneration

as an evolutionary response to frequent lethal events (predation, biomass destruction). Such a three-way trade-off has been determined empirically using multivariate analysis of life-history traits for fishes (Winemiller & Rose 1992; Winemiller 1992, 1995), birds and mammals (Gaillard *et al.* 1989), and CSR strategies have now been used in the interpretation of organisms as diverse as coral holobionts (Murdoch 2007), butterflies (Dennis *et al.* 2004), ants (Andersen 1995), echinoderms (Lawrence 1990), birds (Hodgson 1991), phytoplankton (Reynolds 1984, 1991; Elliott *et al.* 2001; Weithoff *et al.* 2001; Bonilla *et al.* 2005; König-Rinke 2008), lichens (Rogers 1988), and fungi (Pugh 1980). Grime & Pierce (2012) also discuss evidence, based on physiology and life-history traits, for the operation of the three-way trade-off amongst the Squamata, Amphibia, Insecta, Aracnida, Crustacea, Mollusca, Annelida, Archaea, various clades of Eubacteria and even amongst the viruses. Thus CSR plant strategy theory (Grime 2001) is now regarded as a specialised field under the wider umbrella of *universal adaptive strategy theory* (UAST; Grime & Pierce 2012). Because humped-back curves and CSR strategies are both extremely widespread phenomena, our study of plant communities may be representative of a general condition whereby the evolution of taxonomic diversity is favoured by intermediate productivities, where precise, fine-scale niches are not obscured by the large-scale foraging of giant monopolists and the abiotic environment is not so harsh as to limit adaptive specialisation.

In synthesis, our data provide the first empirical support, in wild communities, for the hypothesis that biodiversity is limited at productivity extremes by a requirement for extreme adaptive specialisation, whilst divergence in resource economics and reproductive timing at intermediate productivities creates the potential for the survival of a greater range of species. The conclusion that diversity in resource economics and reproductive timing are key to taxonomic diversity creation is likely to be of widespread relevance, particularly for biodiversity conservation. For instance, the majority of rare or endangered species in herbaceous plant communities are found at intermediate productivities (Schaffers 2002) where management regimes involving cutting, mowing or grazing prevent dominance by large, C-selected forms. The present study demonstrates the mechanism whereby a greater range of phenotypes can survive, and biodiversity is favoured, where large, fast-growing species are prevented from attaining dominance and extreme adaptation to a harsh abiotic environment is not a prerequisite for survival.

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3 – Effects of substrate nitrogen content on biomass production, biodiversity and community dynamics in early stages of experimental sowings

3.1 Introduction

Humans have soon learned how to improve some plant species performances in terms of biomass production by providing soils with limiting resources as nutrients or water. It is quite obvious to think that, according to their physiological needs, single plant specimens should react thriving to the absence of limiting factors. Things get a little bit more complicated when we work with sets of individuals or sets of species living together. In fact we have to account for interactions between individuals and between different species that react in different ways and derive different benefits from greater resources availability. Shedding light upon consequences of changes in nutrients availability for plant communities has become of main concern as, since industrial revolution, global energy use and food production have increased nutrients input (especially nitrogen) to ecosystems worldwide (Clark *et al.* 2007; Galloway *et al.* 2008; Reay *et al.* 2008).

Many studies investigated plant communities dynamics in terms of physiological responses (namely biomass allocation patterns) to different degrees of resources availability. Tilman (1982, 1988) asserted that, in order to obtain a higher portion of one resource, plants must allocate more biomass to structures involved in the acquisition of that resource at the expense of allocation of biomass to structures involved in the acquisition of another resource. Fowler (1990) and Wilson & Shay (1990) supported this idea. Tilman's hypothesis has been tested in experiments with nitrogen addition resulting in decreased belowground biomass allocation but no change in total biomass allocation for most species (Wilson & Tilman 1991, 1993, 1995). Weiner (1990) stated that plants developing above ground structures larger than their neighbours' ones, obtaining advantages in light interception, do not seem to enjoy a similar disproportionate advantage in capturing belowground resources. For more, in a study with evergreen and deciduous heathland species (Aerts *et al.* 1991), both the evergreens *Erica tetralix* L. and *Calluna vulgaris* (L.) Hull and the perennial deciduous grass *Molinia caerulea* (L.) Moench allocated relatively more biomass to the roots at low nutrients supply. The idea that allocating more biomass into below ground structures should results in better performances according to environmental conditions is supported by Schwinning (1996) and Schwinning & Weiner (1998) that suggested the possibility that larger root systems would have a disproportionate advantage in a patchy soil environment because they should be more likely to encounter a high-

nutrient patch. These studies said that in nutrient-rich habitats (where limiting resource is mainly light) plants should allocate more biomass into above ground structures, while in nutrient-poor environments (where limiting resource is mainly substrate nutrients content) plants should allocate more biomass to roots, in both cases with no change in total biomass production. The idea behind is that the relative importance of above and below ground biomass allocation amount changes as plants must face an unavoidable trade-off between the abilities to acquire for above and below ground resources, as postulated by Tilman's resource ratio model (Tilman, 1988). Otherwise Grime (1974, 1979, 1988) suggested that, in nutrient-poor conditions, plant traits leading to a high nutrient retention would be far more important than a high ability for nutrient uptake, thus allocating a lot of biomass in roots is rather unimportant in nutrient-poor environments while more productive sites should exhibit greater overall rates of above and belowground biomass allocation. Grime's hypothesis was supported by some studies (Reader 1990; Campbell & Grime 1992). Both schools of thought, anyway, assumed that resource acquisition ability (above or below ground) goes hand in hand with biomass allocation patterns. Other studies shown instead that this ability, in particular for below-ground resources, also depends on other morphological characteristics, notably specific root length (Berendse & Elberse 1989; Olff *et al.* 1990; Aerts 1999; Aerts & Chapin, 2000).

Plants attitude towards resources acquisition (according to their availability) and its effect on populations and communities diversity have been the object of many other ecological studies. Many authors have collected data showing that increasing in substrate resources (and in particular nitrogen availability) results in declining species diversity (Bobbink *et al.* 1998; Stevens *et al.* 2004; Suding *et al.* 2005; Clark *et al.* 2007; Xia & Wan 2008; Reich 2009; Kleijn *et al.* 2009). Several hypotheses on the mechanisms of plant diversity declining with nitrogen enrichment have been proposed which focus either on random or competitive processes. Goldberg & Miller (1990), Oksanen (1996) and Stevens & Carson (1999) proposed that random deaths of small individuals of all species after nitrogen enrichment lead to community-level thinning and the extinction of rare species. In contrast, different functionally-based hypotheses emphasize the differences between species in terms of plant functional traits that determine their competitive abilities. Grime (1973a, 1974) defined the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space as competition. Some individuals or species (namely competitors) show an higher ability in acquisition and control of resources obtaining, in lack of limiting factors, advantages in terms of survival (Grime & Pierce 2012). Competition affect populations or communities structures as it prevents some individuals or species with a lower ability in resource acquisition to reach, in turn,

enough resources for growth, survival or reproductive purposes (Casper & Jackson 1997). Newman (1973) and Tilman & Pacala (1993) supported the aboveground competition hypothesis suggesting that a shift from belowground competition to aboveground competition after nitrogen enrichment results in the loss of poor aboveground competitors. Rajaniemi *et al.* (2003) In contrast, proposed the belowground competition hypothesis suggesting that nitrogen higher availability creates resource patches in the substrate. Individuals or species with greater extent of root system have a greater probability to acquire more resources, subtracting them from the others that undergo growth, survival or reproductive reduction. Last but not the least, Grime (1973b), argued that diversity loss due to nitrogen enrichment resulted from the enhanced intensity of both above and below ground competition, with the superior competitors excluding the inferior ones.

According to these considerations, the present study has the main purpose to detect the effects of substrate nitrogen content on biomass production, biodiversity and community dynamics in early stages of some pasture communities experimental sowings verifying the following hypothesis:

- substrate nitrogen enrichment increase sowings biomass production and decrease sowings diversity
- competition between plants is the main mechanism that lay behind sowings diversity decreasing after nitrogen enrichment

3.2 Methods

Seeds were collected from three different kinds of pastures typical of north Italy mountain belt. For each vegetation we recorded taxonomic identities and estimated species abundances with the methodology proposed by Braun-Blanquet (1928) modified by Pignatti (1952); (Fig. 3.2.1). Table 3.2.1 lists investigated herbaceous plant communities including elevations recorded using a Garmin eTrex Summit GPS receiver (with an electronic barometer). To each vegetation was assigned a label based on comparison of the dominant species with those of vegetation types recorded in Mucina *et al.* (1993a, b), Grabherr & Mucina (1993) and Aeschimann *et al.* (2004).

Table 3.2.1: lists of investigated herbaceous plant communities.

Label	Survey period	Site	Elevation (m a.s.l.)	# of species per plot	Most representative Species	Number and type of protected habitat
<i>A. ela</i>	6/2009	Pirola (BG)	1085	32	<i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. & C. Presl	6510 - lowland hay meadows

Label	Survey period	Site	Elevation (m a.s.l.)	# of species per plot	Most representative Species	Number and type of protected habitat
<i>B.ere</i>	7/2009	Fogarolo (BG)	1200	43	<i>Bromus erectus</i> Huds.	6210 - semi-natural dry grasslands and scrubland <i>facies</i> on calcareous substrates
<i>F.rub</i>	8/2009	Piani di Artavaggio (LC)	1600	24	<i>Festuca rubra</i> L.	6520 - mountain hay meadows

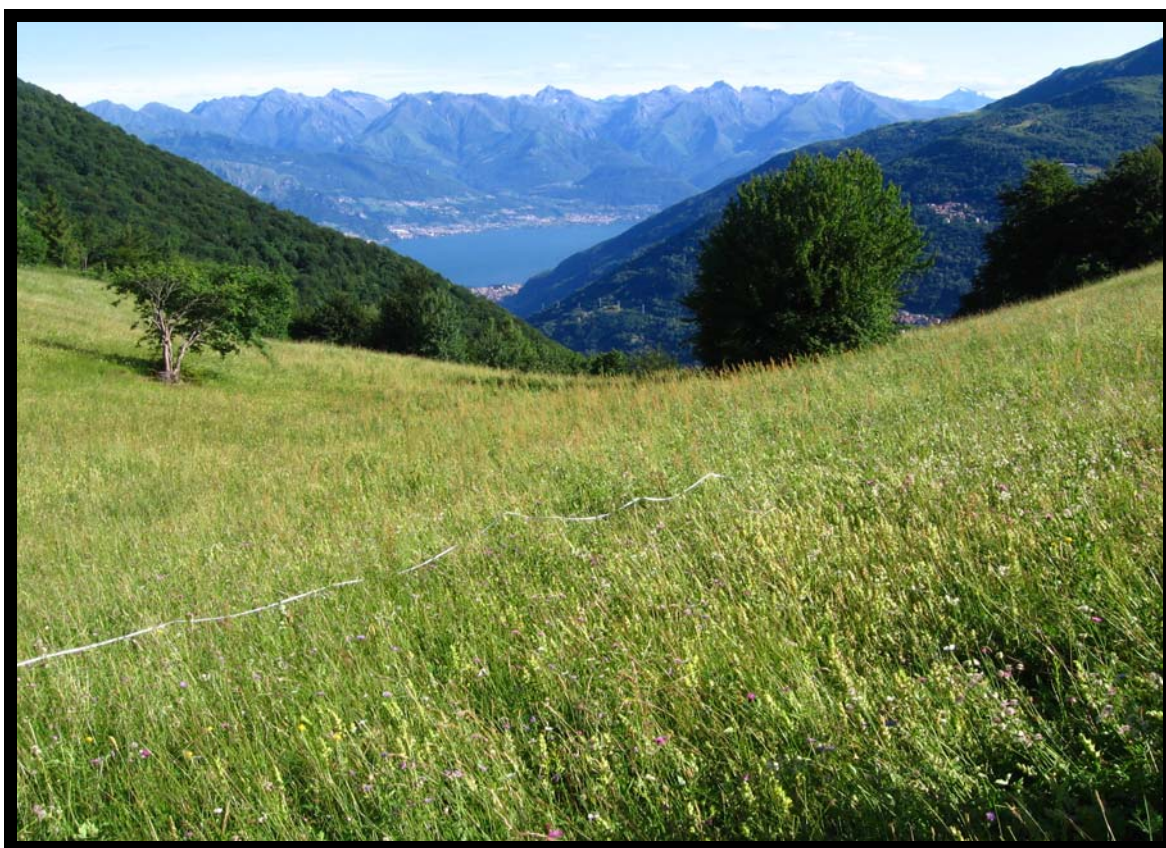


Figure 3.2.1: Floristic and vegetation survey in a community dominated by *Bromus erectus* Huds.

According to the EU Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora, source vegetations could be considered protected habitat types. Specifically:

- *A.ela* (characterized by the presence of *Arrhenatherum elatius* (L.) P. Beauv. ex J. & C. Presl, *Trisetaria flavescens* (L.) Baumg., *Pimpinella major* (L.) Huds., *Centaurea jacea* L., *Knautia arvensis* (L.) Coult., *Tragopogon pratensis* L., *Daucus carota* L., *Leucanthemum vulgare* Lam., *Sanguisorba officinalis* L., *Campanula patula* L., *Leontodon hispidus* L., *Leontodon autumnalis* L., *Colchicum autumnale* L., *Dactylis glomerata* L., *Poa pratensis* L., *Homalotrichon pubescens* (Huds.) Banfi, Galasso & Bracchi, *Filipendula vulgaris* Moench, *Holcus lanatus* L., *Rumex acetosa* L., *Achillea millefolium* L., *Anthoxanthum*

odoratum L., *Bromus hordeaceus* L., *Centaurea nigrescens* Willd., *Galium mollugo* L., *Lathyrus pratensis* L., *Lolium perenne* L., *Lotus corniculatus* L., *Poa trivialis* L., *Ranunculus bulbosus* L., *Rhinanthus alectorolophus* (Scop.) Pollich, *Taraxacum officinale* Weber., *Trifolium pratense*, *Trifolium pratense* L., *Cynosurus cristatus* L., *Salvia pratensis* L., *Plantago lanceolata* L., *Ranunculus acris* L., *Galium verum* L. and *Silene vulgaris* (Moench) Garcke) can be considered as belonging to “**lowland hay meadows – habitat 6510**”;

- *B.ere* (characterized by the presence of *Bromus erectus* Huds., *Anthyllis vulneraria* L., *Campanula glomerata* L., *Centaurea scabiosa* L., *Dianthus carthusianorum* L., *Leontodon hispidus* L., *Primula veris* L., *Sanguisorba minor* Scop., *Scabiosa columbaria* L.) belongs to “**semi-natural dry grasslands and scrubland facies on calcareous substrates – habitat 6210**” and because of the presence of *Dactylorhiza maculata* (L.) Soó, *Gymnadenia conopsea* (L.) R. Br. and *Platanthera bifolia* (L.) Rchb. can be mentioned as “**important orchid sites**”;
- *F.rub* (characterized by the presence of *Festuca rubra* L., *Trisetaria flavescens* (L.) Baumg., *Heracleum sphondylium* L., *Astrantia major* L., *Carum carvi* L., *Bistorta officinalis* Delarbre, *Silene dioica* (L.) Clairv., *Silene vulgaris* (Moench) Garcke, *Anthoxanthum odoratum* L. subsp. *nipponicum* (Honda) Tzvelev, *Crocus vernus* (L.) Hill subsp. *albiflorus* (Kit.) Ces., *Trollius europaeus* L., *Pimpinella major* (L.) Huds., *Viola tricolor* L., *Chaerophyllum hirsutum* L., *Agrostis capillaris* L., *Centaurea nigrescens* Willd., *Dactylis glomerata* L., *Festuca pratensis* Huds., *Galium mollugo* L., *Leontodon hispidus* L., *Rhinanthus alectorolophus* (Scop.) Pollich, *Trifolium pratense* L., *Trifolium repens* L., *Veratrum album* L., *Veronica chamaedrys* L., *Poa alpina* L. subsp. *alpina* , *Anthriscus sylvestris* (L.) Hoffm., *Campanula scheuchzeri* Vill., *Bistorta vivipara* (L.) Delarbre, *Lotus corniculatus* L. and *Vicia cracca* L.) belongs to “**mountain hay meadows – habitat 6520**”.

