Fine-root seasonal pattern, production and turnover rate of European beech (Fagus sylvatica L.) stands in Italy Prealps: Possible implications of coppice conversion to high forest

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Abstract

The aim of this study was to investigate the possible effects of coppice conversion to high forest on the beech fine-root systems. We compared the seasonal pattern of live and dead fine-root mass ($d < 2$ mm), production and turnover in three beech stands that differed in management practices. Tree density was higher in the 40-year-old coppice stand than in the stands that were converted from coppice to high forest in 1994 and 2004, respectively. We found that a reduction in tree density reduced the total fine-root biomass (Coppice stand, 353.8 g m^{-2}; Conversion 1994 stand, 203.6 g m^{-2}; Conversion 2004 stand, 176.2 g m^{-2}) which continued to be characterised by a bimodal pattern with two major peaks, one in spring and one in early fall. Conversion to high forest may also affect the fine-root soil depth distribution. Both fine-root production and turnover rate were sensitive to management practices. They were lower in the Coppice stand (production 131.5 g m^{-2} year^{-1}; turnover rate 0.41 year^{-1}) than in the converted stands (1994 Conversion stand: production 232 g m^{-2} year^{-1}, turnover rate 1.06 year^{-1}; 2004 Conversion stand: production 164.2 g m^{-2} year^{-1}, turnover rate 0.79 year^{-1}).

Keywords: *Conversion to high forest,* Fagus sylvatica *L., fine-root production, fine-root seasonal pattern, fine-root turnover rate*

Introduction

Consequent to the continuous increase of CO_2 in the atmosphere, the function of forests in sequestering carbon has become one of the most intensely investigated topics in forestry research. In forest ecosystems, the below-ground carbon pool accounts for 10–46% of the total tree stand carbon pool (Helmisaari et al. 2002). Given this high percentage, models of the below-ground tree biomass are required to calculate the overall carbon stock and the related stock changes (Godbold & Brunner 2007). Therefore, there is a need to better understand some of the aspects of root development and life cycle that might influence below-ground carbon stock turnover (Tobin et al. 2007).

Within a root system, very fine and fine roots (0.5 mm < *diameter* and 0.5 < *diameter* < 2 mm; Zobel & Waisel 2010) represent the most dynamic component of a root apparatus (Hendrick & Pregitzer 1992; Barlow 2010) despite their relatively minor contribution to the overall root biomass (Vogt et al. 1996). In fact, their turnover accounts for as much as 33% of annual net primary productivity (NPP) (Jackson et al. 1997). Moreover, given their simple anatomical organisation, fine roots are the most sensitive component within the overall root system in that they respond rapidly to variations in the rooting environment. Therefore, the fine-root compartment should be investigated when studying nutrient cycling and carbon accumulation in a forest ecosystem (Helmisaari et al. 2002).

It is more difficult to model carbon allocation in the below-ground compartment than into the above-ground compartment. Firstly, collection of field data is highly labour-intensive, and secondly, models must include a variety of internal (e.g. genotype of plant species) and external (e.g. temperature,

precipitation, soil properties, nutrient availability and competition between plants) factors (Majdi et al. 2005). A major external factor is the effect of anthropological disturbances on forest ecosystem including management practices (Diaci et al. 2010; Liira & Kohv 2010; Rötzer et al. 2010). Interestingly, a recent review of root biomass data of the three main types of European ecosystems demonstrated that the fine-root biomass (FRB) undergoes considerable fluctuations in relation to above-ground characteristics (Finér et al. 2007, 2011). Moreover, various studies have shown that forest-use intensity and disturbance has a profound impact on fine-root characteristics (Chertov et al. 2005; Leuschner et al. 2008). European beech (*Fagus sylvatica* L.) is a major tree species in European forests and one of the most thoroughly scientifically investigated in diverse field due to its wide distribution (Magri et al. 2006). In Italy, beech forest represents one of the most widespread deciduous trees accounting 17.3% of the total area covered by deciduous species (Manes et al. 2010). In recent reviews by Finér et al. (2011a,b) on FRB, production and turnover rate in forest ecosystem, very little data exist in beech forests in south Europe area, and there are practically no data for Italy.

Fine-root growth intra-annual dynamics (seasonal pattern) is crucial for estimating fine-root dynamics and carbon cycling in forest ecosystems (Gill & Jackson 2000; Fukuzawa et al. 2010) generally reflects changes in seasonal variations of water and consequent nutrient availability (Coners & Leuschner 2005; Vanguelova et al. 2005; Mainiero & Kazda 2006) as well as an ontogenic response to local conditions (Chiatante et al. 2005; Claus & George, 2005). In general, fine-root production increases in spring and peaks in late spring to mid-summer before decreasing in the fall (Brassard et al. 2009). On the contrary, long-term dynamics of FRB (inter-annual) is still not clearly understood. The variability of site and species assemblage over time may largely be responsible for the different FRB stand development trends (Brassard et al. 2009). Various studies have investigated the ability of beech for vegetative regeneration by sprouting from stumps or roots (Papalexandris & Milios 2010). Few authors describe general changes in fine-root production with increasing stand age or altering site conditions. In most forest tree species, clear-cut harvesting leads to the disappearance of all fine roots followed by a rapid recovery of their biomass within a few years (Claus & George 2005). On the contrary, results about dependence of FRB on the age of forest stand are not coherent (Claus & George 2005). Brassard et al.'s review (2009) reported that differences in FRB among forest stands may be due to changes from stand initiation to a later stage of the stand development (canopy closure), pointing out that forest management may directly influence below-ground C dynamics.

Despite coppice represents the great majority of forest habitats in Europe, data on this type of forest are still not exhaustive. In Italy in recent years, regional and governmental policy direct forest management practices to conversion from coppice to high-standard condition. Natural beech forests have been subjected for centuries to coppice management in order to produce high yields of merchantable wood (Nocentini 2009; Ciancio & Nocentini 2011). A coppice stand (CpS) is usually characterised by a high stand tree density due to a dense distribution of stools, each of which includes a number of stems. Only one stem in each stool is left during conversion to high forest management. Thus, conversion practice considerably changes tree density and consequently canopy cover, which in turn alters most of the stand environmental factors like, light/shade distribution and surface soil layer temperature. Given the importance of these variations, it is reasonable that the contemporaneous variation of so many environmental factors might affect the life cycle of fine roots.

