



Forest canopy reduction stimulates xylem production and lowers carbon concentration in fine roots of European beech



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ABSTRACT

Forest canopy reduction is well known to affect the coarse and fine root biomass production. Seasonality, to the same extent, is acknowledged to vary the non-structural carbon content. However, the fine root response in terms of carbon concentration to both canopy cover and seasonal change remains unclear.

To this aim, morphological and anatomical traits like xylem percentage, carbon concentration and starch content were measured in mid-summer and early-fall on fine roots of three beech stands differing in canopy cover and basal area.

The results highlighted a significant effect of canopy cover on the xylem area percentage throughout the <2 mm diameter fine root population, as the lower the canopy cover is, the larger the xylem area is. Moreover, an inverse relationship occurred between carbon concentration and xylem area percentage, highlighting the key role played by this anatomical trait. In order of magnitude, the significant carbon concentration decrease observed 5 years after felling was 15 kg ha⁻¹ for a mean fine root biomass of 200 g m⁻². For a given xylem percentage, starch concentration seasonal change partially explained the carbon concentration decrease with the incipient dormancy. Root tissue density significantly decreased with soil depth in mature and 15-yr-old conversion stands, whereas it did not in recently cut (5-yr-old) conversion stand.

Outcomes are that canopy closure in the mature stand, which increases the fine root standing crop, produced a higher total carbon input into the soil. Moreover, fifteen years since felling appeared sufficient for detecting a clear trend in the recovery of fine root biomass to pre-thinning levels.

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1. Introduction

Belowground biomass significantly influences the biogeochemical processes, particularly the soil carbon cycling rates (Hendrick and Pregitzer, 1993; Jackson et al., 1997; Nadelhoffer and Raich, 1992; Röderstein et al., 2005). Fine-roots (diameter <2 mm) rarely represent more than 5% of the total tree biomass, but their production amount to 33–67% of the total annual net primary production in most ecosystems (Jackson et al., 1997; Joslin and Henderson, 1982; Matamala et al., 2003; McLaugherty et al., 1982) and can be used as indicator of forest adaptation (Montagnoli et al., 2016) and health state (Xue et al., 2015). Therefore, knowledge of fine root structure and function is essential for a detailed understanding of their role as carbon (C) sources of soil litter input.

Thinning practices modify stand characteristics in terms of tree density, stand basal area, canopy cover and related environmental variables (i.e. soil moisture and temperature), leading to increased stem and crown growth along with changes in the ecophysiological behaviour at stand level (Aussenac, 2000; Cullotta et al., 2015). The work reported here builds on previous studies on beech forests subjected to thinning operations for the conversion into high forest, focusing in particular on the belowground portion, namely fine (Montagnoli et al., 2014, 2012; Terzaghi et al., 2013) and coarse (Di Iorio et al., 2013) roots. At root system level, depending on cutting intensity, forest harvesting generally result in the partial or complete death of coarse roots (Di Iorio et al., 2013; O'Loughlin and Watson, 1979) and in the change of fine root density and production (Montagnoli et al., 2012), with the fine-root biomass decreasing from dense mature coppice to recently thinned stands. On the other hand, readjustments in crown closure of remaining trees stimulate the production of photosynthate and, consequently, the cascade-driven radial growth (i.e. xylem production) of stem

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(Vincent et al., 2009) and structural roots (Di Iorio et al., 2013; Fayle, 1975; Vincent et al., 2009; Urban et al., 1994) along with fine root biomass production (Montagnoli et al., 2012), which becomes more evident several years after felling. However, whether thinning practices affect or not to the same extent the chemical composition of fine roots in terms of carbon and nitrogen concentrations is still matter of debate. Biomass is a complex plant matter, mainly composed of organic molecules with varying proportions of carbon. The most widely used value for carbon concentration is 50%, as the average molecular formula for plant matter is $\text{CH}_{1.44}\text{O}_{0.66}$ (Pettersen, 1984). However, different analyses showed carbon concentration values ranging from 47 to 59%, as a function of tree compartment or species (Lamloom and Savidge, 2003 and references therein). Consequently, carbon content uncertainty may raise to about 20–25% (Bert and Danjon, 2006). However, potential variations within and between compartments have been frequently neglected, in particular because of sampling only one compartment (the stem as a rule) and/or only during one limited period. Lignin (18–35% of biomass) and holocellulose (65–75% of biomass) are the principal chemical components in wood, as minor amounts of organic extractives and inorganic mineral (ash) usually account only for 4–10% of wood biomass. Lignin and holocellulose, made up of α -cellulose and hemicelluloses, are complex, polymeric materials and their chemical formula is not unique. Anyhow, it is widely recognized that C content is higher for lignin than holocellulose, within the range of 63–66% (Bert and Danjon, 2006; Hancock et al., 2007).