Experimental sowing has been set in may 2010 in an opened tunnel protected by a anti-hail net and regularly irrigated; (Fig. 3.2.2). Seeds from each vegetation type were planted in plastic pots (45360 cm³ in volume) differing in nitrogen content according to their substrate nature (specifically: soil + sand (SO-SA) = low nitrogen content, soil (SO) = medium nitrogen content, soil + fertilizer (SO-FE) = high nitrogen content); (Table 3.2.2). Sowings were different also for seed densities (number of seeds per pot: Low, Medium, High); (Table 3.2.3).

Table 3.2.2: substrate types used in the experiment and their nitrogen content.

Substrate	Label	N content per pot (g)
Soil + Sand	SO-SA	12.8

Substrate	Label	N content per pot (g)
Soil	SO	25.6
Soil + Fertilizer	SO-FE	33.2

As a soil a universal soil produced from Vigorplant Italy s.r.l. (via A. Volta , 2, 26861, Fombio (LO)) was used, while, as fertilizer, Osmocote® (brevet owned by The Scotts Company LLC, 14111 Scottslawn Road Marysville, OH, USA), distributed in Italy by ITAL-AGRO (Via Vittorio Veneto, 81, 26857 Salerano sul Lambro (LO)).

Table 3.2.3: seed densities used in the experiment.

Seed densities	Label	# of seeds per pot
Low	L	~12000
Medium	M	~13500
High	H	~15000

Overall 81 pots were set (3 vegetation types x 3 substrates x 3 seed densities x 3 replicates) to which 9 control pots were added. Experiment lasted almost 4 months (117 days). Counts of the number of seedlings were made each 15 days using a quadrat size of 25 cm² three times randomly placed in each pot; (Fig. 3.2.3). At the end of the experiment the number of species in each pot was recorded, as well as canopy height (maximum height of the dominant species detected with standard methods (Hodgson *et al.* 1999; Cornelissen *et al.* 2003)). Leaf Area Index was indirectly measured using the plant canopy analyzer LAI-2000 described in Welles & Norman (1991), and available from LI-COR, Box 4425, Lincoln, NE 68504, USA. It uses hemispherical optics and a ringed detector that simultaneously measures diffuse radiation in five distinct angular bands about the zenith. Three LAI measurements, consisting in 6 replicates following the succession ac, uc, uc, uc, uc ac (ac = above canopy, uc = under canopy), were taken in each vegetation pot. A small cap was applied on LAI-2000 sensors to minimize detector's influence. Then, the whole standing crop plus litter was harvested using a battery-powered clipper and scissors; (Fig. 3.2.4 and 3.2.5). Dry weight was measured following drying in a forced-air oven at 95°C for eight hours then dry weight per m² at each pot was calculated. Below ground biomass was sampled collecting a soil core from each pot using a cylindrical soil core sampler (diameter: 15 cm, height: 15 cm); (Fig. 3.2.6). Soil cores were washed with current water in sieves whose mesh size was 1.5 mm. Roots dry weight was measured following drying in a forced-air oven at 95°C for eight hours. Normal distribution of variables was verified with the W test for normality (Shapiro & Wilk 1965). In order to obtain a normal distribution, a logarithmic transformation (with

natural logarithm) was applied to data of above ground and below ground dry mass (g m^{-2}), canopy height (mm), plant densities (number of plants m^{-2}) and species richness (number of species detected in each single pot). Data have been organized in a matrix with 10 columns (representing source pasture, treatments and detected variables) and 81 rows (representing pots); (Table 3.2.4).



Figure 3.2.2: pots in the tunnel.

Table 3.2.4: data matrix: x1 = source pasture label; x2 = substrate; x3 = seed densities, a = $\ln(\text{above ground dry mass (g m}^{-2}\text{)})$; b = $\ln(\text{below ground dry mass (g m}^{-2}\text{)})$; pd = $\ln(\text{plant densities(\# of plants m}^{-2}\text{)})$; sr = $\ln(\text{species richness (\# of species per pot)})$; h = $\ln(\text{canopy height (mm)})$; l = leaf area index ($\text{m}^2 \text{m}^{-2}$).

x1	x2	x3	a	b	pd	sr	h	l
<i>A.ela</i>	SO-SA	H	5.52	5.39	9.18	2.30	4.29	7.13
<i>A.ela</i>	SO-SA	H	5.49	4.54	8.26	2.20	4.40	6.55
<i>A.ela</i>	SO-SA	H	5.39	5.18	9.16	1.95	3.73	5.45
<i>A.ela</i>	SO-SA	M	5.36	5.19	8.86	2.56	4.42	4.25
<i>A.ela</i>	SO-SA	M	5.24	5.33	9.57	2.08	3.74	3.82
<i>A.ela</i>	SO-SA	M	5.55	4.82	9.00	2.08	4.75	5.98
<i>A.ela</i>	SO-SA	L	5.10	5.97	8.70	1.79	4.20	2.92
<i>A.ela</i>	SO-SA	L	5.29	5.16	8.78	1.95	4.12	4.65
<i>A.ela</i>	SO-SA	L	5.21	6.00	9.60	2.08	4.36	5.24
<i>A.ela</i>	SO	H	5.51	5.51	8.95	2.08	4.21	3.34
<i>A.ela</i>	SO	H	5.80	5.83	8.80	2.48	4.09	5.80

x1	x2	x3	a	b	pd	sr	h	l
<i>A.ela</i>	SO	H	5.60	5.99	9.14	1.95	4.68	6.90
<i>A.ela</i>	SO	M	5.65	5.72	8.92	1.79	4.40	5.88
<i>A.ela</i>	SO	M	5.63	5.10	8.72	2.08	4.74	5.35
<i>A.ela</i>	SO	M	5.37	5.06	9.22	1.61	4.00	4.68
<i>A.ela</i>	SO	L	5.43	5.46	8.82	2.20	4.36	5.29
<i>A.ela</i>	SO	L	5.42	6.21	9.22	2.30	4.70	4.48
<i>A.ela</i>	SO	L	5.72	5.88	8.90	2.30	4.31	6.62
<i>A.ela</i>	SO-FE	H	6.08	4.10	6.28	1.95	6.65	6.58
<i>A.ela</i>	SO-FE	H	6.45	2.47	7.09	2.08	7.31	5.49
<i>A.ela</i>	SO-FE	H	6.20	0.35	6.97	1.95	6.59	5.10
<i>A.ela</i>	SO-FE	M	6.24	3.11	6.50	1.39	6.50	4.24
<i>A.ela</i>	SO-FE	M	6.10	-0.86	7.67	1.95	6.80	6.42
<i>A.ela</i>	SO-FE	M	6.16	2.39	6.84	1.95	7.36	2.95
<i>A.ela</i>	SO-FE	L	6.14	-0.57	7.67	1.61	5.87	7.41
<i>A.ela</i>	SO-FE	L	6.17	1.54	6.50	2.08	8.17	4.53
<i>A.ela</i>	SO-FE	L	5.92	0.24	7.20	1.39	6.44	6.67
<i>B.ere</i>	SO-SA	H	5.13	5.95	9.22	1.79	5.31	4.75
<i>B.ere</i>	SO-SA	H	5.35	5.33	8.82	2.08	4.55	6.49
<i>B.ere</i>	SO-SA	H	5.17	6.34	9.22	2.08	4.35	4.53
<i>B.ere</i>	SO-SA	M	5.48	5.11	9.31	1.95	5.22	4.27
<i>B.ere</i>	SO-SA	M	5.47	5.99	9.13	2.20	4.93	5.26
<i>B.ere</i>	SO-SA	M	5.16	5.84	8.53	2.08	4.67	3.74
<i>B.ere</i>	SO-SA	L	5.18	5.37	8.86	2.48	4.63	3.77
<i>B.ere</i>	SO-SA	L	5.29	5.96	9.22	2.48	5.00	3.44
<i>B.ere</i>	SO-SA	L	5.19	5.60	8.48	1.79	5.49	2.01
<i>B.ere</i>	SO	H	5.62	6.00	8.53	1.39	5.63	3.79
<i>B.ere</i>	SO	H	5.56	6.43	9.32	1.95	4.16	6.53
<i>B.ere</i>	SO	H	5.50	5.42	9.32	1.39	5.25	4.50
<i>B.ere</i>	SO	M	5.50	5.97	9.24	2.08	4.64	5.99
<i>B.ere</i>	SO	M	5.40	5.80	9.00	2.08	4.27	5.14
<i>B.ere</i>	SO	M	5.26	6.28	9.51	1.61	4.51	4.89
<i>B.ere</i>	SO	L	5.59	5.70	8.29	2.08	6.33	3.34
<i>B.ere</i>	SO	L	5.28	6.08	9.25	2.48	4.22	3.91
<i>B.ere</i>	SO	L	5.17	5.67	8.19	1.95	4.67	2.45
<i>B.ere</i>	SO-FE	H	6.37	5.29	7.29	1.39	7.39	7.42
<i>B.ere</i>	SO-FE	H	6.56	4.46	7.20	2.20	7.28	8.32
<i>B.ere</i>	SO-FE	H	6.55	5.12	8.07	1.79	7.34	5.58
<i>B.ere</i>	SO-FE	M	6.11	3.91	6.50	1.61	7.73	8.35
<i>B.ere</i>	SO-FE	M	6.48	5.43	6.97	2.30	8.01	7.88
<i>B.ere</i>	SO-FE	M	6.27	3.98	6.68	1.95	6.88	6.44

x1	x2	x3	a	b	pd	sr	h	l
<i>B.ere</i>	SO-FE	L	6.26	4.65	7.20	1.95	8.28	5.70
<i>B.ere</i>	SO-FE	L	6.48	4.33	7.46	2.08	7.22	9.52
<i>B.ere</i>	SO-FE	L	6.56	5.07	6.97	1.79	8.42	7.37
<i>F.rub</i>	SO-SA	H	4.42	3.38	7.78	1.39	4.75	2.06
<i>F.rub</i>	SO-SA	H	5.21	5.08	9.32	1.39	5.26	3.37
<i>F.rub</i>	SO-SA	H	5.37	4.98	9.00	1.79	4.39	5.53
<i>F.rub</i>	SO-SA	M	5.15	4.24	9.70	1.95	4.49	3.18
<i>F.rub</i>	SO-SA	M	4.89	5.49	8.78	1.79	3.79	3.64
<i>F.rub</i>	SO-SA	M	5.19	4.94	9.56	1.61	4.35	4.15
<i>F.rub</i>	SO-SA	L	4.97	4.77	8.42	1.61	4.25	3.95
<i>F.rub</i>	SO-SA	L	5.50	4.67	9.39	1.61	3.99	3.24
<i>F.rub</i>	SO-SA	L	5.09	4.80	8.74	1.79	3.95	3.31
<i>F.rub</i>	SO	H	5.42	5.76	8.53	1.10	4.12	5.20
<i>F.rub</i>	SO	H	5.57	6.49	9.60	1.39	4.24	4.32
<i>F.rub</i>	SO	H	5.60	6.17	9.46	1.39	5.01	3.57
<i>F.rub</i>	SO	M	5.31	5.70	9.18	1.61	3.92	4.26
<i>F.rub</i>	SO	M	5.44	6.03	8.58	1.79	4.65	5.43
<i>F.rub</i>	SO	M	5.14	5.19	9.24	1.39	4.47	4.12
<i>F.rub</i>	SO	L	5.42	5.12	8.29	1.39	4.57	5.03
<i>F.rub</i>	SO	L	5.44	6.07	9.05	1.61	4.63	3.98
<i>F.rub</i>	SO	L	5.44	6.08	8.48	2.08	4.30	6.76
<i>F.rub</i>	SO-FE	H	6.17	4.60	6.84	1.61	7.52	6.47
<i>F.rub</i>	SO-FE	H	6.15	4.29	7.09	1.61	7.05	7.84
<i>F.rub</i>	SO-FE	H	6.44	4.50	7.38	1.61	6.96	8.91
<i>F.rub</i>	SO-FE	M	6.31	4.12	6.97	1.39	7.19	7.30
<i>F.rub</i>	SO-FE	M	6.06	4.09	6.84	1.61	7.75	4.52
<i>F.rub</i>	SO-FE	M	6.25	3.94	6.50	1.39	9.13	9.25
<i>F.rub</i>	SO-FE	L	6.35	5.10	7.38	1.61	7.86	4.83
<i>F.rub</i>	SO-FE	L	6.26	4.20	7.31	1.95	7.77	7.62
<i>F.rub</i>	SO-FE	L	6.27	3.43	6.50	1.79	7.52	7.21

ANOVA was performed on data collected for above and below ground dry mass, plant densities and species richness considering as treatments seed densities (sd), substrate nitrogen content (snc) and their interaction. Post hoc tests were performed on data collected for above ground dry mass, below ground dry mass and plant densities, considering only substrate nutrients content treatment. Further elaborations have involved above ground dry mass, canopy height and LAI data.



Figure 3.2.3: quadrat size of 25 cm² used for seedlings counts.



Figure 3.2.4: Content of a pot right before clipping above ground biomass.



Figure 3.2.5: harvest of standing crop and litter.



Figure 3.2.6: soil core sampling.

3.3 Results

Results from ANOVA performed for each vegetation type on four variables (above ground dry mass, below ground dry mass, plant densities and species richness) in relation to two factors (substrate nitrogen content and seed density) and their interaction, are summarized in Table 3.3.1.

Table 3.3.1: summarize of ANOVA results: snc = substrate nitrogen content, sd = seed densities, snc*sd = interaction, n.s = not significant, "*" = statistically significant.

		Variables											
		Above ground dry mass			Below ground dry mass			Plant densities			Species richness		
		<i>A.ela</i>	<i>B.ere</i>	<i>F.rub</i>	<i>A.ela</i>	<i>B.ere</i>	<i>F.rub</i>	<i>A.ela</i>	<i>B.ere</i>	<i>F.rub</i>	<i>A.ela</i>	<i>B.ere</i>	<i>F.rub</i>
Factors	snc	*	*	*	*	*	*	*	*	*	n.s.	n.s.	n.s.
	sd	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	snc*sd	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Except for vegetation *A.ela* (whose above ground biomass was affected by seed densities), substrate nitrogen content was the only treatment that produced significant effects on three of the four variables considered (above ground dry mass, below ground dry mass and plant densities) in all vegetation types. Bonferroni post hoc tests were performed considering only these variables data according to variations in substrate nitrogen content. Results are summarized in Table 3.3.2.