We selected three beech forest stands differing in use intensity and cutting age (an undisturbed 40-year-old CpS and two CpSs converted to high forest in 1994 and 2004, respectively) in the Italian Southern Alps in order to test the following hypothesis: (a) harvesting above-ground biomass causes a general decline in fine-root standing biomass; (b) management practice affects stand developmental stage influencing inter/intra-annual fine-root dynamics. The three stands reflect different cutting ages: the more recent the cutting operation, the more severe the forest-use intensity and the disturbance effect. In particular, we evaluated for each stand: (1) the fine-root standing biomass and necromass seasonal pattern during the 2008 growing season; (2) the annual fine-root production and turnover rate; (3) how the aforementioned fine-root traits vary in relation to the soil profile.

Materials and methods

Site description

The study area is located in the catchments of the Telo stream in the Lombardy Alps (Intelvi Valley, NW Italy, 45° 59′N, 9° 07′E) approximately from 1160 to 1200 m above sea level between Lakes Como and Lugano. This area is characterised by a sub-continental climate, with a mean annual precipitation of 1600 mm, mainly concentrated in two main periods (April–May and October–November),

and a mean annual temperature of 10–11°C. Rainfall (mm) and air temperature (°C) were recorded at 60 min interval. Sensors (Thermometer DMA572 and Rain gauge DQA030; LSI Latstem s.r.l.) were mounted on a 3-m high mast and set up on a hill (Alpe di Ponna) 0.8 km from the experimental site. An intense snow fall on 22 November 2008 (http://www.centrometeolombardo.com/content.asp?contentid=3900) prevented sampling until the following spring.

According to the World Reference Base (WRB) for Soil Resources (http://www.fao.org FAO/IS-RIC/IUSS 2006), soil type is Leptosol 40–50 cm deep. Sampling plots were placed in three stands subjected to different types of forest management. Specifically, three beech stands were considered: a residual CpS, the only one left in the area, cut once 40 years ago and then allowed to re-grow from stumps and never recut; two converted stands from coppice to high forest cut in 1994 (CvS 1994) and 2004 (CvS 2004), respectively. Cutting consisted in reducing the number of stems per stool to one per stool, and eliminating exceeding stools thereby reducing stand tree density, and transforming the coppice to high forest. Moreover in CvS 2004, the soil had been recently disturbed consequent to management practices as observed by Gondard et al. (2002) and Hartanto et al. (2003) in their studies. The three stands were adjacent to each other and located on the same slope facing south-west, with slope average between 28° and 30°.

Species and cover composition of the understorey differed among the three stands. A vegetation survey conducted in June 2008 in CpS showed that beech seedling cover was less than 5%: herbaceous species covered 5% of the stand soil surface and mosses covered 35%. Five herbaceous species were found and the most abundant species were *Luzula nivea* with a cover of 20% and *Maianthemum bifolium* (up to 4%). In the CvS 1994, beech seedlings covered up to 15% of the soil surface. The herbaceous species covered from 20 to 50% with 16 species of which the most abundant were *Pteridium aquilinum* (from 8 to 20%), *Maianthemum bifolium* (up to 20%) and *Silene rupestris* (up to 35%). Mosses covered only 5% of the soil surface. In CvS 2004, beech seedlings covered up to 15% and seedlings of birch (*Betula pendula* Roth) covered 2%. Herbaceous species covered up to 85% and mosses only 1%. The number of herbaceous species was 19, the most abundant were *Carex pallescens* (25%), *Veronica officinalis* (15%), *Rumex acetosella* (10%) and *Luzula pilosa* (10%). Soil temperature was measured on each fine-root sampling date at the soil core sampling point at three depths (5, 15

and 25 cm). Measurements were taken by Checktemp 1 thermometer with an NTC thermistor sensor (Hanna Instruments®) (±0.3°C).

Seven sampling plots per stand along a 140-m transect were surveyed to establish the number of trees and diameter at breast height (dbh). In the case of CpS each stem was counted as a single tree. The plots were circular-shaped with a 20-m diameter for a total of 2199 m^2 area per stand. In July 2008, canopy cover was measured by hemispherical photos analysed with the Can-eye freeware (https://www4.paca.inra.fr/can-eye, 2011). Ten hemispherical photos per stand were taken at 7.5-m intervals along a transect. In November 2008, the above-ground biomass was measured. For each stand, three sample trees representing the range of tree sizes were selected for destructive harvesting, and the dbh was measured. The trunk and branches of each tree were sliced into sections almost one-tenth of the respective total length. The total fresh weight of each tree was measured using a forest skidding tractor and a portable dynamometer. For each tree, the dry weights of two sub-samples of trunk and branch at the small-end and large-end were determined after oven drying at 70°C to a constant weight (2–3 weeks). Finally, a site-specific allometric relationship was developed to estimate the woody biomass from the tree dbh. The best fit ($r^2 = 0.97$) was obtained by a unique power function suitable for all three stands (no stand effect, ANCOVA $p = 0.74$). The power Equation 1 is:

$$W = aD^b \qquad (1)$$

where W is dry weight (kg), D is dbh (cm), $a = 1.0594$ and $b = 1.8237$.

Fine-root measurements

Fine-root biomass (hereafter named all roots with diameter smaller than 2 mm including very fine-root with diameter smaller than 0.5 mm; Zobel & Waisel 2010) was determined in soil cores (Vogt & Persson 1991). In each stand, four permanent 10-m^2 plots were established. Each plot was the centre of a circular-shaped plot with a 20-m diameter where above-ground characteristics were also measured. The top 30 cm of soil accumulates most of the root biomass (Jackson et al. 1996) therefore two 30 cm deep soil cores (4 cm diameter) were randomly collected in each plot using a motor-driven portable core sampler (adapted from Ponder & Alley 1997). We established sampling times in relation to the growing seasons of beech forests from May to October 2008, when the soil was free of snow. During winter period, experimental site was difficult to reach due to snow cover, therefore we could not

sample. In accordance with others (Crider 1928; Claus & George 2005; Chen et al. 2011), we assumed that fine-root production and decomposition are low during winter. Moreover, we collected core samples in April 2009 after snowmelt. Therefore, the kinetics of biomass variation was investigated from May 2008 to April 2009. Each core sample was divided into three portions according to the depth from the soil surface: 0–10 (including the first 2–3 cm of a humus layer), 10–20 and 20–30 cm. The mean distance between plots was 50 m, which is 6- to 10-fold the distance between trees in all stands.