Seasonality strongly influences the phenology of fine roots, but little is known about its effects on their chemical properties. In beech stands of Southern Europe, the seasonal trend of fine root live mass shows a bimodal pattern with a first peak in July and, a second lower one in September–October (Montagnoli et al., 2014, 2012). Fine root C and N concentrations show a reverse pattern compared to each other, with the highest and lowest values for [C] in July and October, respectively (Terzaghi et al., 2013). This behaviour is hypothesized to be related to the starch concentration, which has a low carbon concentration (44.4%), and is well known to decrease in spring and increase in autumn in mature beech stands (Barbaroux et al., 2003), in poplar clones (Nguyen et al., 1990) and teak (Singh and Srivastava, 1986). Moreover, in beech total non-structural carbon (soluble sugars plus starch) has higher concentrations in root wood than other plant organs (Barbaroux et al., 2003).

Few studies showed root-conduit (i.e. vessel) size increment with increasing soil depth (Di Iorio et al., 2007; Gebauer and Volařík, 2013; McElrone et al., 2004; Wang et al., 2016), and even less investigated the occurrence or not of such a pattern for fine roots within the first 30 cm soil depth. For a same plant individual, vessels are often more than four times as large in deep roots as in stems and are intermediate in shallow roots (Jackson et al., 2000; McElrone et al., 2004). Variations in xylem conduit diameter can radically affect the functions of different portions of the conducting system because of the fourth-power relationship between radius and flow through a capillary tube, as described by the Hagen-Poiseuille law (Tyree and Ewers, 1991; Zimmermann, 1983). Thus, anatomical changes in terms of root-conduit size increase in the first 30 cm soil depth may influence the hydraulic architecture and the root tissue density (RTD) alongside the C content of the fine root compartment.

The present study aimed at gaining a better understanding of the fine root response in terms of C concentration and anatomical characteristics to canopy cover modification, seasonality and soil depth. The hypothesis tested were (1) the reduced canopy cover-derived higher photosynthate production should stimulate the xylem production (i.e. secondary growth), and (2) the higher concentration in early fall of low [C]-bearing molecular species as

starch should lower the C concentration. RTD was expected to decrease with depth and amplify this response accordingly. To this aim, anatomical traits like xylem percentage and total lumen vessel area together with C concentration and starch content were measured in mid-summer and early-fall on fine roots of three beech stands differing in tree density and canopy cover.

2. Materials and methods

2.1. 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 m to 1200 m above sea level between Lakes Como and Lugano. This area is characterized by a sub-continental climate, with a mean annual precipitation of 1600 mm, occurring in two main periods (April–May and October–November) and a mean annual temperature of 10–11 °C. Generally, the area is snow-covered from late October to late March. According to the World Reference Base for Soil Resources (FAO/ISRIC/ISSS, 2006), soil type is Leptosol 40–50 cm deep.

General characteristics of this area were already described in a previous work carried out on the same site (Montagnoli et al., 2012). Briefly, three beech stands were selected and labelled by ascending cutting age: two conversions thinning from coppice to high forest cut in 2004 (Conversion Stand [CvS] 2004) and 1994 (CvS 1994) respectively; a residual coppice stand cut in 1968 (CpS 1968) and then allowed to re-grow from stools. The three stands were adjacent to each other and located on the same slope facing south-west, with slope inclination averaging between 28 and 30°. Above ground stand characteristics (Table 1) such as canopy cover (%), above ground biomass (Mg ha^{-1}), diameter at breast height (DBH, cm) and stand basal area ($\text{m}^2 \text{ha}^{-1}$), were evaluated on seven circular-shaped (20 m diameter) sampling plots per stand along a transect almost 120 m long for a total of 1884 m^2 area per stand. In the case of CpS 1968, each stool was counted as a single tree.

2.2. Fine root collection and measurement

Soil cores were harvested in summer after leaves had fully expanded (July 1–3, 2009) and the following autumn during the leaf fall (October 19–21, 2009). These dates correspond to maximum and minimum annual standing crop respectively, as determined in a previous non-destructive experiment in the same stands (Montagnoli et al., 2012). In each stand, four smaller permanent 10 m^2 replicated plots were set within four out of the previously described seven larger plots and used for fine root measurements. One soil core (4 cm diameter \times 30 cm deep) was randomly collected in each plot at each sampling date and successively divided into 10 cm depth increments: 0–10 (including the first 2–3 cm of a humus layer), 10–20 and 20–30 cm for a total

Table 1
Beech above-ground characteristics for the three investigated stands. Values are the mean of 4 replicates (SE).

	Canopy cover (%)	Above-ground biomass (Mg ha^{-1})	DBH (cm)	Basal area ($\text{m}^2 \text{ha}^{-1}$)
CpS 1968	94.2 (0.6)	248.5 (15.6)	17.2 (0.7)	32.18 (2.05)
CvS 1994	74.2 (5.5)	123.7 (7.3)	22.6 (1.5)	18.55 (2.14)
CvS 2004	54.3 (3.2)	91.8 (20.2)	31.9 (1.9)	13.65 (1.21)

Data shown are means \pm SE.

DBH, diameter at breast height.

Canopy cover values are the mean of 10 replicates.

Above-ground biomass values are the mean of seven replicates.

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