Table 3.3.2: summarize of Bonferroni post hoc tests results conducted independently for each vegetation type on three variables (above ground dry mass (g m^{-2}), below ground dry mass (g m^{-2}) and plant densities (number of plants m^{-2}) in relation to three steps of nitrogen content according to substrate nature (specifically: soil + sand (SO-SA) = low nitrogen content, soil (SO) = medium nitrogen content, soil + fertilizer (SO-FE) = high nitrogen content). Different letters mean a statistically significant difference. Average values of the variable increase according to the letter: $A < B < C$.

		Variables								
		Above ground dry mass			Below ground dry mass			Plant densities		
		<i>A.ela</i>	<i>B.ere</i>	<i>F.rub</i>	<i>A.ela</i>	<i>B.ere</i>	<i>F.rub</i>	<i>A.ela</i>	<i>B.ere</i>	<i>F.rub</i>
Snc	SO-SA	A	A	A	B	B	A	B	B	B
	SO	B	A	B	B	B	B	B	B	B
	SO-FE	C	B	C	A	A	A	A	A	A

Above ground dry mass increased significantly from pots with low nitrogen content to pots with medium and high nitrogen content (namely SO and SO-FE) for vegetations *A.ela* and *F.rub*. No differences were detected instead between pots with low and

medium nitrogen content for vegetation *B.ere*. Below ground dry mass shown no differences between pots with low and medium nitrogen content for vegetations *A.ela* and *B.ere*, while an increasing was detectable in vegetation *F.rub*. All vegetations shown instead a decreasing in below ground dry mass from pots with medium nitrogen content to pots with high nitrogen content. No differences were detected in plant densities between pots with low and medium substrate nitrogen content. All vegetations' plant densities decreased from pots with medium nitrogen content to pots with high nitrogen content.

Box plot in Figure 3.3.1 represent general variables trends (independently from vegetation type) according to three different steps of substrate nitrogen content (soil + sand (SO-SA) = low nitrogen content, soil (SO) = medium nitrogen content, soil + fertilizer (SO-FE) = high nitrogen content). Greatest differences are detectable from pots with low and medium nitrogen content to pots with high nitrogen content, specifically above ground dry mass increases while below ground dry mass and plant densities decrease.

Bars in Figure 3.3.2 represent average values of ratio between above ground and below ground dry mass for each vegetation in relation to three steps of nitrogen content with error bars representing 95% confidence interval. Average ratios of pots with low and medium nitrogen content were never significantly different from 1. On the contrary, pots with high nitrogen content show average ratios significantly greater than 1.

Figure 3.3.3 is a scatter plot considering as variables natural logarithm of above ground dry mass (g m^{-2}) and natural logarithm of canopy height (mm). When above ground biomass increase, canopy height increase.

Figure 3.3.4 is a scatter plot considering as variables natural logarithm of above ground dry mass (g m^{-2}) and LAI ($\text{m}^2 \text{m}^{-2}$). When above ground biomass increased, LAI increased.

Scatter plot in figure 3.3.5 considers as variables natural logarithm of above ground dry mass (g m^{-2}) and natural logarithm of plant densities (number of plants m^{-2}). Data in scatter plot have been differently coloured according to their nitrogen content. When nitrogen availability allowed above ground biomass to increase, plant densities decreased.

Figure 3.3.6 shows trends in plant densities trough experiment time according to substrate nitrogen content. A statistically significant negative relation was evident in each treatment (a: $f = 1.24\text{e}+04 - 3.45\text{e}+01x$, $R^2=4.99\text{e}-01$, $p<0.05$; b: $f = 1.34\text{e}+04 - 4.42\text{e}+01x$, $R^2=5.99\text{e}-01$, $p<0.05$; c: $f = 1.39\text{e}+04 - 1.17\text{e}+02x$, $R^2=8.63\text{e}-01$, $p<0.001$). Pots with fertilizer shown the steeper negative relationship between time and plant densities (angular coefficient = $1.17\text{e}+02$), (Fig. 3.3.6c).

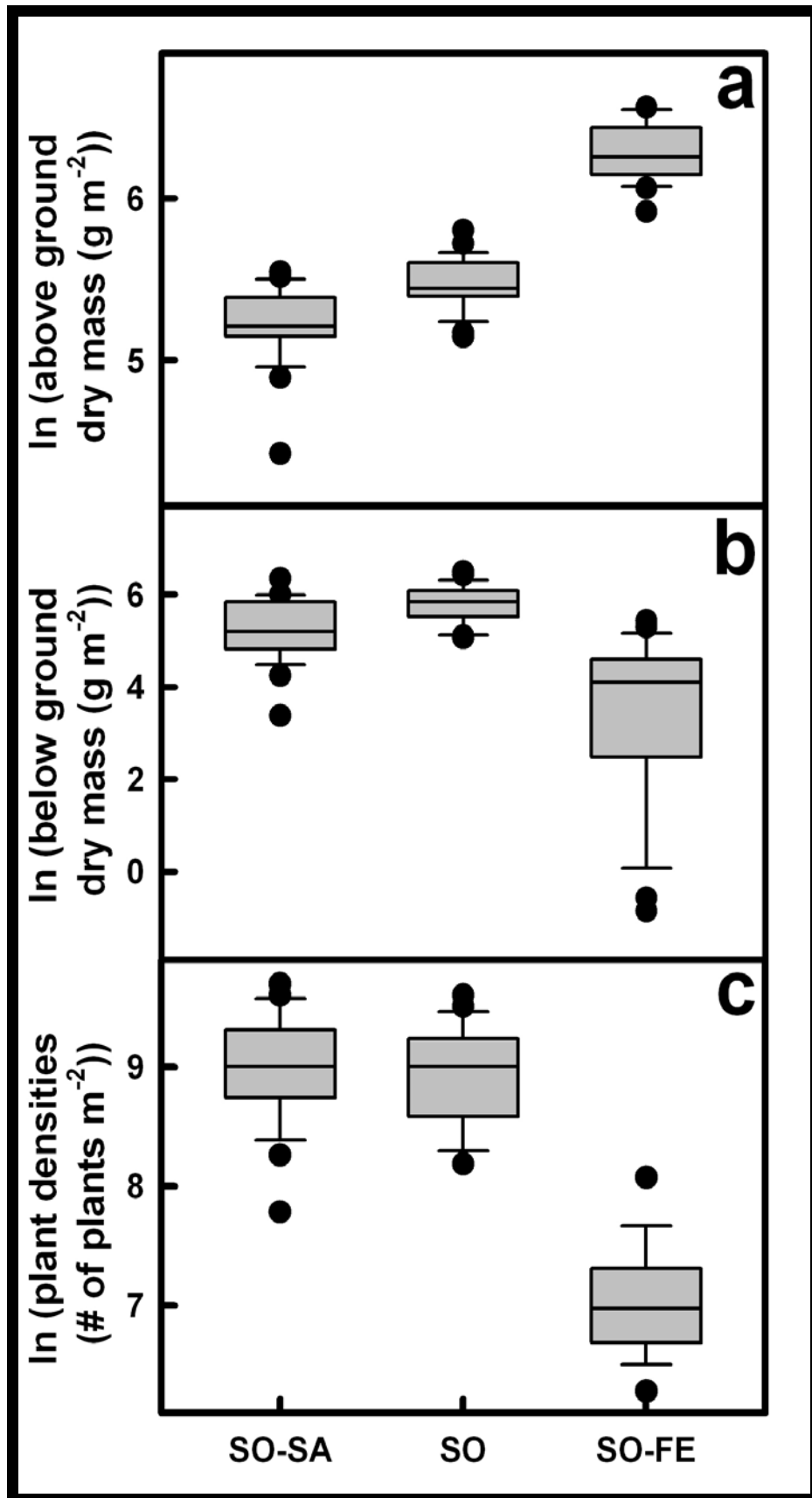


Figure 3.3.1: box plots each showing variation in a considered variable (a = natural logarithm of above ground dry mass, b = natural logarithm of below ground dry mass, c = natural logarithm of plant densities) according to different degree of substrate nutrient content and independently from vegetation type.

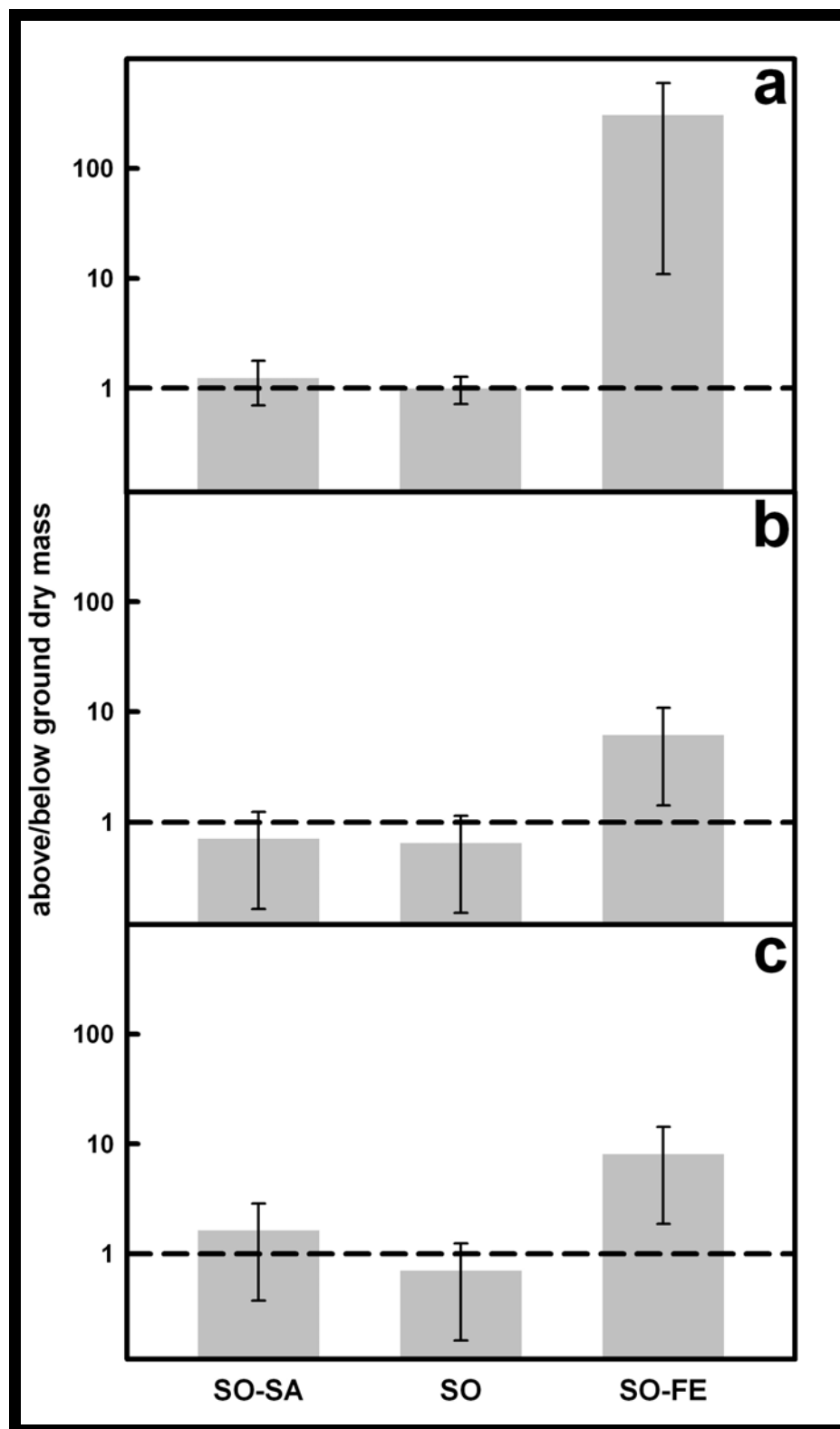


Figure 3.3.2: bars representing average values of ratio between above ground and below ground dry mass for each vegetation (a = *A. elae*; b = *B. ere*; c = *F. rub*) in relation to three steps of substrate nitrogen content (specifically: soil + sand (SO-SA) = low nitrogen content, soil (SO) = medium nitrogen content, soil + fertilizer (SO-FE) = high nitrogen content). Error bars represent 95% confidence interval.

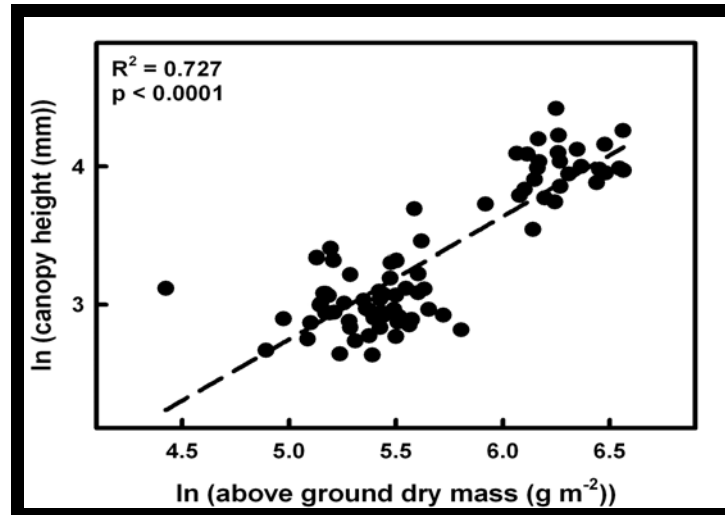


Figure 3.3.3: trend of ln (canopy height (mm)) according to ln (above ground dry mass (g m⁻²)).

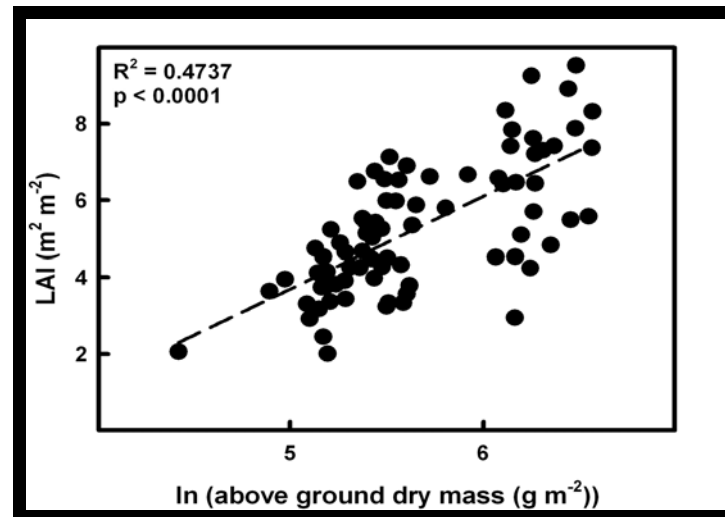


Figure 3.3.4: trend of LAI (m² m⁻²) according to ln (above ground dry mass (g m⁻²)).