Samples were stored in plastic bags at 4°C until processed. For processing, each sample was placed in a nylon bag (300 μm mesh) that was contained in a plastic cylinder (6 mm mesh) and washed automatically in a washing machine (adapted by Benjamin and Nielsen 2004). We distinguished beech roots from other understory roots by identifying morphological characteristics at the microscope. The morphological characteristics of beech fine roots were previously established from samples dug near the tree. Beech fine roots were reddish and stiffer than the understorey roots (herbaceous). The fine roots of beech were classified as ''live'' (dry weight hereafter termed FRB) or ''dead'' (dry weight hereafter termed fine-root necromass [FRN]) depending on their colour, texture and shape (Vogt & Persson 1991). Live roots were resilient, translucent and white to tan; dead roots fragmented easily, were dull, and grey to black. The reliability of the criteria we used was confirmed by observations at the binocular microscope. These visual and manual criteria were based on readily observable morphological features. These criteria yielded reproducible results and hence provide a practical approach to classifying roots on the scale required in this study. The following root traits were determined for each stand: (1) mean live (FRB; g m^{-2}) and dead (FRN; g m^{-2}) fine-root dry mass; (2) FRB and FRN seasonal pattern; (3) fine-root annual production (FRP; g m^{-2} year^{-1}) and turnover rate (FRT; year^{-1}); (4) fine-root depth distribution.

In a study conducted in a *Fagus–Quercus* mixed forest, Hertel and Leuschner (2002) compared four methods used to evaluate fine-root production and found that the minimum–maximum method would yield a more realistic result (25% overestimation). We therefore estimated FRP using the minimum–maximum method procedure (Edwards & Harris 1977; McClaugherty et al. 1982). This method calculates and sums the difference between minimum and maximum of total fine-root dry mass (FRB plus FRN). Only significant differences between minimum and maximum were considered. Fine-root turnover rates of FRB were calculated as Annual Root Production divided by Maximum Standing Biomass (Gill & Jackson 2000).

Statistical analysis

Four permanent plots were established within each stand. According to Godbold et al. (2003), this is a point comparison approach rather than a replicated experiment on the ecosystem scale. Each single plot was considered as the experimental unit and each pair of soil cores per plot was pooled and treated as one ($n = 4$). FRB and FRN were evaluated throughout a soil depth of 0–30 cm and at three different soil depths (0–10, 10–20 and 20–30 cm). For the whole 0–30 cm soil depth, FRB, FRN and FRP were calculated by summing values obtained in each of the three soil layers. The data were not normally distributed neither could satisfyingly be transformed. Therefore, differences (FRB and FRN, total mean FRB per number of trees) among the three forest stands and the different three soil depths were analysed using a non-parametric analysis of variance (Kruskal–Wallis test). The effect of tree density on FRB was assessed using a linear regression function. Mann–Whitney two samples test was used for FRP estimation (i.e. difference between maximum and minimum). To test the significance of each peak in the seasonal pattern, the Dunnett's *t*-test (unilateral alternative, $p < 0.05$) was applied to differences among the peak (reference mean) and both prior and subsequent first minimum values (Montagnoli et al. 2012). Differences were considered significant at $p \leq 0.05$ unless otherwise stated. Large spatial variation is a common problem in fine-root dynamics quantification, justifying the use of an alpha value of 0.10. Statistical analysis was carried out with the statistical software package SPSS 17.0 (SPSS Inc, Chicago IL, USA).

Results

Above-ground stand characteristics

As shown in Table I, above-ground structure differed among the three forest stands, tree density and above-ground biomass were higher in the CpS than in CvS 2004, whereas dbh and height were greater in CvS 2004. In CvS 1994, values of all the parameters tested were intermediate between those of CpS and CvS 2004. The differences in canopy cover percentage measured by the hemispherical photo analysis reflected those recorded for tree density, namely canopy cover was the highest in the CpS and the lowest in CvS 2004 (Table I). Soil temperatures were

Table I. Beech above-ground biomass characteristics and soil temperature of the three stands.

Forest stand	Density (trees ha^{-1})	Above-ground biomass (Mg ha^{-1})	Mean dbh (cm)	Mean tree height (m)	Canopy cover (%)[a]	Soil temperature (°C)			
						0–30 cm[b]	5 cm	15 cm	25 cm
CpS	724 ± 35	248.5 ± 15.6	17.2 ± 0.7	12.1 ± 0.3	94.2 ± 0.6	10.2 ± 0.3 a	10.6 ± 0.6 a	10.2 ± 0.5 a	9.9 ± 0.5 a
CvS 1994	279 ± 24	123.7 ± 7.3	22.6 ± 1.5	12.8 ± 0.7	74.2 ± 5.5	11.3 ± 0.3 b	11.7 ± 0.6 ab	11.1 ± 0.5 ab	10.9 ± 0.5 b
CvS 2004	167 ± 20	91.8 ± 20.2	31.9 ± 1.9	18.9 ± 0.8	54.3 ± 3.2	12.2 ± 0.4 c	12.7 ± 0.7 b	12.0 ± 0.6 b	11.9 ± 0.6 c

Data shown are the mean and standard error (SE). dbh, diameter at breast height. [a]Canopy cover values are the mean of 10 replicates. Beech above-ground biomass values are the mean of seven replicates. [b]Soil temperature (0–30 cm) is referred to the mean of three soil depths (5, 15 and 25 cm) and each value is the mean of four replicates for eight sampling dates (May 2008–April 2009).

invariably lower in the CpS where the canopy cover was elevated and the shading effect was higher, whereas soil temperature was the highest in CvS 2004 where the percentage of canopy cover was the lowest. Soil temperature slightly decreased with increasing soil depth (Table I). Rainfalls were maximum in Spring and Autumn with minimum in August. Seasonal variation of the soil temperature roughly followed the air temperature, increasing from spring to summer with maximum at the beginning of August. This trend was similar in the three stands (data not shown).

Fine-root standing mass and seasonal pattern

Figure 1 shows the seasonal variations of FRB and FRN in the three stands and for three soil depths. In general, FRB seasonal trend showed a bimodal pattern that became more evident with increasing soil depth. However, seasonal trend differed in the timing of the two peaks formation usually ranging between June–July the first and September–October the second. For the whole 0–30 cm soil profile, in both Conversion stands, only the first peak value was significantly higher than prior and subsequent minima ($p < 0.05$). On the whole, this response was maintained across the three soil layers. In contrast, CpS did not show significant peaks with the only exception of two maxima in the 20–30 cm layer. In general, FRN seasonal trend showed a unimodal pattern with one peak ranging between July and August. This peak was significant ($p \leq 0.05$) in both Conversion stands for the whole 0–30 cm and at different soil depth depending on the stand considered. For the CpS, the peak value was marginally significant ($p < 0.1$) only for the whole 0–30 cm soil profile and 10–20 cm soil layer. The mean 0–30 FRB and FRN values were significantly higher in CpS (Kruskal–Wallis test, $p < 0.05$; Table II) than both Conversion stands. Fine-root biomass in CvS 1994 was significantly higher than that in CvS 2004, whereas no differences occurred for FRN.

In order to obtain an estimation of the FRB per tree, for each selected plot, we divided the mean FRB (0–30 cm) ($n = 4$; data not shown) by the tree number. In both Conversion stands (CvS 2004, 7.15 ± 0.6 kg tree^{-1}; CvS 1994, 5.19 ± 0.5 kg tree^{-1}), this ratio resulted significantly higher ($p < 0.05$; Kruskal–Wallis test) than in CpS (3.18 ± 0.2 kg tree^{-1}). The difference between Conversion stands marginally missed the 5% level ($p = 0.06$; Kruskal–Wallis test). Moreover, FRB showed a significant direct linear relationship ($F = 47.901$, $p < 0.001$) with the tree density (Figure 2).

For all the stands considered, on average, the uppermost soil layer (0–10 cm) contain 59 and 58% of the total biomass and necromass, respectively. In fact, the biomass of live and dead fine roots decreased with depth (Table II) although the trend slightly differed among stands. In CpS, the decrease was significant for both FRB and FRN. In CvS 1994, only FRB values in the first soil layer significantly exceed those in the two deeper layers, whereas FRN significantly decreased along the soil depth profile. In CvS 2004, biomass did not differ significantly between the first two soil layers (0–10 and 10–20 cm), but significantly decreased in the deepest layer (20–30 cm).

Fine-root production and turnover

When evaluated in the whole 0–30 cm thickness of the soil, annual FRP showed the lowest value in CpS and the highest in CvS 1994 (Table III). In the uppermost soil layer, annual FRP was higher in both Conversions than in CpS. Fine-root annual production showed the lowest values in the deepest soil layer (20–30 cm) at all the three stands. Interestingly, CvS 2004 and CpS showed the highest FRP values in the middle soil layer (10–20 cm), whereas it regularly decreased with depth in CvS 1994.

In the whole 0–30 cm thickness of the soil, FRT showed the same trend of annual FRP with the lowest value in CpS and the highest in CvS 1994 (Table III). Moreover, only CpS showed the lowest
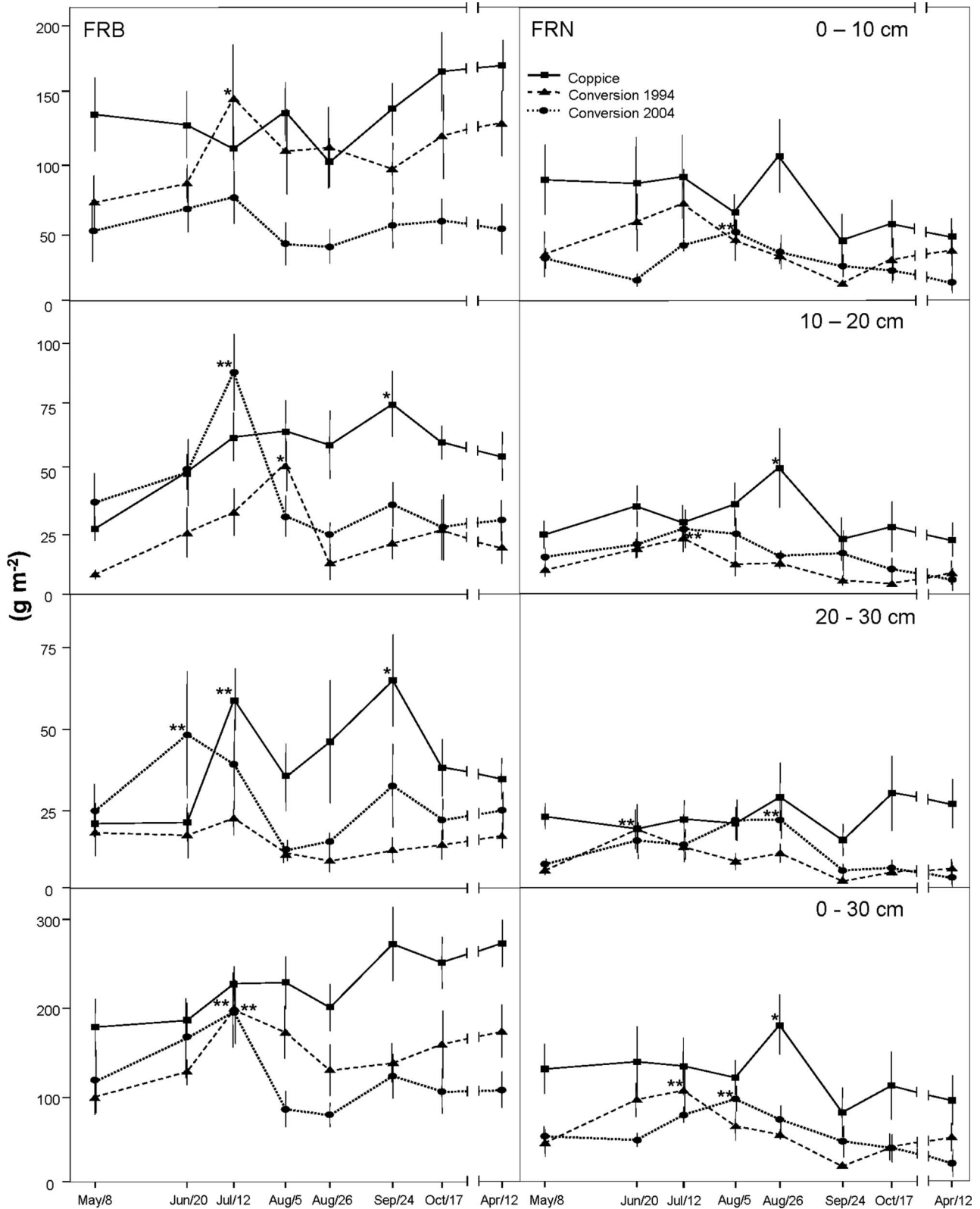
Figure 1. Seasonal pattern of live (FRB) and dead (FRN) fine-root mass (g m^{-2}) (columns) according to soil depth (rows) and type of forest management. Each value represents the mean of four samples and the vertical bars indicate standard error. Scale ranges are not standardised between each panel in order to allow a more clear presentation. Asterisks indicate statistically significant peaks (*$p < 0.1$ and **$p < 0.05$).