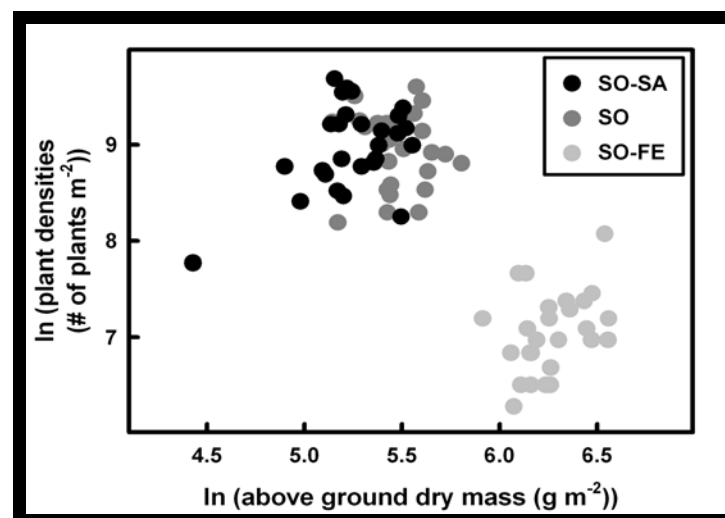


Figure 3.3.5: distribution of plant densities data according to above ground dry mass and independently from vegetation. Dots are differently colored on the basis of pots nitrogen content (specifically: soil + sand (SO-SA) = low nitrogen content, soil (SO) = medium nitrogen content, soil + fertilizer (SO-FE) = high nitrogen content).

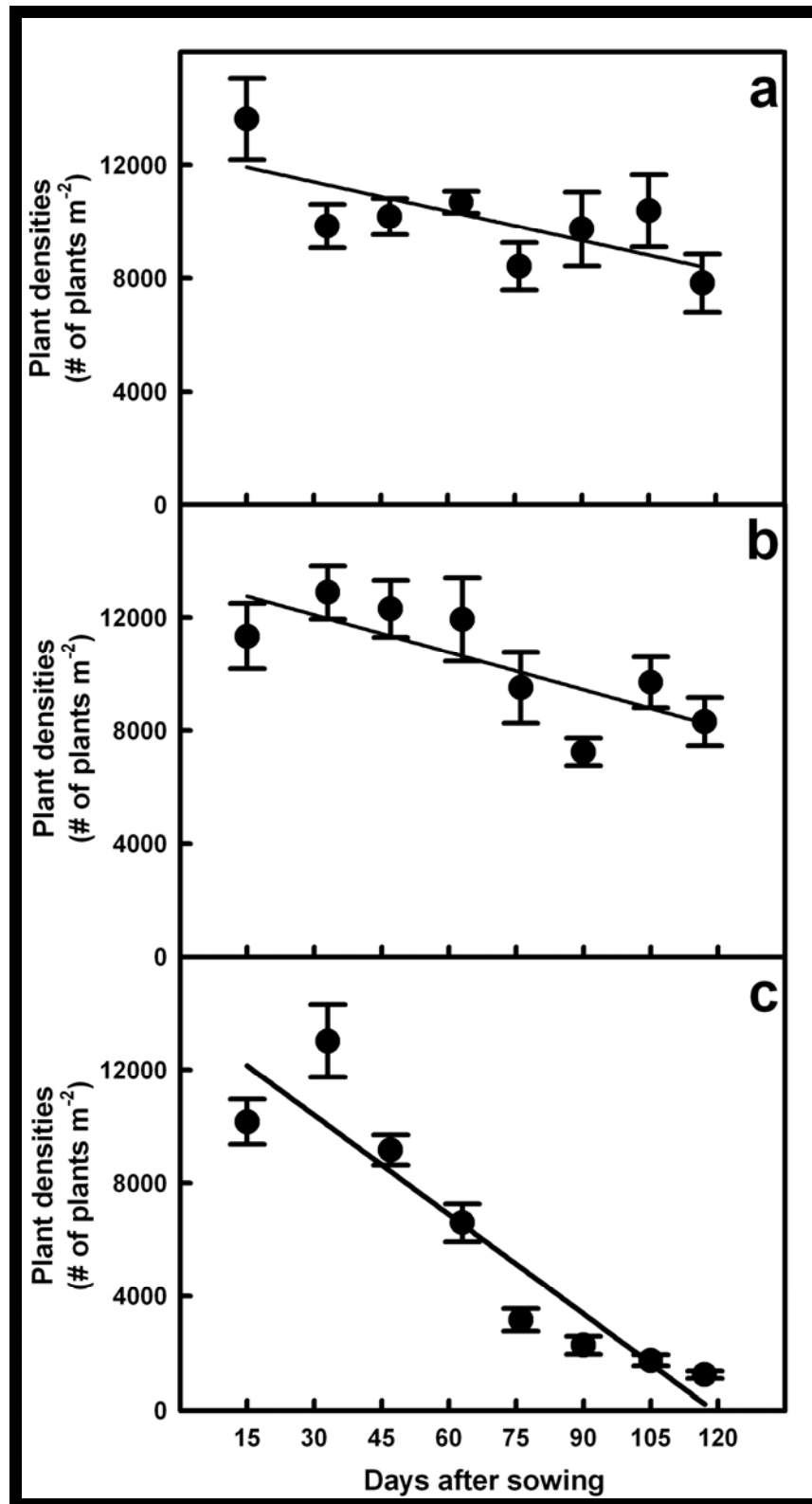


Fig. 3.3.6: trends of average plant densities trough experiment time according to substrate nutrients content: a = soil + sand (low nutrient content), b = soil (medium nutrient content), c= soil + fertilizer (high nutrient content). Standard deviation is shown.

3.4 Discussion

Variations in substrate nitrogen content affected both above and below ground biomass production in experimental sowings; (Tab. 3.3.2). Plant communities on study reacted to the improved availability of nitrogen in the substrate allocating more biomass to the above ground compartment; (Fig. 3.3.1a). Below ground biomass didn't follow the same trend as lower values have been detected in pots with high nitrogen content; (Fig. 3.3.1b). These results "at first glance" agreed with Tilman's resource ratio model (Tilman 1988). Anyway, we won't assume that a trade-off exists between above and below ground patterns of biomass allocation. In fact our results show that high substrate nitrogen content favours above ground production disproportionately more than below ground production, but it's not clear if these observed differences are linked by reciprocal physiological constraints. Histograms in Figure 3.3.3 show that only in conditions of high substrate nitrogen content the ratio between above and below ground dry mass is significantly greater than 1, while in pots with low and medium nitrogen content plants allocate equally biomass between the two compartments. It seems that only in the high nitrogen content pots the threshold after which plants need to worry less about looking for nutrients in the soil is passed. Thus, according to our data, it seems reasonable to think that, in the presence of higher nutrient availability, a relatively small root system is enough to acquire resources to thrive above ground, further corroborating the idea that greater biomass allocation in root systems is not necessarily involved in high uptake of resources (Berendse & Elberse 1989; Olf *et al.* 1990; Campbell & Grime 1992; Aerts 1999; Aerts & Chapin 2000). It is possible that, as time goes by and resources are depleted, root systems extend themselves into the soil both to find nutrients and water and (or) for simple structural reasons, nearing reality to Grime's model (Grime 1974, 1979, 1988). This is partially confirmed also by data collected from the author in natural and semi-natural communities showing that some herbaceous plants developed extended root systems to support huge above ground apparatus (e.g. *Fallopia japonica* (Houtt.) Ronse Decr., Verginella unpublished data).

Increase in plant canopy height (a functional trait directly correlated to the degree of above ground competition in plant communities, chapter 2) detected for increasing values of above ground dry mass, according to higher substrate nutrients content (Fig. 3.3.3), is a sign of selection toward traits that improve plants competitive ability for above ground resources. In fact, higher vegetations with more above ground biomass have a greater ability to intercept light (Fig. 3.3.4), resource for which competition mainly occurs in the epigeal compartment (Freckleton & Watkinson 2001; Hautier *et al.* 2009). Further evidences that plant individuals thriving in pots with high nitrogen content lead to a competitive exclusion of other individuals, come from plant densities

data showing lower values in pots with high nitrogen availability (Tab 3.3.2 and Fig. 3.3.1.). At this early stage, success of larger above ground individuals (producing more biomass) from each species, in substrates with high nutrients content, excluded smaller shaded plants from pots, reducing total number of individuals (Fig 3.3.5). This agreed with the idea that, in the lack of environmental stress, individuals with greater ability in resource acquisition (namely competitors *sensu* Grime 2001 and Grime & Pierce 2012) monopolise resources, limiting neighbours survival and occupying more physical and ecological space. According to the decreasing in plant densities trough experiment times, detected for all levels of substrate nitrogen content (Fig. 3.3.6), we may assume that some thinning process (random or driven by competitive exclusion) is going on even in pots with low and medium nitrogen content where a slight decreasing of plant densities trough experiment time is detectable (Fig. 3.3.6a; Fig 3.3.6b). Anyway, only in pots with high nitrogen availability this process act fiercely and fast with a clear direction: selection of competitors. According to this we can also affirm that nitrogen addition has negative effects on community genetic and functional diversity.

Albeit increasing in nitrogen supply frequently resulted in declining species diversity (Bobbink *et al.* 1998; Stevens *et al.* 2004; Suding *et al.* 2005; Clark *et al.* 2007; Xia & Wan 2008; Reich 2009; Kleijn *et al.* 2009), number of species per pot was not affected in the short term by nutrients availability. This could be explained considering that our experiment was concluded in a relatively short time and that communities in our study included pasture species assemblages already used to tolerate nitrogen availability variations.

A sharable conclusion of our experiment could be the fact that greater above ground biomass production in pasture plant communities growing on nitrogen rich substrates is an effect of faster resources monopolization by competitors. These stronger individuals are able to exploit substrate favorable conditions producing a lot of above ground biomass, thus monopolizing light availability and competitively excluding smaller shaded individuals.

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4 – Measurements of LAI (Leaf Area Index) as a tool for non-destructive biomass evaluation of natural and semi-natural grasslands

4.1 Introduction

Since the beginning of civilization plant biomasses have occupied a relevant role towards human economic activities. Nowadays management of biomass is still a matter of great concern as billions of people are starving principally because of agriculture failure and new renewable energetic sources are required. Pastoral economies are based principally on natural, semi-natural or artificial vegetation primary production that sustains livestock. Estimating productivity of plant communities grazed by cattle could be of great concern, permitting to calculate the amount of livestock that a site can sustain. As stated by Harmoney *et al.* (1997), the most accurate method for determining biomass is still by cutting and weighing it from known areas. However ecologists have made several attempts to find a non-destructive, simple and reliable method to evaluate plant biomass. There is at least a good reason to prefer a non destructive way of estimating biomass: in contrast to meadows and pastures, some grasslands studied by ecologists and conservation managers are vegetation protected by laws and, besides the complication of obtaining the authorizations to work in protected sites, it could be fancy to obtain ecological data without modifying communities structure and viability.

A lot of examples of non destructive methods can be found in literature concerning with different studies testing and comparing methodologies as: visual estimation method (Pechanec & Pickford 1937; Wilm *et al.* 1944), capacitance meters (Dowling *et al.* 1955; Fletcher & Robinson 1956; Campbell *et al.* 1962; Hyde & Lawrence 1964; Alcock 1964; Johns *et al.* 1965; Johns & Watkin 1965; Alcock & Lovett 1967; Morse 1967; Back 1968; Kreil & Matschke 1968; Van Dyne *et al.* 1968; Back *et al.* 1969; Jones & Haydock 1970; Bryant *et al.* 1971; Currie *et al.* 1973), forage disk meters (Alexander *et al.* 1962; Michalk & Herbert 1977; Vartha & Matches 1977; Bransby *et al.* 1977; Baker *et al.* 1981; Karl & Nicholson 1987;), weighted disc (Jagtenburg 1970), sight obstruction measurements using a Robel pole (Robel *et al.* 1970; Michalk & Herbert 1977), Sward height (Michalk & Herbert 1977), β -attenuation (Teare *et al.* 1966; Mitchell 1972; Johnson *et al.* 1976), remote sensing (spectral) methods (Pearson & Miller 1972; Colwell 1974; Deering *et al.* 1975; Maxwell 1976; Pearson *et al.* 1976; Colwell *et al.* 1977; Duggin 1977; Tucker 1977a; Tucker 1977b; Deering 1978; Kriebel 1978; Tucker 1978; Kriebel 1979; Tucker 1979; Wiegand *et al.* 1979; Holben *et al.* 1980a; Holben *et al.* 1980b; Tucker *et al.* 1980a; Tucker *et al.*

1980b; Pinter *et al.* 1981; Tucker *et al.* 1981) and Leaf Area Index (Pearce *et al.* 1965; Engel *et al.* 1987; Trott *et al.* 1988; Welles & Norman 1991; Ganguli *et al.* 1999; Ganguli *et al.* 2000). Each study shows pros and cons of methodologies (as summarized by Table 4.1.1), often underlining the necessity of an empirical calibration of the selected methodology according to vegetation types.

Table 4.1.1: list of indirect methods for above ground biomass estimation reported in literature.

Method	Pros	Cons	Tools	References
Visual estimation procedures	Rapidity (after calibration)	Subjective; not sufficiently accurate for many experimental purposes	Pair of shears, plot marking material, paper sacks, scales (only for calibration)	Pechanec & Pickford 1937; Wilm <i>et al.</i> 1944
Capacitance meters	Rapidity and simplicity	Erroneous measurements with wet-weather and dew, frequent need for recalibration	Electronic device for measuring the capacitance	Alcock & Lovett 1967; Alcock 1964; Back <i>et al.</i> 1969; Back 1968; Bryant <i>et al.</i> 1971; Campbell <i>et al.</i> 1962; Currie <i>et al.</i> 1973; Dowling <i>et al.</i> 1955; Fletcher & Robinson 1956; Hyde & Lawrence 1964; Johns & Watkin 1965; Johns <i>et al.</i> 1965; Jones & Haydock 1970; Kreil & Matschke 1968; Morse 1967; Van Dyne <i>et al.</i> 1968
Forage disc meters	Rapidity and simplicity	It doesn't account for litter; dependent on species composition	Wood or metal or plywood plate, yardstick	Alexander <i>et al.</i> 1962; Baker <i>et al.</i> 1981; Bransby <i>et al.</i> 1977; Karl & Nicholson 1987; Michalk & Herbert 1977; Vartha & Matches 1977
Weighted disc	Rapidity and simplicity	Dependent from species composition and from time of year	Weighted disc	Castle 1976; Jagtenburg 1970; Phillips & Clarke 1971; Powell 1974
Robel pole	Rapidity and simplicity	Relies on human eyesight	Robel pole, yardstick	Michalk & Herbert 1977; Robel <i>et al.</i> 1970
Sward height	Rapidity and simplicity	Difficult to account for vegetation density	Yardstick	Michalk & Herbert 1977
β -attenuation	Relatively inexpensive	Limited usage on moderately to heavily grazed pastures and on micro topographical variations	β - particles emitter and detector	Johnson <i>et al.</i> 1976; Mitchell 1972; Teare <i>et al.</i> 1966
Remote sensing techniques	Relatively inexpensive; not affected by moisture, wet or damp soil or by uneven micro topography; useful to investigate large areas.	Sensitive to illumination conditions (solar zenith angle and clouds)	Remote sensing system	Colwell 1974; Colwell <i>et al.</i> 1977; Deering 1978; Deering <i>et al.</i> 1975; Duggin 1977; Holben <i>et al.</i> 1980; Kriebel 1978; Kriebel 1979; Maxwell 1976; Pearson & Miller 1972; Pearson <i>et al.</i> 1976; Pinter <i>et al.</i> 1981; Tucker 1977a; Tucker 1977b; Tucker 1978; Tucker 1979; Tucker 1980; Tucker 1980a; Tucker 1980b; Tucker <i>et al.</i> 1981; Wiegand <i>et al.</i> 1979
Leaf area index	Not destructive	Quite expensive	Canopy analyzer	Engel <i>et al.</i> 1987; Ganguli <i>et al.</i> 1999; Ganguli <i>et al.</i> 2000; Pearce <i>et al.</i> 1965; Trott <i>et al.</i> 1988; Welles & Norman 1991

Engel *et al.* (1987) have shown a positive linear relationship between leaf area and standing crop. On the other hand, many studies found out also an almost low correlation between Canopy Analyzer measurements and standing crop (Harmony *et*

al. 1997; Miller-Goodman *et al.* 1999; Volesky *et al.* 1999). Ganguli *et al.* (1999) obtained better results defining the specific area that Canopy Analyzer was measuring. Despite of this, Canopy Analyzer technique has been considered to produce poor estimates of standing crop (Ganguli *et al.* 2000). In this study, indirect measurements of LAI and canopy height have been collected in order to develop a model to estimate in a non destructive way plant above ground peak dry mass of natural and semi-natural herbaceous vegetations including some communities protected by Habitats Directive (EU Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora).