value in the uppermost soil layer, remarkably increasing with depth. CvS 1994 showed the opposite trend with slight differences among the three soil layers, whereas CvS 2004 showed an intermediate behaviour with the highest value in the middle (10–20 cm).

Table II. Annual mean fine-root livemass and deadmass of three forest management treatments in the 0–10, 10–20 and 20–30 cm soil layer.

Soil depth	Coppice		Conversion 1994		Conversion 2004	
	FRB (g m^{-2})	FRN (g m^{-2})	FRB (g m^{-2})	FRN (g m^{-2})	FRB (g m^{-2})	FRN (g m^{-2})
0–10	135.4 ± 8.9 ax	71.5 ± 8.9 ax	106.5 ± 9.1 bx	38.7 ± 5.3 bx	53.6 ± 5.7 cx	28.9 ± 3.0 bx
10–20	55.8 ± 4.1 ay	30.1 ± 3.2 ay	23.9 ± 3.8 by	11.5 ± 1.3 by	39.5 ± 4.3 cx	16.4 ± 2.0 by
20–30	38.8 ± 4.1 az	22.2 ± 2.5 az	14.4 ± 1.7 by	8.6 ± 1.2 bz	26.4 ± 3.8 cy	11.4 ± 1.6 bz
Profile 0–30	230.0 ± 17.2 a	123.8 ± 14.6 a	144.8 ± 14.7 b	58.8 ± 7.8 b	119.4 ± 13.7 c	56.8 ± 6.6 b

Profile 0–30 values are sums of each soil layer. Values are the mean of 32 samples ± SE (eight sampling time × four plots). a, b and c indicate significant differences between forest management treatments within the same soil depth (Kruskal–Wallis test, $p < 0.05$). x, y and z indicate significant differences between soil depth within the same forest management treatment (Kruskal–Wallis test, $p < 0.05$).
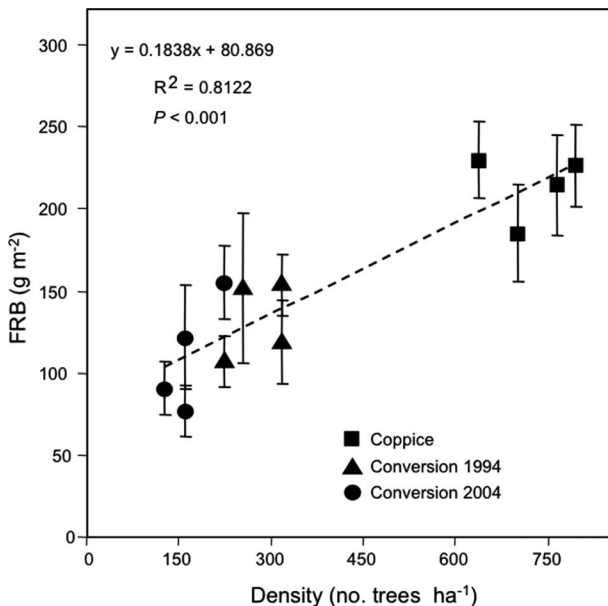
Figure 2. The relationship between tree density (number of trees ha^{-1}) and fine-root biomass (g m^{-2}). Each point represents a sampling plot. Above-ground characteristics were measured around each plot by a circular-shaped area with a 20-m diameter. Fine-root biomass for each sampling plot is the mean of 16 samples (from May 2008 to April 2009) ± SE.

Discussion

Fine root mass (biomass+necromass) data in the present study (Table II) ranged from 176.2 to 353.8 g m^{-2} and were of the same magnitude as other published values for the same tree species (Finér et al. 2007) and for temperate deciduous forests (Finér et al. 2011). Our values of annual FRP (from 131.5 to 232 g m^{-2} year^{-1}) and turnover rate (from 0.41 to 1.06 year^{-1}) fall within the range reported in literature for temperate forests (Finér et al. 2011).

In the present study, the focus was on the variation of tree fine-root standing biomass and its dynamics at three forest stands with differing forest management practices and age. Consistently with our *a* hypothesis, we observed a general decrease of the total FRB

in the Conversion stands. We may assert that the reduction of tree density leads to the death of roots belonging to the dying stools. Our findings showed that management practices may influence biomass distribution also along the soil profile. In fact, fine-root mass differed significantly between all the three soil layers only in CpS, whereas such differences were significant only in the two deepest and two uppermost soil layers in CvS 1994 and CvS 2004, respectively. Padula et al. (1987) found that in aging coppiced stands soil characteristics are improved with a slow progressive formation of a typical well-differentiated forest soil profile which may favourite the typical decreasing root depth distribution. On the contrary logging operation in forest due to the harvesting practices cause disturbance to the soil surface (Gondard et al. 2002) as well as soil erosion (Hartanto et al. 2003). This may alter the distribution of fine roots in the stands.

When investigating the effect of conversion of a stand from coppice to high forest it is necessary to consider that the consequent overall rejuvenation of the stand would also directly affect the life-cycle of the roots. Our data are in line with the FRB successional trend throughout a forest's stand development suggested by Claus and George (2005) and reported in a recent review by Brassard et al. (2009), where FRB increases from stand initiation to a maxima at a later stage of stand development, which can vary from canopy closure to maturity. In this context, the three stands considered in this study may be safely considered three different stages in a beech forest successional development with CvS 2004 and CpS representing the younger and older stage, respectively. Indeed, the more recent CvS 2004 represents the initiation stage occurring after cutting in which together with low fine-root standing mass, there is a rapid increase in fine-root production. CvS 1994 represents the second stage with a relatively slow decrease in FRP and increase of standing biomass. The CpS represents the third phase of the succession where FRP reaches equilibrium with canopy closure. Therefore, in our study,

Table III. Seasonal maximum and minimum of total fine-root dry mass (FRB plus FRN), net annual fine-root production (FRP) (according to minimum–maximum method) and turnover rate (production/seasonal maximum FRB) of three forest management treatments in the 0–10, 10–20 and 20–30 cm soil layers.

Soil depth (cm)	Total fine-root dry mass (g m^{-2})			FRP (g m^{-2} year^{-1})	Seasonal maximum FRB (g m^{-2})	Turnover rate (year^{-1})
	Seasonal minimum	Seasonal maximum	p			
Coppice						
0–10	180.9	224.0	*	43.1	178.6	0.24
10–20	49.2	99.5	**	50.3	74.7	0.67
20–30	38.2	76.3	**	38.1	63.6	0.60
0–30				131.5	316.9	0.41
Conversion 1994						
0–10	87.7	244.6	**	157.0	145.2	1.08
10–20	17.2	71.7	**	54.4	51.4	1.06
20–30	13.5	34.1	*	20.6	21.4	0.96
0–30				232.0	218.0	1.06
Conversion 2004						
0–10	62.1	114.0	**	51.9	74.1	0.70
10–20	35.0	112.8	**	77.8	87.1	0.89
20–30	27.1	61.6	*	34.5	47.1	0.73
0–30				164.2	208.3	0.79

* and ** indicate significant difference between maximum and minimum at $p < 0.1$ and $p < 0.05$, respectively. Profile 0–30 cm FRP and seasonal maximum FRB are sums of each soil layer.

forest stand above-ground management seems to result in a temporary stimulation of fine-root emission according to what described by Helmisaari et al. (2002). Moreover, the higher FRP and FRB: tree number ratio observed in both Conversions are in accordance with our second hypothesis suggesting that the cutting operation may alters FRB production.

Also fine-root turnover rate showed possible implication of conversion from coppice to high forest stand management. In fact, there was an increase in fine-root turnover that probably reflects the need to construct a different type of root system when a single large stem remains on the stool. In addition to this direct influence, we also found that the lower the mean soil temperature the lower the fine-root turnover rate. Jackson et al. (1997) found that within the same plant functional type, fine-root turnover rate increased as temperature increased. In the stands of the present study, canopy cover increased with tree density and both these factors were inversely related to soil temperature. All these findings supported our second hypothesis that fine-root inter-annual dynamics may be indirectly influenced by harvesting and cutting operations.

The seasonal pattern in fine roots is endogenously controlled in the first place (Hendrick & Pregitzer 1997) and secondly attributed to exogenous factors such as water, nutrient availability and soil temperature (Chiatante et al. 2005; Coners & Leuschner 2005; Vanguelova et al. 2005; Mainiero & Kazda 2006; Mainiero et al. 2010). Previous studies on the seasonal variations in fine-root standing biomass reported forests showing no distinct seasonal pattern (Persson 1978) and those with one (McClaugherty et al. 1982) or two (Grier et al. 1981) statistically significant peaks. Peaks in standing FRB have been measured in spring (Grier et al. 1981; Burton et al. 2000), summer (Burton et al. 2000) and fall (Vogt et al. 1981) in temperate climates (Yang et al. 2004).

In our beech stands, FRB showed a general trend characterised by two main peaks occurring in June–July and September–October. In both Conversion stands, only the first peak was significant whereas in CpS only the second peak was characterised by a significant increase being followed by a gentle decrease. From the beginning of May to mid of July, FRB increased together with air and soil temperature while monthly precipitation was still higher than 100 mm although in a decreasing trend (Figure 1). This initial increase is consistent with the need to enlarge the volume of soil exploited for water and nutrient searching. In fact, subalpine beech generally shows a significant direct correlation between ammonium ions uptake and soil temperature in July (Gessler et al. 1998).

Our data show that FRN increased together with biomass. This simultaneous fine-root formation and mortality was broadly in line with that found in *Quercus ilex* (Lopez et al. 2001) and in *F. sylvatica* (Mainiero & Kazda 2006). This result suggests that newly formed fine roots replaced inefficient older ones as water absorption balance strategy. The subsequent decrease of biomass and necromass coincided with the lowest precipitation value, and this might have affected their vitality. In beech stand,

in fact, Mainiero and Kazda (2006) observed a suppression of fine-root formation as soil dried though they underlined that increasing soil temperature seems to overrule the effect of soil water depletion making root formation rate roughly correlated with the seasonal course of soil temperature.

For all the stands and with lesser intensity, with the only exception of CpS, another peak of FRB was observed at the end of September. The soil moisture increase associated with a decrease of soil temperature after the dry-warm summer might explain this different behaviour. In line with previous studies (Chiatante et al. 2005, 2006; Di Iorio et al. 2011), we suggest that this second flush of FRB is a recovery mechanism whereby the plants uptake water and nutrients for winter storage (Cerasoli et al. 2004). A decline and consequent arrest of new root production in the autumn coincided with lower temperatures and leaf shedding. The significant second increase in CpS may be due to the lower spring soil temperature, on average 3° lower than Conversion stands, which reduced the growth rate and postponed in time the seasonal fine-root standing biomass maximum. Therefore, our *b* hypothesis was confirmed and we can assert that the conversion to high forest may affect intra-annual variations.