4.2 Methods

The study investigate 21 natural and semi-natural herbaceous communities located at a range of elevations and geographic locations spanning the Po Plain of Lombardy to the Alpine zone; (Table 4.2.1). A Garmin eTrex Summit GPS receiver (with electronic barometer) was used to record geographic locations, including elevations, which are reported in Table 4.2.1.

Table 4.2.1: community label, survey date, North coordinate, East coordinate, altitude (m a.s.l.), slope (°), exposure (°) and physiognomic description for each vegetation surveyed is given.

Label	Survey Date	North coordinate	East coordinate	Elevation (m a.s.l.)	Slope (°)	Exposure (°)	Physiognomic description
<i>A.fat</i>	24/5/2010	45°31'11.8"	10°13'40.1"	130	0	0	Wasteland dominated by <i>Avena fatua</i> L.
<i>F.min</i>	9/6/2010	45°35'56.6"	8°43'27.2"	207	0	0	Meadow dominated by <i>Filago minima</i> (Sm.) Pers.
<i>B.ere</i>	29/6/2010	45°32'45.6"	10°16'45.7"	790	20	150	Meadow dominated by <i>Bromus erectus</i> Huds.
<i>H.pyr</i>	5/7/2010	45°54'00.2"	10°24'12.4"	2010	15	185	Pasture grassland dominated by <i>Horminum pyrenaicum</i> L.
<i>C.sem</i>	5/7/2010	45°53'46"	10°23'51.9"	2020	30	250	Pasture grassland dominated by <i>Carex sempervirens</i> Vill.
<i>R.alp</i>	9/7/2010	45°44'48.8"	10°09'56.6"	1571	0	0	Seasonal livestock enclosure dominated by <i>Rumex alpinus</i> L.
<i>A.ela</i>	12/7/2010	45°38'41.4"	10°09'00.3"	720	15	198	Meadow dominated by <i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. & C. Presl
<i>F.pan</i>	15/7/2010	45°44'45.2"	10°10'14.7"	1492	30	235	Grassland dominated by <i>Festuca paniculata</i> (L.) Schinz & Thell. subsp. <i>paniculata</i>
<i>S.hal</i>	19/7/2010	45°37'25.1"	10°04'36.1"	190	0	0	Wasteland dominated by <i>Sorghum halepense</i> (L.) Pers.
<i>P.alp</i>	22/7/2010	45°44'56"	10°09'44.6"	1621	10	190	Meadow dominated by <i>Phleum alpinum</i> L.
<i>N.str</i>	4/8/2010	45°52'01.1"	10°22'39.5"	2150	5	300	Pasture dominated by <i>Nardus stricta</i> L.
<i>S.alp</i>	4/8/2010	45°52'46.3"	10°23'17.1"	1890	25	266	Stream margin dominated by <i>Senecio alpinus</i> (L.) Scop.
<i>G.mon</i>	6/8/2010	45°45'18.7"	10° 9'50.12"	1780	20	260	Pasture dominated by <i>Geum montanum</i> L.

Label	Survey Date	North coordinate	East coordinate	Elevation (m a.s.l.)	Slope (°)	Exposure (°)	Physiognomic description
<i>S.cae</i>	18/8/2010	45°48'22.8"	10°24'26.1"	1726	15	74	Grassland dominated by <i>Sesleria caerulea</i> (L.) Ard.
<i>S.vir</i>	31/8/2010	45°27'20"	10°10'18.1"	97	0	0	Wasteland dominated by <i>Setaria viridis</i> (L.) P. Beauv.
<i>P.aqu</i>	15/9/2010	46°01'52.7"	8°36'62.4"	1018	10	100	<i>Pteridium aquilinum</i> (L.) Kuhn subsp. <i>aquilinum</i> stand
<i>M.cae</i>	15/9/2010	46°02'11.2"	8°35'19.4"	1380	30	165	Abandoned oldfield meadow dominated by <i>Molinia caerulea</i> (L.) Moench subsp. <i>arundinacea</i> (Schrank) K. Richt.
<i>H.tub</i>	11/10/2010	45°36'34.3"	10°12'25.3"	211	0	0	Wasteland dominated by <i>Helianthus tuberosus</i> L.
<i>A.ver</i>	13/10/2010	45°32'57.9"	8°48'40.7"	180	0	0	Wasteland dominated by <i>Artemisia verlotiorum</i> Lamotte
<i>S.can</i>	13/10/2010	45°34'15.1"	8°42'22.2"	192	0	0	Margin dominated by <i>Solidago canadensis</i> L.
<i>F.jap</i>	28/10/2010	45°45'20.8"	10°35'47.5"	602	1	272	Stream margin dominated by <i>Fallopia japonica</i> (Houtt.) Ronse Decr.

Sampling was carried out at the peak of biomass production of each vegetation type, between April and October, during 2009 to 2010. Dates as early as April were necessary for communities of therophytes on disturbed ground at low elevations that peaked extremely early, but these communities were nonetheless sampled during the peak of biomass and the fruiting phase of the majority of species within the community. In each community a standard quadrat size of 16m² was employed during floristic surveys and point analysis, in which counting the species touched by a needle inserted at 75 points provided a measure of species relative abundance (e.g. Pierce *et al.* 2007a; Cerabolini *et al.* 2010a). Vegetation was assigned a label based on comparison of the dominant species with those of vegetation types recorded in Mucina *et al.* (1993a,b), Grabherr & Mucina (1993) and Aeschimann *et al.* (2004). Leaf Area Index was indirectly measured using the plant canopy analyzer LAI-2000 described in Welles & Norman (1991), and available from LI-COR, Box 4425, Lincoln, NE 68504, USA. It uses hemispherical optics and a ringed detector that simultaneously measures diffuse radiation in five distinct angular bands about the zenith. Three LAI measurements, consisting in 6 replicates following the succession ac, uc, uc, uc, uc ac (ac = above canopy, uc = under canopy), were taken in each vegetation plots. A small cap was applied on LAI-2000 sensors to minimize detector's influence. Canopy height was measured directly in the field for species touched by the needle during point analysis four or more times, following the method of Hodgson *et al.* (1999) and Cornelissen *et al.* (2003). Bibliographic data have been used for species not touched by the needle or touched only three times or less. These data were basis for several calculations: average height of species in phytosociological survey (hsur) ; average

height of species in point analysis (hpa); average height of species with relative abundance >10% (hdom); height of highest species between dominants (hd). Being hd the easier variable to calculate and because of its correlation with all other height measurements (Pearson product-moment correlation: $r=8.86e-01$ and $p<0.001$ with hsur; $r=8.42e-01$ and $p<0.001$ with hpa; $r=9.51e-01$ and $p<0.001$ with hdom) it has been the only one considered as a variable for our models. Three epigeal biomass samples, including litter, were taken for each community employing a standard quadrat size of 0.25m^2 (e.g. Al-Mufti *et al.* 1977). Normal distribution of variables was verified with the W test for normality (Shapiro & Wilk 1965). Biomass values were not normally distributed, therefore a transformation was carried out employing natural logarithm. Thus we've obtained a matrix with 21 communities and 4 variables; (Table 4.2.2).

Table 4.2.2: matrix A. label = vegetations label; b = above ground peak dry mass (g m^{-2}); lai = leaf area index ($\text{m}^2 \text{m}^{-2}$); hd = height of highest species between dominants (mm).

label	bl	lai	hd
<i>F.min</i>	376	0.3	97
<i>H.pyr</i>	481	1.9	42
<i>P.alp</i>	599	4.3	308
<i>G.mon</i>	604	4.7	140
<i>C.sem</i>	684	3.6	337
<i>B.ere</i>	744	2.7	465
<i>N.str</i>	836	2.8	140
<i>S.cae</i>	913	4.3	146
<i>A.ela</i>	967	5.5	767
<i>A.fat</i>	987	4.0	1268
<i>F.pan</i>	1039	6.1	447
<i>S.vir</i>	1040	5.8	662
<i>S.alp</i>	1131	6.9	887
<i>S.hal</i>	1189	4.9	1472
<i>R.alp</i>	1280	7.1	640
<i>M.cae</i>	1441	6.4	633
<i>P.aqu</i>	1619	7.0	858
<i>S.can</i>	1732	5.5	1972
<i>A.ver</i>	2275	5.9	1558
<i>H.tub</i>	2377	6.4	2083
<i>F.jap</i>	2592	3.0	1800

Several models have been created using hd and lai as variables.

4.3 Results

A linear model fm1 was fitted introducing LAI (lai) as independent variable and natural logarithm of above ground peak dry mass (bl) as dependent variable. Results are shown; (Table 4.3.1).

Table 4.3.1

	Estimate	Std. Error	t value	Pr(> t)
Intercept	6.10e+00	2.61e-01	23.3e+00	<0.001
Lai	1.79e-01	5.17e-02	3.46e+00	<0.01

The model shows an almost low adjusted R^2 (0.355), resulting statistically significant ($F = 12.0$ on 1 and 19 DF, p -value <0.01). According to its equation for each increase of one unit of LAI we have an increase of 0.179 units of $\ln(\text{above ground peak dry mass (g m}^{-2}\text{)})$; (Fig. 4.3.1). It is remarkable that the intercept is different from 0. Bonferroni outlier test has shown that herbaceous community dominated by *Fallopia japonica* (Houtt.) Ronse Decr. act as an outlier (Bonferroni $p <0.01$; Fig. 4.3.1). For this reason it has been excluded from further data analysis.

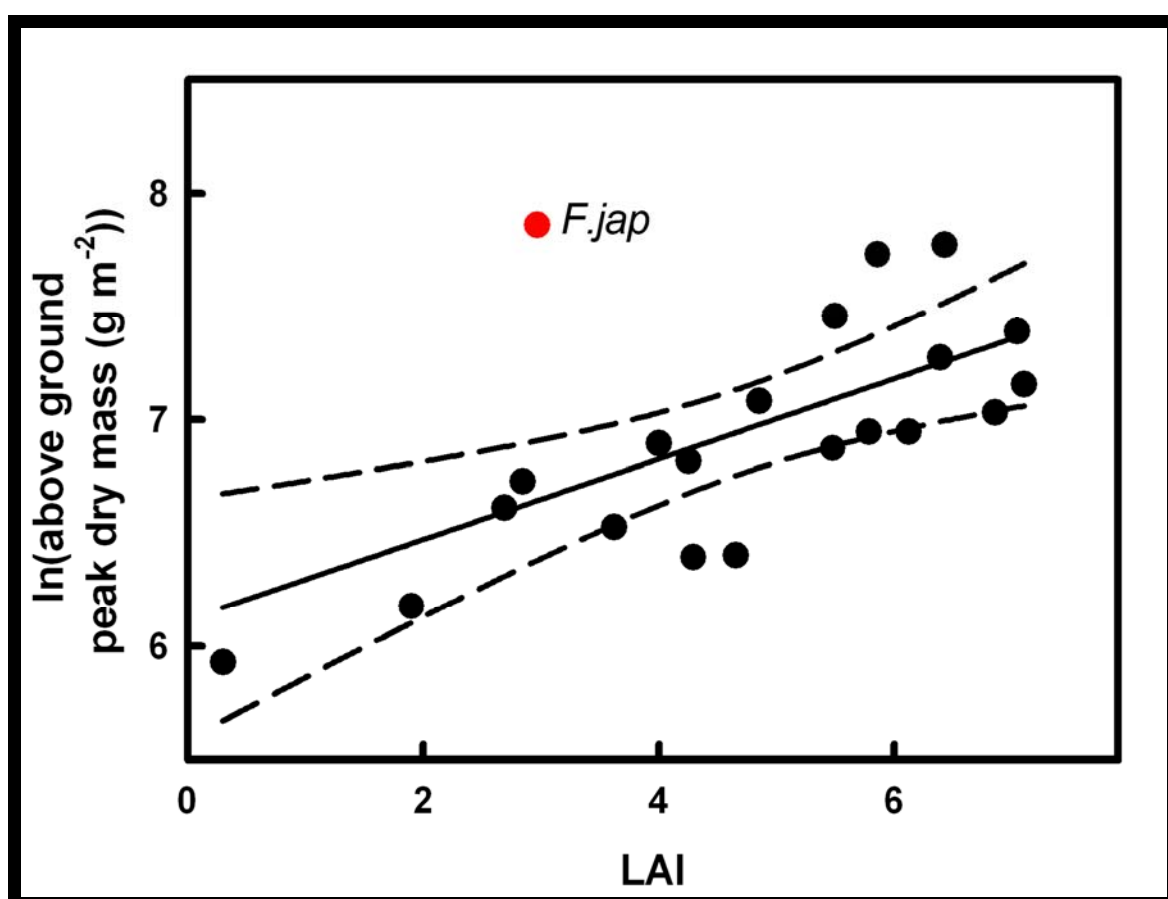


Figure 4.3.1: linear model fm1 ($f=6.1+0.179x$; $\text{adj.}R^2=0.355$; $p<0.01$). Community dominated by *Fallopia japonica* (*F.jap*) is an outlier.

A new model fm2 has been created using the new subset of communities, lai as independent variables and bl as dependent variables. Results are shown (Table 4.3.2).

Table 4.3.2

	Estimate	Std. Error	t value	Pr(> t)
Intercept	5.87e+00	1.95e-01	29.9e+00	<0.001
Lai	2.14e-01	3.82e-02	5.61e+00	<0.001

The model shows an higher adjusted R^2 (0.616) compared with fm1, resulting statistically significant ($F = 31.6$ on 1 and 18 DF, $p\text{-value} < 0.001$). According to its equation for each increase of one unit of lai we have an increase of 0.214 units of $\ln(\text{above ground peak dry mass})$ (Fig. 4.3.2).

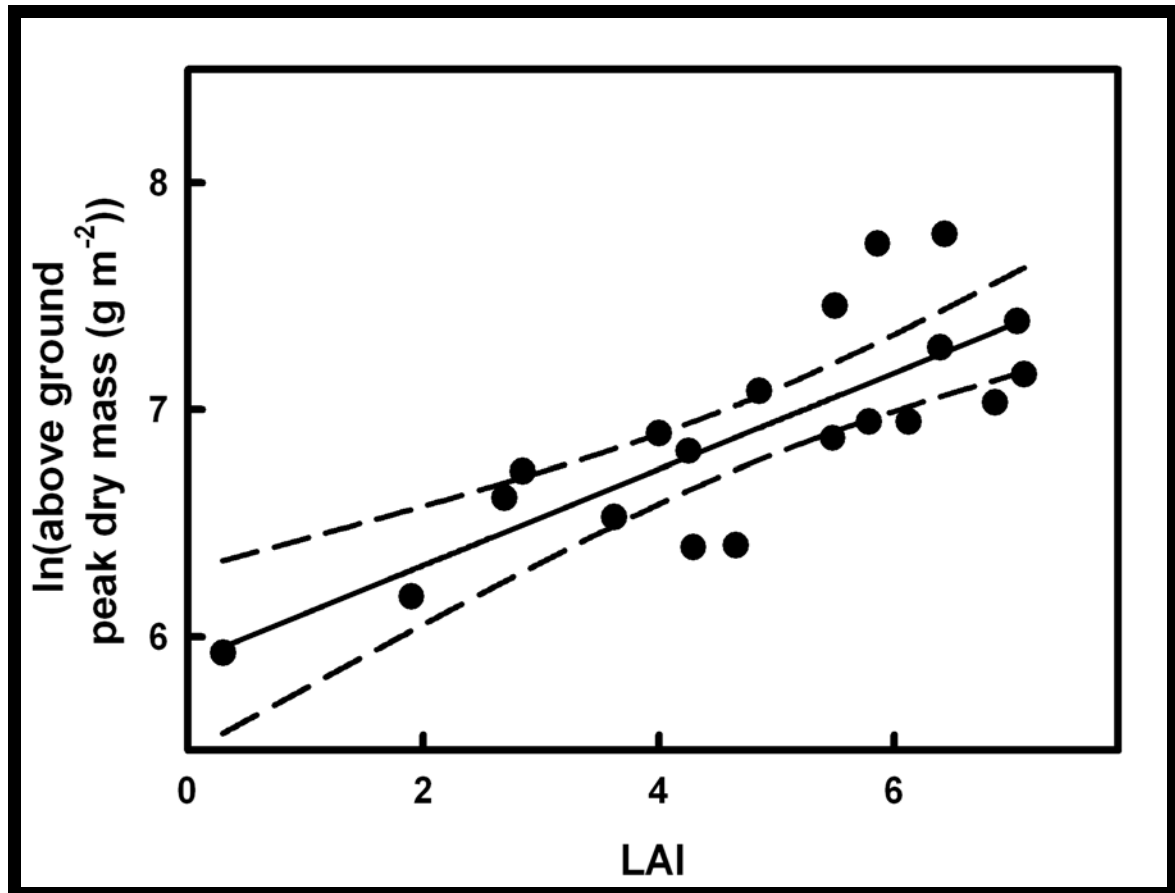


Figure 4.3.2: linear model fm2 ($f=5.87+0.214x$; $\text{adj.}R^2=0.616$; $p<0.01$).

A new model fm3 has been created including as independent variable height of highest species between dominants (hd), interaction between variables lai and hd (lai*hd), lai^2 (lai*lai) and hd^2 (hd*hd). Results are shown; (Table 4.3.3).

Table 4.3.3

	Estimate	Std. Error	t value	Pr(> t)
Intercept	5.94e+00	1.96e-01	30.1e+00	< 0.001
Lai	1.93e-01	1.19e-01	1.62e+00	> 0.05
Hd	-1.52e-04	5.05e-04	-3.01e-01	> 0.05
lai*hd	1.51e-04	1.49e-04	1.01e+00	> 0.05
lai*lai	-1.48e-02	2.05e-02	-7.24e-01	> 0.05
hd*hd	-1.01e-07	2.46e-07	-4.11e-01	> 0.05

This model shows an $\text{adj. } R^2$ of 0.845 resulting statistically significant ($F = 21.7$ on 5 and 14 DF, $p\text{-value} < 0.001$). Intercept is different from 0. Estimated coefficients for hd, lai*lai and hd*hd are negative values, so we perform a forward step wise

regression to choose the most explanatory variables. The results are shown in Table 4.3.4.

Table 4.3.4

Step	Model	AIC				
		lai	lai*hd	hd	hd*hd	lai*lai
1	bl~lai	-45.44	-65.76	-64.51	-64.49	-43.46
2	bl~lai + lai*hd	lai+lai*hd		lai*lai	Hd	hd*hd
		-65.76	-64.28	-63.84	-63.79	

Step wise regression suggested that lai and lai*hd account for most of variability. A new model fm4 was created using as independent variables lai and lai*hd. Even in this model intercept is different from 0. Results are shown; (Table 4.3.5).

Table 4.3.5

	Estimate	Std. Error	t value	Pr(> t)
Intercept	6.04e+00	1.18e-01	50.8e+00	< 0.001
Lai	1.08e-01	2.87e-02	3.77e+00	<0.01
lai*hd	8.26e-05	1.40e-05	5.90e+00	< 0.001

This model shows an adj. R^2 of 0.867 resulting statistically significant ($F = 62.9$ on 2 and 17 DF, p -value <0.001). Models fm1 and fm4 were compared with ANOVA resulting significantly different ($F = 34.8$, p -value <0.001).

4.4 Discussion

Many authors have assessed direct and indirect LAI measurements as an instrument to estimate above ground peak biomass in herbaceous community (Pearce *et al.* 1965; Engel *et al.* 1987; Trott *et al.* 1988; Welles & Norman 1991; Ganguli *et al.* 1999; Ganguli *et al.* 2000). In this study above ground peak dry mass measurements, LI-COR 2000 canopy analyzer's LAI estimates and canopy height values have been collected from 21 different herbaceous community. Data have been elaborated in order to develop a predictive model to estimate, non-destructively, above ground peak biomass of natural and semi-natural herbaceous communities. First model developed accounted for natural logarithm of above ground peak dry mass as dependent variable and for lai as the only explanatory independent variable. Even if statistically significant (F -statistic: 12.03 on 1 and 19 DF, p -value<0.01) the model shown an almost low adj. R^2 (0.355). Being an outlier, vegetation dominated by *Fallopia japonica* (Houtt.) Ronse Decr. has been excluded from the communities under study. Low LAI values obtained for this high above ground peak dry mass vegetation can be explained considering that a lot of biomass harvested by hand clipping was located in *F.japonica* wooden branches, while its sparse foliage allowed a consistent amount of sunlight to reach the ground. This particular situation must be considered as a warning for the

need to better define the features that an herbaceous community must have for being investigated with LI-COR 2000 canopy analyzer. Even sampling procedures should be calibrated to improve the relationship between LAI measurements and above ground peak dry mass values (as already noticed by Ganguli *et al.* 2000).

Models developed with the new data set shown intercepts always different from zero. That's easy to explain, as LI-COR 2000 sensors are located at the extremity of a kind of rod about 5cm thick: sensor could take measures only in plant communities that allocate a substantial proportion of epigeal biomass at least 5 cm above the ground level. This technical consideration should be added to those reported in Ganguli *et al.* (1999) and in Volesky *et al.* (1999), in order to improve field usage of canopy analyzer as an instrument for standing crop evaluations. New instruments and new field procedures are required, instead, for all herbaceous plant communities shorter than 5cm.

In the first model fm1, LAI is the only variable used to estimate plant biomass, showing an almost high adjusted R^2 of 0.616. Adding as an independent variable interaction between LAI and a measure of canopy height a new model fm4 was created. Adjusted R^2 increased to 0.867. Comparison between models fm1 and fm4 performed with ANOVA shown that there was a significant difference between models. Thus our model fm4 ($bl \sim lai + lai*hd$) can be used to estimate in a non destructive way herbaceous communities. Anyway, to obtain a best fitted model, is necessary to consider community canopy height, and to introduce into the model interaction between LAI and canopy height.

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5 - Linking plant functional traits, biomass production and floristic features for preliminary ES assessment: an example from herbaceous plant communities

5.1 Introduction

The Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005) documented the importance of ecosystem services (ES) to human well-being and showed that continued supply of these services is threatened by unsustainable anthropogenic activities (Balmford *et al.* 2002). Understanding the factors that cause changes in ecosystems and Ecosystem Services and the effects of environmental change on the human well-being is essential to the design of interventions that enhance positive and minimize negative impacts (Millennium Ecosystem Assessment 2005).

Different papers provided conceptual frameworks to link ES to Net Primary Production (NPP), Biodiversity (BD) and/or plant functional traits (Balvanera *et al.* 2006, Diaz *et al.* 2007), but applications for practical purposes are still rare. In fact, the economic value of ES has often been estimated merely from tabulated standard economic values (Costanza *et al.* 1997) and land use changes (Kreuter *et al.* 2001; Wang *et al.* 2006, Tianhong *et al.* 2010), without considering ecosystems properties and functions.

The mass ratio hypothesis (Grime 1998) predicts that the influence of a species or group of species on ecosystem functioning is proportional to their contribution to total biomass and to primary production. On the other hand biodiversity-ecosystem multifunctionality studies have found that more species are needed to provide multiple functions, because different species promote different functions (Balvanera *et al.* 2006; Isbell *et al.* 2011). Recent works (Mokany *et al.* 2008) indicate that the mass ratio hypothesis provides a more appropriate framework for explaining how plant communities influences key ecosystem processes in comparison to the diversity hypothesis, especially for the native grasslands. In this light, the mass ratio hypothesis can be the basis on which develop practical tools for rough evaluation of ES, for example using key plant functional traits and species abundance estimation in plant communities of interest. This approach can give access to a huge amount of literature data (i.e. phytosociological relevés, PFTs etc.) facilitating preliminary ES assessments based on measured ecological data.

Major aims of this work are: (i) to estimate if and how 60 plots of herbaceous plant communities representative of wide ecological range of Alps and central Europe vegetation differ in average key plant functional traits, in above and below ground

biomass and in the quality of present species; (ii) to formulate simple indexes on the basis of these data that can be used for estimating main ES offered by plant communities; (iii) to evaluate the relationships between these indexes and functional signature of plant communities within CSR theory.

5.2 Methods

Analysis were performed on a data set regarding 60 plots of natural and semi-natural herbaceous plant communities covering a wide range of ecological conditions representative of Alps and continental Europe vegetation. Each plot was included in the data set according to floristic, biomass and plant functional traits data availability. Taxonomic composition and species abundance of each plot was determined by the mean of 16 m² phytosociological survey. Species abundance was derived from ground coverage indexes assessed using the Braun-Blanquet scale modified by Pignatti (1952). Starting from the taxonomic composition, for each plot were calculated as rates of the total recorded species the percentage of species with noticeable blooming, the percentage of protected species and the percentage of Black List species. Protected species and Black List species were considered those belonging to the lists decreed by Lombardy Regional Law 10/2008.

Biomass was assessed as above ground biomass plus litter (AGDW) and below ground coarse roots biomass (BGDW). For sampling methods see Chapter 2, Ossola *et al.* (2009) and Cerabolini *et al.* (2010a). Biomass data were expressed in g m⁻².

For plot inclusion in the data set, plant functional traits had to be available for species covering on whole 90% of the survey area at least. As plant functional traits were considered: plant canopy height (CAN_H in mm), leaf dry matter content (LDMC as percentage of leaf fresh weight), specific leaf area (SLA in mm² mg⁻¹), leaf nitrogen content (LNC as percentage of leaf dry weight) and leaf carbon content (LCC as percentage of leaf dry weight). Sampling and measuring methods of CAN_H, LDMC and SLA followed standard methodology recommended in literature (Hodgson *et al.* 1999; Cornelissen *et al.* 2003). CAN_H was log transformed before multivariate and correlation analysis. LNC and LCC were determined from dry leaf material with a CHN-analyzer (NA-2000 N-Protein; Fisons Instruments S.p.A., Rodano (MI), Italy). Plant CSR strategies were calculate using the spreadsheet of Hodgson *et al.* (1999), starting from data published in the FIFTH Database (Cerabolini *et al.* 2010b). For missing species in the FIFTH Database further measures were taken on populations living in the analyzed plant communities.

Plant functional traits and CSR radii for each plot were calculated as average of species traits and CSR radii weighted by their relative abundance in the plot. As

abundance values were employed the relative values of the ground coverage indexes after their conversion as follows: 5 → 90%; 4 → 70%; 3 → 50%; 2 → 30%; 1 → 10%; + → 0.5%; r → 0.1%.

We performed the first Principal Component Analysis (PCA) on a matrix considering 10 key traits for the 60 plots. The employed variables were: Flowering Species %, Protected Species %, Black List Species %, AGDW, BGDW, CAN-H (ln), LDMC, SLA, LNC and LCC. We performed a second PCA summarizing variables used in the first analysis in four indexes, each one accounting for a different ES on study. Algorithms for calculating ES indexes were adjusted to make indexes vary within a similar ranges (from 10 to 14 points). Plot key traits and algorithms for each ES are listed in Table 5.2.1 and 5.2.2.

Table 5.2.1: Ecosystem Services and vegetation traits.

CODE	ECOSYSTEM SERVICES / PARAMETERS	LNC	SLA	AGDW	CAN-H	BGDW	LDMC	LCC	Flowering Sp. %	Protected Sp. %	Black list Sp. %
	SUPPORTING										
ES_SU N	Nutrient cycling	X	X								
	PROVISIONING										
ES_PROV	Food, Fiber, Fuel			X	X						
	REGULATING										
ES_RE C	Climate regulation (Carbon storage)					X	X	X			
	CULTURAL										
ES_CULT	Aesthetic, Educational etc.								X	X	X

Table 5.2.2: Ecosystem Services and algorithms.

ES_SU N	$RADQ (LNC * SLA)$
ES_PROV	$RADQ (AGDW * \ln CAN_H / 10) / 3$
ES_RE C	$RADQ (BGDW * LDMC * LCC / 100000)$
ES_CULT	$[Flowering\ Sp.\ \% + Protected\ Sp.\ \% + (100 - Black\ List\ Sp.\ \%)] / 10$

After multivariate analysis, ES indexes values were range standardized and divided in five classes (1 very low, 2 low, 3 medium, 4 high, 5 very high). Multivariate analysis were performed using MSVP 3.13o software (Kovach Computing services, Pentraeth, Anglesey, UK), Pearson correlation coefficients between variables and between variables and PCA axes were calculated using the software R 2.6.2 (R Development Core Team 2008), triangular diagrams were made with SigmaPlot ® 7.0 software (SPSS Inc.). The list of the vegetation plots employed in the analysis is

reported in **Annex 1**, together with AGDW, BGDW and number of species data. ES indexes and CSR radii are also reported.