In regards to differences observed for the depth-related seasonal pattern among the stands, in our study significant increments in the uppermost soil layer occurred only for CvS 1994. On the contrary, fine roots in CpS and CvS 2004 showed a stronger seasonality at the subsurface soil layer. Between-layer differences in seasonal variability of below-ground biomass might be related to microclimatic subsoil conditions. During the summer, the highest soil temperature measured in the uppermost soil layer in CvS 2004 together with mechanical soil disturbance due to that the recent cutting operations represent adverse condition for the development of fine roots, which are easily dehydratable. Relocation of fine-root growth in deeper, still moist and milder soil layers during drought and warm period, was suggested for several tree species being an important response to efficiently exploit available soil water (Lyr & Hoffmann 1967; Dickmann et al. 1996; Torreano & Morris 1998; Ponti et al. 2004; Mainiero & Kazda 2006). Therefore, seasonal differentiation of fine-root activity in depth highlighted the ability to counteract the control by endogenous factors. This may be also the case of old CpS where the very high fine-root standing biomass in the first soil layer reduced the nutrient availability in favour of greater recourses exploration at higher depth.

In conclusion, this study demonstrates that considerable variations in the fine-root compartment occur during the conversion of beech forests from old coppice to high forest. Given the importance of fine-root production, which constitutes almost 30% of the total NPP, the lower fine-root production in the CpS suggests that there is an immediate advantage in converting a CpS to a high forest stand because of the increase of primary production in the fine-root compartment. This study, on the other hand, shows that harvesting in the converted stands causes a general decrease in the total standing biomass of fine roots with a consequent increase of turnover rate and carbon release. Therefore, the coppice management practice seems to favour a higher amount and lasting in time below-ground carbon stock accumulation, at least at the fine-root compartment scale.

Acknowledgements

References

Barlow PW. 2010. Plastic, inquisitive roots and intelligent plants in the light of some new vistas in plant biology. Plant Biosyst 144: 396–407.

Benjamin JG, Nielsen DC. 2004. A method to separate plant roots from soil and analyze root surface area. Plant soil 267: 225–234.

Brassard BW, Chen HYH, Bergeron Y. 2009. Influence of environmental variability on root dynamics in northern forests. Crit Rev Plant Sci 28: 179–197.

Burton AJ, Pregitzer KS, Hendrick RL. 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. Oecologia 125: 389–399.

Cerasoli S, Maillard P, Scartazza A, Brugnoli E, Chaves MM, Pereira JS. 2004. Carbon and nitrogen winter storage and remobilisation during seasonal flush growth in two-year-old cork oak (Quercus suber L.) saplings. Ann Forest Sci 61: 721–729.

Chen WN, Wu Y, Wu N, Wang Q. 2011. Effect of snowmelt time on growth and reproduction of Pedicularis davidii var. pentodon in the eastern Tibetan Plateau. Plant Biosyst 145: 802–808.

Chertov O, Komarov A, Mikhailov A, Andrienko G, Andrienko N, Gatalsky P. 2005. Geovisualization of forest simulation modelling results: A case study of carbon sequestration and biodiversity. Comput Electron Agric 49: 175–191.

Chiatante D, Di Iorio A, Sciandra S, Scippa GS, Mazzoleni S. 2006. Effect of drought and fire on root development in *Quercus pubescens* Willd. and *Fraxinus ornus* L. seedlings. Environ Exp Bot 56: 190–197.

Chiatante D, Di Iorio A, Scippa GS. 2005. Root responses of *Quercus ilex* L. seedlings to drought and fire. Plant Biosyst 139: 198–208.

Ciancio O, Nocentini S. 2011. Biodiversity conservation and systemic silviculture: Concepts and applications. Plant Biosyst 145: 411–418.

Claus A, George E, 2005. Effect of stand age on fine-root biomass and biomass distribution in three European forest chronosequences. Can J Forest Res 35: 1617–1625.

Coners H, Leuschner C. 2005. In situ measurements of fine root water absorption in three temperate tree species – Temporal variability and control by soil and atmospheric factors. Basic Appl Ecol 6: 395–405.

Crider FJ. 1928. Winter root growth of plants. Science 1765: 403–404.

Diaci J, Rozenbergar D, Boncina A. 2010. Stand dynamics of Dinaric old growth forest in Slovenia: Are indirect human influences relevant? Plant Biosyst 144: 194–201.

Dickmann DI, Nguyen PV, Pregitzer KS. 1996. Effects of irrigation and coppicing on above-ground growth, physiology, and fine-root dynamics of two field-grown hybrid poplar clones. Forest Ecol Manage 80: 163–174.

Di Iorio A, Montagnoli A, Scippa GS, Chiatante D. 2011. Fine root growth of *Quercus pubescens* seedlings after drought stress and fire disturbance. Environ Exp Bot 74: 272–279.

Edwards NT, Harris WF. 1977. Carbon cycling in a mixed deciduous forest floor. Ecology 58: 431–437.

Finér L, Helmisaari HS, Lohmus K, Majdi H, Brunner I, Børja I, et al. 2007. Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.), and Scots pine (*Pinus sylvestris* L.). Plant Biosyst 141: 394–405.

Finér L, Ohashi M, Noguchi K, Hirano Y. 2011a. Factors causing variation in fine root biomass in forest ecosystems. Forest Ecol Manage 261: 265–277.

Finér L, Ohashi M, Noguchi K, Hirano Y. 2011b. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. Forest Ecol Manage 262: 2008–2023.

Fukuzawa K, Dannoura M, Kanemitsu S, Kosugi Y. 2010. Seasonal patterns of root production of Japanese oak seedlings and dwarf bamboo grown in rhizoboxes. Plant Biosyst 144: 434–439.

Gessler A, Schneider S, Von Sengbusch D, Weber P, Hanemann U, Huber C, et al. 1998. Field and laboratory experiments on net uptake of nitrate and ammonium by the roots of spruce (*Picea abies*) and beech (*Fagus sylvatica*) trees. New Phytol 138: 275–285.

Gill AR, Jackson RB. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol 147: 13–31.

Grier CC, Vogt KA, Keyes MR, Edmonds RL. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can J Forest Res 11: 155–167.

Godbold DL, Brunner I. 2007. The platform for European root science, COST action E38: An introduction and overview. Plant Biosyst 141: 390–393.

Godbold DL, Fritz H-W, Jentschke G, Meesenburg H, Rademacher P. 2003. Root turnover and root necromass accumulation of Norway spruce (*Picea abies*) are affected by soil acidity. Tree Physiol 23: 915–921.

Gondard H, Romane F, Aronson J, Shater Z. 2002. Impact of soil surface disturbances on functional group diversity after clear-cutting in Aleppo pine (*Pinus halepensis*) forests in southern France. Forest Ecol Manage 180: 165–174.