5.3 Results

The first PCA analysis (Fig. 5.3.1), carried out on the matrix of 10 key traits of plant communities, arranged the 60 plots into an approximately triangular multivariate space, with the first two principal components (PCA axis 1 and 2) accounting for 52.4% of total variance (first axis accounted for 27.13%). Pearson coefficients (Table 5.3.1) showed a strong correlation (Pearson coefficient $> |0.5|$) between PCA axis 1 and traits that are considered meaningful to the leaf economic spectrum (LNC, LDMC, SLA), indicating the capability of rapid resources acquisition, and therefore a rapid nutrient cycling, toward the negative end of the PCA axis 1, and a conservative resources economy with investment in durable tissues, and therefore an efficient carbon storage, toward the positive end of the axis. Others Important key traits for carbon storage showed a weaker correlation with axis 1 (BGDW 0.44, LCC 0.46).

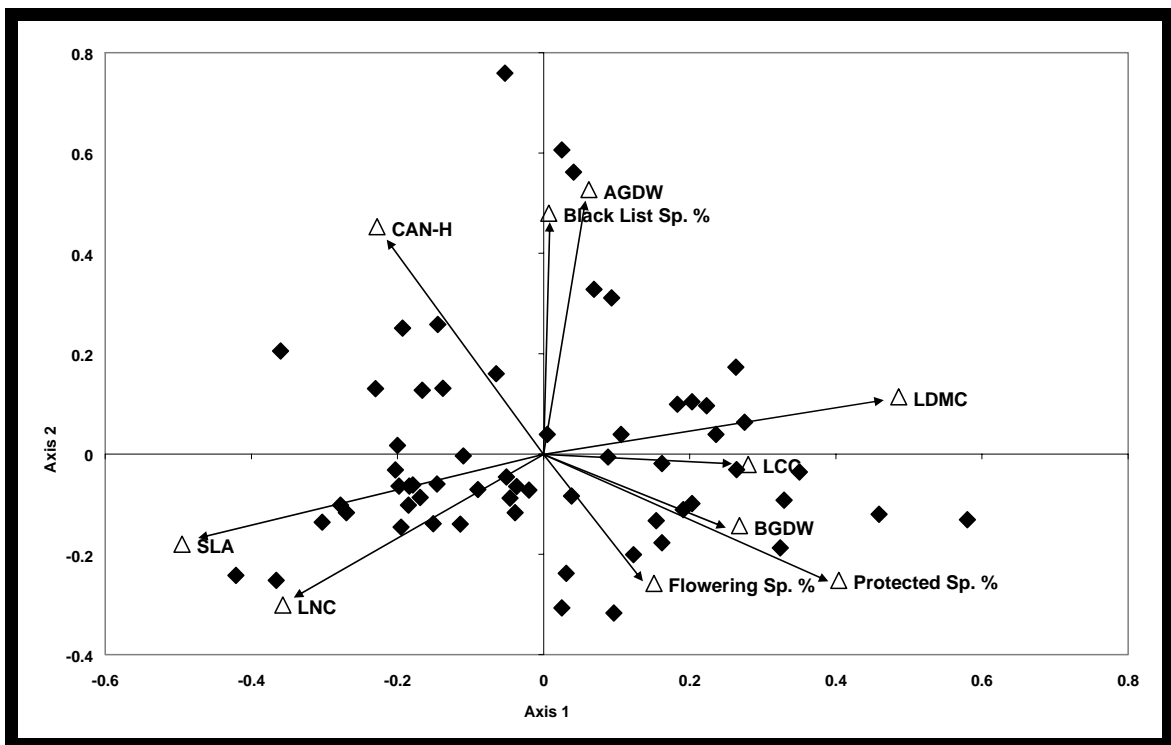


Figure 5.3.1: Principal components analysis (PCA) of 10 key trait variability for 60 herbaceous plant communities representative of Alps and continental Europe. Axis 1 and 2 account respectively for 27.13% and 25.23% of total variability. Traits are: Flowering Sp. % percentage of noticeable blooming species, Protected Sp. % percentage of protected species after Lombardy LR 10/2008; Black List Sp. % percentage of Black List species after Lombardy LR 10/2008, CAN_H canopy height, LCC leaf carbon content, LNC leaf nitrogen content, SLA specific leaf area, LDMC leaf dry matter content, AGDW aboveground standing crop biomass plus litter, BGDW belowground coarse roots biomass.

Plant communities traits that resulted highly correlated with PCA axis 2 are AGDW and CAN_H, indicating a sizeable production of exploitable biomass toward the positive

end of the axis. Floristic traits showed contradictory patterns of difficult interpretation. Black List Species % resulted highly correlated with biomass production due to the fact that dataset included plots dominated by large exotic species (*Solidago gigantea* Aiton, *Solidago canadensis* L., *Helianthus tuberosus* L., *Artemisia verlotiorum* Lamotte). Protected Species % was quite strongly correlated with the positive part of axis 1 due to the fact that a large amount of Protected species lives in communities that experiment harsh environmental factors and though show a high investment in durable tissues. Flowering Species % did not show any particular pattern.

Table 5.3.1: Pearson correlation coefficients between key plant communities traits, key traits and PCA axis. In bold values > |0.5|.

	Flowering Sp %	Protected Sp %	Black List Sp %	AGDW	BGDW	CAN_H (ln)	LNC	LCC	LDMC	SLA	Axis.1	Axis.2
Flowering Sp %	1											
Protected Sp %	0.32	1										
Black List Sp %	-0.14	-0.22	1									
AGDW	-0.20	-0.20	0.57	1								
BGDW	-0.12	0.41	-0.19	-0.06	1							
CAN_H (ln)	-0.41	-0.43	0.41	0.55	-0.12	1						
LNC	-0.09	-0.21	-0.36	-0.36	0.11	0.00	1					
LCC	0.23	0.12	0.17	0.08	0.33	-0.19	0.03	1				
LDMC	-0.08	0.32	0.02	0.11	0.34	-0.13	-0.51	0.27	1			
SLA	-0.06	-0.37	-0.10	-0.30	-0.15	0.09	0.57	-0.28	-0.67	1		
Axis.1	0.25	0.66	0.01	0.10	0.44	-0.37	-0.59	0.46	0.80	-0.82	1	
Axis.2	-0.41	-0.40	0.76	0.84	-0.23	0.72	-0.48	-0.03	0.18	-0.29	0.00	1

The second PCA performed on ES indexes still showed a broad triangular arrangement of plant communities in the multivariate space (Fig. 5.3.2). Note that PCA diagram have been modified to facilitate the comparison with the former PCA results. In particular axis 1 and 2 have been swapped and both are presented with inverse scale. PCA axis 1 ES accounted for 38.0% of total variability and resulted strongly correlated with provisioning ES (negative end) and with cultural ES (positive end). PCA axis 2 ES accounted for the 34.1% of total variability showing to be correlated (Table 5.3.2) with supporting ES regarding nutrient cycling (positive end) and with climate regulating ES via carbon storage (negative end). The PCA performed on ES indexes clearly showed an inverse relationship between cultural and provisioning ES on one side and between supporting and regulating on the other side, at least for the ecosystem functions considered. PCA also showed a strong independence of the two couple of analyzed ES.

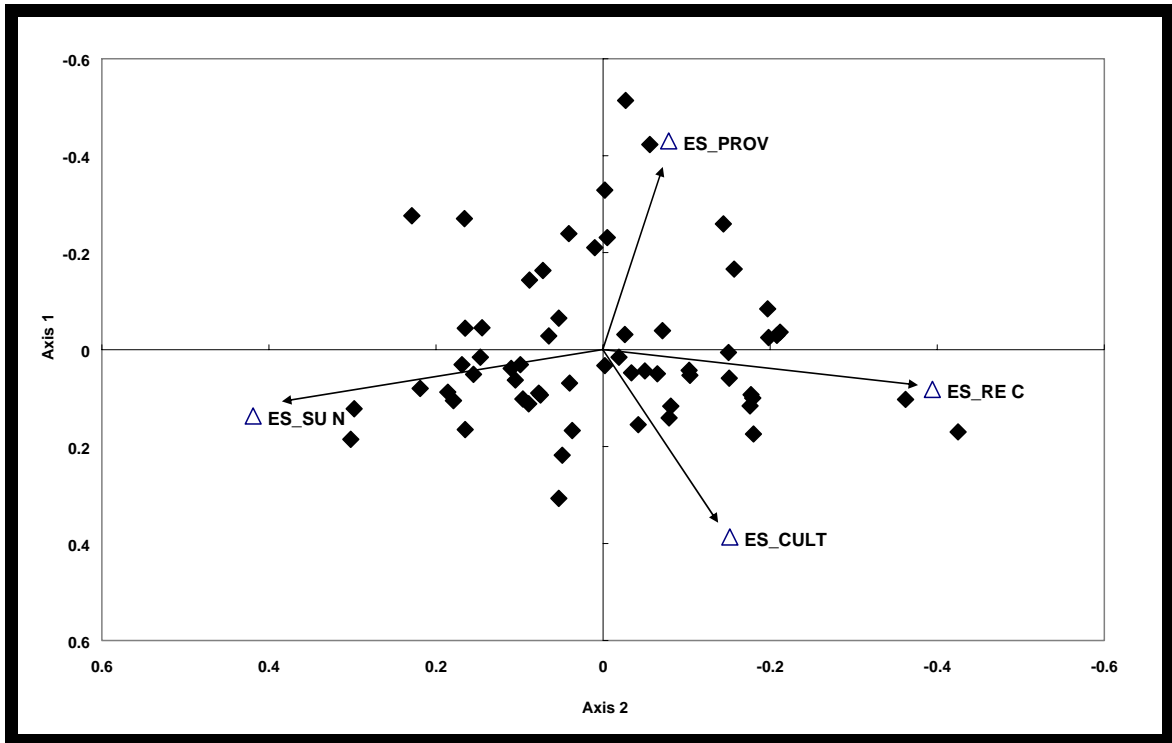


Figure 5.3.2: Principal components analysis (PCA) of 4 ES indexes variability for 60 herbaceous plant communities representative of Alps and continental Europe. Axis 1 and 2 account respectively for 38.0% and 34.1% of total variability. ES indexes are: ES_SU_N SUPPORTING (Nutrient cycling), ES_PROV PROVISIONING (Food, Fiber, Fuel), ES_RE_C REGULATING (Climate regulation - Carbon storage), ES_CULT CULTURAL (Aesthetic, Educational etc.)

Table 5.3.2: Pearson correlation coefficients between ES indexes, CSR radii and PCA axis. In bold values $> |0.5|$.

	ES_CULT	ES_PROV	ES_SU_N	ES_RE_C	S %	C %	R %	Axis 1 ES	Axis 2 ES
ES_CULT	1								
ES_PROV	-0.46	1							
ES_SU_N	-0.08	-0.29	1						
ES_RE_C	0.15	-0.06	-0.30	1					
S %	0.31	-0.21	-0.58	0.51	1				
C %	-0.46	0.73	0.09	-0.19	-0.64	1			
R %	0.06	-0.44	0.66	-0.48	-0.66	-0.15	1		
Axis 1 ES	0.79	-0.88	0.28	0.17	0.23	-0.67	0.36	1	
Axis 2 ES	-0.30	-0.15	0.81	-0.77	-0.68	0.18	0.70	0.00	1

Since three plant functional traits used in the present work are the same used for CSR plant strategies classification of species (LDMC, CAN_H and SLA) and allometric and leaf economic spectrum gradient appeared from the multivariate analyses, PCA results have been related to CSR radii calculated for each plot. Note that in the initial dataset the three CSR variables are added as weighted averages of the whole community, and not just as a single species or population trait, and that they were analyzed together with community "holistic" parameters (AGDW and BGDW) and floristic features.

Competitive radius (C %) of plots resulted strongly correlate with provisioning ES, Stress-tolerant radius (S %) with climate regulating ES (carbon storage) and Ruderal radius (R %) with supporting ES regarding nutrient cycling. Cultural ES were correlated with none of the CSR radii, since they rest on the value of species present in the plot in terms of geographical distribution, rarity, level of protection and aesthetic quality. These latter features are not prominent to survival strategy of species and thus do not influence quantitative functions and services offered by plant communities. The CSR radii correlation with examined ES quite clearly appeared even when plots were built in CSR triangular diagrams with ES indexes respective values; (Fig. 5.3.3).

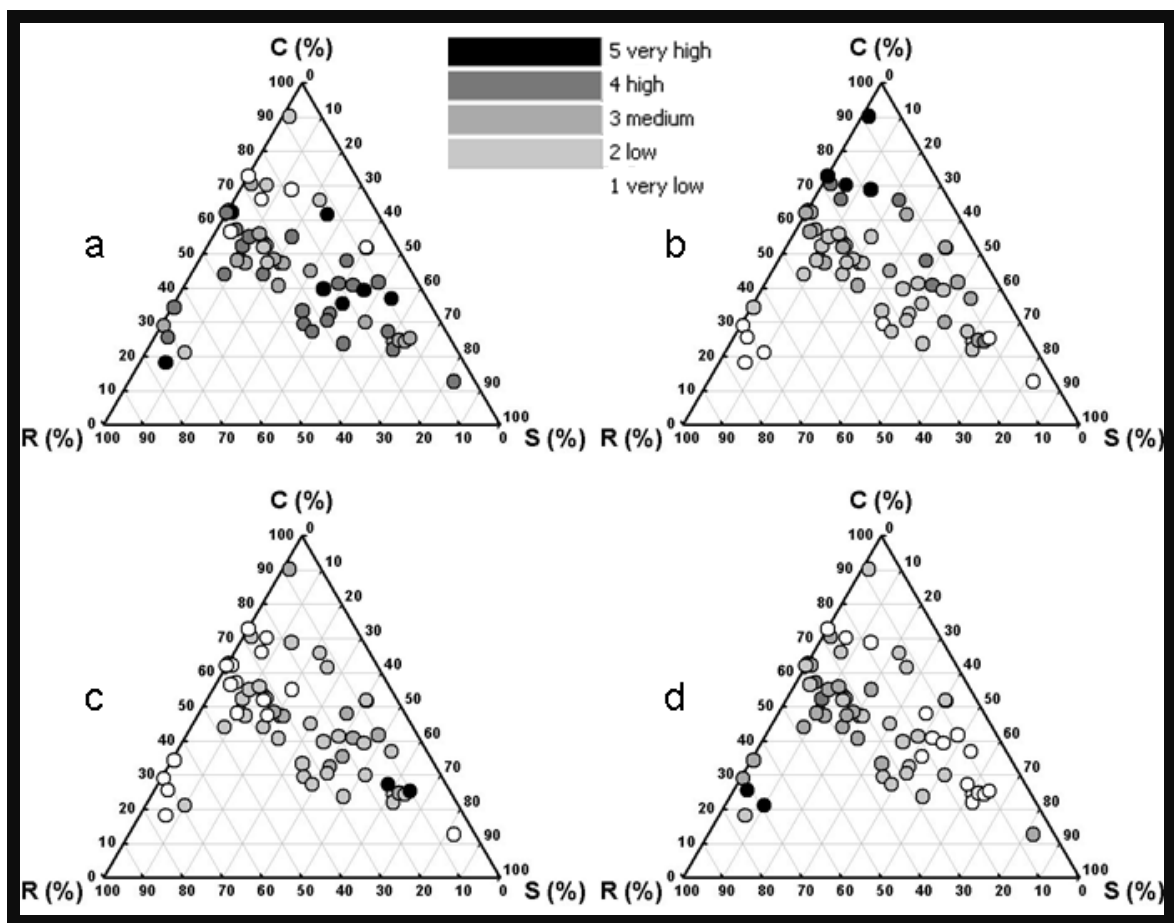


Figure 5.3.3: CSR Spectra of the analyzed plant communities with relative value of ES indexes. a) CULTURAL ES (Aesthetic, Educational etc.) b) PROVISIONING ES (Food, Fiber, Fuel) c) REGULATING ES (Climate regulation - Carbon storage) d) SUPPORTING (Nutrient cycling).

5.4 Discussion

Despite a great effort to define ecosystem functioning, functions and services it has not been found yet a unified approach for practical evaluation of ES, starting from ecological data. This work is an attempt to fill this gap, using (i) phytosociological data for estimating species abundance and floristic features, (ii) plant functional traits that can account for ecosystem functions via weighted averages of their values within the community. In practice the mass ratio hypothesis and the “hard trait – soft traits” concept (Hodgson *et al.* 1999) were linked to formulate simple indexes to describe and evaluate main ES.

Surely the approach of evaluation on whole of economic value of ES (Kreuter *et al.* 2001; Wang *et al.* 2006, Tianhong *et al.* 2010) may be useful in first instance for land management and policy, but does not allow to consider single ES and to properly evaluate their importance and changes, concerning their specific contribution to ecosystem and to humans. From this point of view, cultural ES are a striking example.

On the contrary the Millennium Ecosystem Assessment (MA) has acted following a more integrated approach to the problem, being able to define an ES classification following a multi-functional approach. Therefore from this work comes out that logical framework of the MA is the correct way to relate to land management, and thus to policy makers and public administrators, since ES cannot be considered on whole as they rely on different ecosystem functions and features (i.e. different fonts of variation in the multivariate space).

For this type of approach is necessary to: (i) divide ES that have a strong quantitative basis related to the ecosystem functioning from those that are more purely qualitative, such as cultural ES (ii) define certain indexes for each ES, based on parameters that are relatively easy to measure and estimate.

With regard to Ecosystem Services measured quantitatively, the scientific debate sees the opposite supporters of the close relationship between BD and ES and those who support the existence of positive relationship between Mass Ratio Hypothesis (MRH) and ES. However in this work was chosen to use mainly the MRH approach on the basis of evidence of Mokany *et al.* (2008), since other approaches rely mostly on biodiversity manipulation experiments (Balvanera *et al.* 2006). MRH approach can even be the tool to link ES assessment and CSR plant strategies theory, giving a strong logical framework.

Nevertheless the MRH approach cannot be conceptually applied for cultural ES, because their estimation should be based on the quality of the present species according to their evolutionary history, geographical distribution, rarity and aesthetical value. Indeed there is no correlation with the CSR radii. According to the findings of

this work, there is an evidence that cultural ES are in some way inversely proportional to provisioning ES that are closely related to biomass and then to the NPP.

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ANNEX 1

Site	Vegetation type	Elevation (m a.s.l.)	AGDW (gr m ⁻²)	BGDW (gr m ⁻²)	Number of Species	ES_CULT	ES_PROV	ES_SU N	ES_RE C	S (%)	C (%)	R (%)
BS Caffaro	Abandoned grassland dominated by <i>Poa pratensis</i> L.	130	560.0	951.6	20	3	2	3	1	9.6	48.1	42.3
BS Capriano del Colle	Wasteland dominated by <i>Ranunculus sardous</i> Crantz	92	324.0	324.3	9	3	1	3	1	0.6	29.0	70.4
BS Val Vestino (Moerna)	Verge dominated by <i>Pteridium aquilinum</i> (L.) Kuhn	1050	1154.7	2403.8	25	5	3	2	2	25.8	61.4	12.8
BS Val Grigna Casinone d'Arcina	Nitrophilous meadow dominated by <i>Poa annua</i> L.	1770	246.7	4121.7	6	2	1	5	2	9.9	21.1	69.0
BS Collio	Margins dominated by <i>Stachys sylvatica</i> L.	1000	486.7	809.3	19	4	2	3	1	20.1	55.0	25.0
SO Stelvio	Discontinuous grassland dominated by <i>Luzula alpinopilosa</i> (Chaix) Breistr. subsp. <i>alpinopilosa</i>	2646	477.3	2076.7	24	4	2	3	2	33.5	33.3	33.2
SO Stelvio	Dwarf shrub vegetation dominated by <i>Kalmia procumbens</i> (L.) Gift, Kron & Stevens ex Galasso, Banfi & F. Conti	2608	957.3	1640.4	18	3	2	1	2	61.0	24.4	14.6
SO Stelvio	Grassland dominated by <i>Carex curvula</i> All.	2600	697.3	2013.9	16	4	2	1	2	62.1	22.0	15.9
SO Stelvio	Dwarf shrub vegetation dominated by <i>Salix herbacea</i> L.	2673	324.0	1328.6	16	4	1	2	2	35.8	29.5	34.7
BS Val Grigna Rosello di sopra	Peatland dominated by <i>Trichophorum cespitosum</i> (L.) Hartm.	1742	244.0	8456.5	11	3	1	1	5	64.7	25.4	10.0
BS Val Grigna Rosello di sopra	Peatland dominated by <i>Carex panicea</i> L.	1742	624.0	7571.2	14	4	2	1	5	58.2	27.2	14.6
BS Iseo Bosine	Wasteland dominated by <i>Capsella grandiflora</i> (Fauché & Chaub.) Boiss.	504	610.7	933.7	10	4	2	3	1	0.7	34.3	65.0
BS Oglio (Cascina Ardemagni)	Wasteland dominated by <i>Stellaria media</i> (L.) Vill.	52	360.0	1050.4	10	4	1	5	1	3.5	25.6	70.9

Site	Vegetation type	Elevation (m a.s.l.)	AGDW (gr m ⁻²)	BGDW (gr m ⁻²)	Number of Species	ES_CULT	ES_PROV	ES_SU N	ES_REC	S (%)	C (%)	R (%)
BS Via Duca degli Abruzzi	Wasteland dominated by <i>Avena fatua</i> L.	130	986.7	396.8	7	4	3	2	1	0.0	62.0	38.0
BS Oglio (Borgo S.Giacomo)	Wasteland dominated by <i>Saxifraga tridactylites</i> L.	44	101.3	699.1	5	5	1	2	1	6.7	18.1	75.2
VA Lonate Pozzolo (Tornavento)	Meadow dominated by <i>Filago minima</i> (Sm.) Pers.	207	376.0	469.7	12	4	1	3	1	82.1	12.6	5.3
BS Monte Maddalena	Meadow dominated by <i>Bromus erectus</i> Huds.	790	744.0	965.7	17	5	3	1	2	54.2	36.9	8.9
BS Monte Crocedomini	Pasture grassland dominated by <i>Horminum pyrenaicum</i> L.	2010	481.3	2034.5	41	4	2	2	2	39.0	27.3	33.7
BS Crocedomini (M.te Rondenino)	Pasture grassland dominated by <i>Carex sempervirens</i> Vill.	2020	684.0	2940.3	36	5	2	2	2	35.7	39.7	24.7
BS Malga Guglielmo di Sotto	Seasonal livestock enclosure dominated by <i>Rumex alpinus</i> L.	1571	1280.0	7121.3	8	3	4	5	3	0.2	62.8	37.0
BS Brione	Meadow dominated by <i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. & C. Presl	720	966.7	1933.1	30	3	3	2	2	29.7	45.0	25.3
BS Malga Guglielmo di Sotto	Grassland dominated by <i>Festuca paniculata</i> (L.) Schinz & Thell. subsp. <i>paniculata</i>	1492	1038.7	1808.2	23	3	3	2	2	51.1	30.0	18.9
BS Provaglio d'Iseo	Wasteland dominated by <i>Sorghum halepense</i> (L.) Pers.	190	1189.3	1537.1	12	2	4	2	2	21.8	65.7	12.5
BS Malga Guglielmo di Sopra	Meadow dominated by <i>Phleum alpinum</i> L.	1621	598.7	5320.7	29	4	2	2	3	40.9	32.4	26.7
BS Punta di Auccia	Pasture dominated by <i>Nardus stricta</i> L.	2150	836.0	2538.5	17	4	2	2	2	48.6	23.7	27.7
BS Val d'Arcina	Stream margin dominated by <i>Senecio alpinus</i> (L.) Scop.	1890	1130.7	1253.2	6	5	3	3	1	1.2	62.1	36.7
BS Malga Guglielmo di Sopra	Pasture dominated by <i>Geum montanum</i> L.	1780	604.0	2535.0	29	4	2	2	2	41.2	30.5	28.3

Site	Vegetation type	Elevation (m a.s.l.)	AGDW (gr m-2)	BGDW (gr m-2)	Number of Species	ES_CULT	ES_PROV	ES_SU N	ES_REC	S (%)	C (%)	R (%)
BS Passo delle Portole	Grassland dominated by <i>Sesleria caerulea</i> (L.) Ard.	1726	913.3	3112.0	42	5	2	1	3	42.6	35.4	22.0
BS Poncarale	Wasteland dominated by <i>Setaria viridis</i> (L.) P. Beauv.	97	1040.0	147.3	8	1	3	2	1	3.8	56.5	39.7
VB Monte Zeda	Verge dominated by <i>Pteridium aquilinum</i> (L.) Kuhn	1018	1618.7	2111.0	14	3	4	3	2	2.2	70.3	27.5
VB Monte Zeda	Grassland dominated by <i>Molinia caerulea</i> (L.) Moench subsp. <i>arundinacea</i> (Schrank) K. Richt.	1380	1441.3	3910.9	16	4	4	1	3	37.4	47.9	14.7
BS Bagnolese	Wasteland dominated by <i>Abutilon theophrasti</i> Medik.	95	1132.0	206.7	4	1	4	2	1	6.8	65.9	27.3
BS San Vigilio	Wasteland dominated by <i>Helianthus tuberosus</i> L.	211	2377.3	679.3	6	1	5	1	1	0.2	72.7	27.1
MI Buscate	Wasteland dominated by <i>Artemisia verlotiorum</i> Lamotte	180	2274.7	1411.4	4	1	5	1	2	13.1	68.8	18.2
MI Magnago	Margin dominated by <i>Solidago canadensis</i> L.	192	1732.0	1070.7	6	2	5	1	1	6.0	70.1	23.8
VA Gropello di Gavirate	Meadow dominated by <i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. & C. Presl	240	805.7	1603.7	29	3	3	3	2	23.7	40.7	35.6
VA Varese (Schiranna)	Meadow dominated by <i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. & C. Presl	243	960.6	964.6	23	2	3	2	1	14.4	51.9	33.7
VA Inarzo	Meadow dominated by <i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. & C. Presl	243	619.9	1282.3	22	2	2	3	1	17.6	47.4	35.0
LC Moggio	Meadow dominated by <i>Trisetaria flavescens</i> (L.) Baumg.	1200	783.7	1722.7	27	3	3	3	2	12.0	47.3	40.7
LC Casargo	Meadow dominated by <i>Trisetaria flavescens</i> (L.) Baumg.	905	544.1	2427.2	28	4	2	3	2	8.5	44.1	47.5
LC Culmine S.Pietro	Meadow dominated by <i>Trisetaria flavescens</i> (L.) Baumg.	1275	731.4	1460.9	29	4	2	3	2	18.2	44.0	37.7

Site	Vegetation type	Elevation (m a.s.l.)	AGDW (gr m ⁻²)	BGDW (gr m ⁻²)	Number of Species	ES_CULT	ES_PROV	ES_SU N	ES_REC	S (%)	C (%)	R (%)
VA Vararo	Meadow dominated by <i>Bromus erectus</i> Huds.	780	935.0	2889.3	22	4	3	1	3	48.5	41.7	9.8
LC Monte Barro	Meadow dominated by <i>Bromus erectus</i> Huds.	700	721.0	2370.2	25	5	2	1	2	46.1	39.3	14.6
VA Monte Chiusarella	Meadow dominated by <i>Bromus erectus</i> Huds.	638	719.9	1517.6	27	4	2	2	2	38.7	41.3	20.0
VA Passo della Forcora	Pasture dominated by <i>Nardus stricta</i> L.	1210	1642.0	4116.3	17	4	4	1	3	42.5	40.8	16.7
CO Passo del Giovio	Pasture dominated by <i>Nardus stricta</i> L.	1700	1210.2	3080.5	20	3	3	1	3	62.3	24.7	13.0
CO Alpe Numbruno	Pasture dominated by <i>Nardus stricta</i> L.	1720	1832.6	1800.8	8	3	4	1	2	63.8	24.4	11.8
VA Angera	Grassland dominated by <i>Molinia caerulea</i> (L.) Moench subsp. <i>arundinacea</i> (Schrank) K. Richt.	199	1208.0	2261.0	4	1	3	2	2	40.5	51.6	7.8
VA Gornate Olona	Grassland dominated by <i>Molinia caerulea</i> (L.) Moench subsp. <i>arundinacea</i> (Schrank) K. Richt.	350	778.9	1287.8	16	1	3	2	2	40.3	51.9	7.8
VA Musignano	Verge dominated by <i>Pteridium aquilinum</i> (L.) Kuhn	830	1911.3	4624.3	10	2	5	2	3	1.8	90.1	8.1
BG Valleve (S.Simone)	Seasonal livestock enclosure dominated by <i>Rumex</i> <i>alpinus</i> L.	1780	724.2	2775.0	17	4	2	4	2	8.9	52.3	38.8
BG Valleve (S.Simone)	Seasonal livestock enclosure dominated by <i>Rumex</i> <i>alpinus</i> L.	1780	647.4	3181.8	14	4	2	3	2	9.3	55.0	35.7
BG Valleve (S.Simone)	Seasonal livestock enclosure dominated by <i>Rumex</i> <i>alpinus</i> L.	1780	575.1	1351.8	20	4	2	4	1	10.1	48.3	41.5
BG Valleve (S.Simone)	Seasonal livestock enclosure dominated by <i>Rumex</i> <i>alpinus</i> L.	1780	693.0	1630.0	14	3	2	3	2	11.4	55.8	32.8
BG Valleve (S.Simone)	Seasonal livestock enclosure dominated by <i>Rumex</i> <i>alpinus</i> L.	1780	796.9	1427.6	17	4	3	4	1	5.0	57.1	38.0

Site	Vegetation type	Elevation (m a.s.l.)	AGDW (gr m-2)	BGDW (gr m-2)	Number of Species	ES_CULT	ES_PROV	ES_SU N	ES_REC	S (%)	C (%)	R (%)
BG Valleve (S.Simone)	Meadow dominated by <i>Bistorta officinalis</i> Delarbre	1780	661.3	4003.7	11	3	2	3	3	20.8	47.4	31.8
BG Valleve (S.Simone)	Meadow dominated by <i>Bistorta officinalis</i> Delarbre	1780	679.9	1812.1	16	3	2	2	2	14.0	53.1	32.9
BG Valleve (S.Simone)	Meadow dominated by <i>Bistorta officinalis</i> Delarbre	1780	480.2	4952.6	15	3	2	2	3	21.8	47.2	31.0
BG Valleve (S.Simone)	Meadow dominated by <i>Bistorta officinalis</i> Delarbre	1780	677.3	3273.4	13	3	2	3	2	14.9	52.3	32.8
BG Valleve (S.Simone)	Meadow dominated by <i>Bistorta officinalis</i> Delarbre	1780	587.4	5144.4	16	3	2	3	3	18.7	48.5	32.8