Hartanto H, Prabhub R, Widayatc ASE, Asdakd C. 2003. Factors affecting runoff and soil erosion: Plot-level soil loss monitoring for assessing sustainability of forest management. Forest Ecol Manage 180: 361–374.

Helmisaari HS, Makkonen K, Kellomäki S, Valtonen E, Mälkönen E. 2002. Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. Forest Ecol Manage 165: 317–326.

Hendrick RL, Pregitzer KS. 1992. Spatial variation in root distribution and growth associated with minirhizotrons. Plant Soil 143: 283–288.

Hendrick RL, Pregitzer KS. 1997. The relationship between fine root demography and the soil environment in northern hardwood forests. Ecoscience 4: 99–105.

Hertel D, Leuschner C. 2002. A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus–Quercus* mixed forest. Plant Soil 239: 237–251.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108: 389–411.

Jackson RB, Mooney HA. Schulze ED. 1997. A global budget for fine-root biomass, surface area, and nutrient contents. Proc Natl Acad Sci USA 94: 7362–7366.

Leuschner C, Harteveld M, Hertel D. 2008. Consequences of increasing forest use intensity for biomass, morphology and growth of fine roots in a tropical moist forest on Sulawesi, Indonesia. Agric Ecosyst Environ 129: 474–481.

Liira J and Kohv K. 2010. Stand characteristics and biodiversity indicators along the productivity gradient in boreal forests: Defining a critical set of indicators for the monitoring of habitat nature quality. Plant Biosyst 144: 211–220.

Lopez B, Sabaté S, Gracia CA. 2001. Annual and seasonal changes in fine root biomass of a *Quercus ilex* L. Forest. Plant Soil 230: 125–134.

Lyr H, Hoffmann G. 1967. Growth rates and growth periodicity of tree roots. Int Rev Forest Res 2: 181–236.

Mainiero R, Kazda M. 2006. Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. Forest Ecol Manage 237: 135–142.

Mainiero R, Kazda M, Schmid I. 2010. Fine root dynamics in 60-year-old stands of *Fagus sylvatica* and *Picea abies* growing on haplic luvisol soil. Eur J Forest Res 129: 1001–1009.

Magri D, Vendramin GG, Comps B, Dupanloup I, Geburek T, Gömöry D, Latalowa M, Litt T, Paule L, Roure JM, Tantau I, WO van der Knaap, Petit JR, de Beaulieu J-L. 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. New Phytol 171: 199–221.

Majdi K, Pregitzer KS, Moren AS, Nylund JE, Agren GI. 2005. Measuring fine-root turnover in forest ecosystems. Plant Soil 276: 1–8.

Manes F, Ricotta C, Salvatori E, Bajocco S, Blasi C. 2010. A multiscale analysis of canopy structure in *Fagus sylvatica* L. and *Quercus cerris* L. old-growth forests in the Cilento and Vallo di Diano National Park. Plant Biosyst 144: 202–210.

McClaugherty CA, Aber JD, Melillo JM. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63: 1481–1490.

Montagnoli A, Terzaghi M, Di Iorio A, Scippa GS, Chiatante D. 2012. Fine-root morphological and growth traits in a Turkey-oak stand in relation to seasonal changes in soil moisture in the Southern Apennines, Italy. Ecol Res, DOI: 10.1007/s11284-012-0981-1.

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Nocentini S. 2009. Structure and management of beech (Fagus sylvatica L.) forests in Italy. Iforest-Biogeosciences and Forestry 2: 105–113.

Padula M, C D'Amico, S Ricci, R Gioffredi. 1987. Esperienze di conversione all'alto fusto di boschi cedui invecchiati di Faggio nell'Appennino Settentrionale (Italia). Ann Accad Ital Sci Forest 37: 23–64.

Papalexandris C and Milios E. 2010. Analysis of natural *Fagus sylvatica* L. s.l. regeneration in low elevation stands located in the central part of the Evros region in northeastern Greece: Is sprout origin regeneration significant for species maintenance? Plant Biosyst 144: 784–792.

Persson H. 1978. Root dynamics in a young Scots pine stand in Central Sweden. OIKOS 30: 508–519.

Ponder Jr F, Alley DE. 1997. Soil sampler for rocky soils. Research Note NC-371. St. Paul, MN: USDA Forest Service North Central Forest Experiment Station. 5 pp.

Ponti F, Minotta G, Cantoni L, Bagnaresi U. 2004. Fine root dynamics of pedunculate oak and narrow-leaved ash in a mixed-hardwood plantation in clay soils. Plant Soil 259: 39–49.

Rötzer T, Dieler J, Mette T, Moshammer R, Pretzsch H. 2010. Productivity and carbon dynamics in managed Central European forests depending on site conditions and thinning regimes. Forestry 83: 483–496.

Tobin B, Cermak J, Chiatante D, Danjon F, Di Iorio A, Dupuy L, et al. 2007. Towards developmental modelling of tree root systems. Plant Biosyst 141: 481–501.

Torreano SJ, Morris LA. 1998. Loblolly pine root growth and distribution under water stress. Soil Sci Soc Am J 62: 818–827.

Vanguelova EI, Nortcliff S, Moffat AJ, Kennedy F. 2005. Morphology, biomass and nutrient status of fine roots of Scots pine (*Pinus sylvestris*) as influenced by seasonal fluctuations in soil moisture and soil solution chemistry. Plant Soil 270: 233–247.

Vogt KA, Edmonds RL, Grier CC. 1981. Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer roots in 23- and 180-year-old *Abies amabilis* stands. Can J Forest Res 11: 223–229.

Vogt KA, Persson H. 1991. Root methods. In Lassoie JP and Hinckley TM, editors. Techniques and approaches in forest tree ecophysiology. Boca Raton, FL: CRC Press. pp. 477–502.

Vogt KA, Vogt DJ, Palmiotto PA, Boon P, O'Hara J, Asbjornsen H. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187: 159–219.

Yang YS, Chen GS, Lin P, Xie JS, Guo JF. 2004. Fine root distribution, seasonal pattern and production in four plantations compared with a natural forest in Subtropical China. Ann Forest Sci 61: 617–627.

Zobel RW, Waisel Y. 2010. A plant root system architectural taxonomy: A framework for root nomenclature. Plant Biosyst 144: 507–512.