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Abstract We investigated the effects of seasonal changes in soil moisture on the morphological and growth traits of fine roots (<2 mm in diameter) in a mature Turkey-oak stand (*Quercus cerris* L.) in the Southern Apennines of Italy. Root samples (diameter: <0.5, 0.5–1.0, 1.0–1.5, and 1.5–2.0 mm) were collected with the Auger method. Mean annual fine-root mass and length on site was 443 g m⁻² (oak fine roots 321 g m⁻²; other species 122 g m⁻²) and 3.18 km m⁻² (oak fine roots 1.14 km m⁻²; other species 2.04 km m⁻²), respectively. Mean specific root length was 8.3 m g⁻¹. All fine-root traits displayed a complex pattern that was significantly related to season. In the four diameter classes, both fine-root biomass and length peaked in summer when soil water content was the lowest and air temperature the highest of the season. Moreover, both fine-root biomass and length were inversely related with soil moisture ($p < 0.001$). The finest roots (<0.5 mm in diameter) constituted an important fraction of total fine-root length (79 %), but only 21 % of biomass. Only in this root class, consequent to change in mean diameter, specific root length peaked when soil water content was lowest showing an inverse relationship ($p < 0.001$). Furthermore, fine-root production and turnover decreased with increasing root diameter. These results suggest that changes in root length per unit mass, and pulses in root growth to exploit transient periods of low soil water content may enable trees to increase nutrient and water uptake under seasonal drought conditions.

Keywords Fine-root biomass · Fine-root length · SRL · Soil moisture · *Quercus cerris* L.

Introduction

Biogeochemical processes are significantly influenced by belowground biomass (Nadelhoffer and Raich 1992; Hendrick and Pregitzer 1993; Jackson et al. 1997; Roderstein et al. 2005). The fine-root (<2 mm in diameter) component of a root system rarely represents more than 5 % of the total tree biomass but its production represents a large proportion of the total annual net primary production in most ecosystems (McClougherty et al. 1982; Joslin and Henderson 1987). Fine-root dynamics is influenced by 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). During the summer, forest ecosystems in Mediterranean climate areas undergo natural soil moisture deficit coupled with elevated temperature. Thus, water deficit is subject to seasonal variability and causes mild and/or extreme drought. Soil moisture is a key factor that influences the fine-root biomass and turnover of trees (Meier and Leuschner 2008). Any distortion of the fine-root system by such stressors might affect carbon and nutrient cycling in the ecosystem. Moreover, as the timing of fine-root dynamics changes in relation to soil environmental conditions, turnover rate can be a crucial factor for root resource acquisition efficiency and therefore might be used as index of plant functioning (Mainero et al. 2009).

Plants continuously adapt the growth of different organs to dynamically heterogeneous soil resources (Metcalf et al. 2008). Different tree species appear to use different adaptation strategies to optimize their mineral nutrition (Comas et al. 2002; Curt and Prevosto 2003; Comas and Eissenstat 2004). This species-specific adaptation in response to the local heterogeneity of the

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soil involves two possible strategies that depend on their ability to exclude or tolerate the stress (Manes et al. 2006 and references therein). Briefly, a stress-tolerance plant adopts an 'extensive' strategy (Ostonen et al. 2007), namely it shifts its allocation of carbon towards roots, where photosynthate can be used to increase water uptake. Ostonen et al. (2011) showed that Norway spruce forests across a European climate gradient acclimatize to a cold climate and low N availability by increasing the biomass, length and the number of root tip ectomycorrhizas. In the case of soil water shortage, this strategy leads to an increase in root mass and length in the fine-root system as soil moisture declines (Manes et al. 2006; Ostonen et al. 2007; Di Iorio et al. 2011). Stress-avoidance plants respond to reduction in water availability by closing their stomata thereby reducing CO₂ assimilation and diffusion into the plant (Manes et al. 2006). This change in the total amount of labile carbon available to the plant probably results in a decline in root mass production as soil moisture falls (Metcalf et al. 2008).

Root length is assumed to be proportional to resource acquisition (benefit) and root mass to be proportional to construction and maintenance (cost) (Eissenstat and Yanai 1997). Specific root length (SRL m g⁻¹) is the length-to-mass ratio (L/M) of a root fragment. Fitter (1976, 1985, 1991) firstly apply SRL and proposed the length/mass ratio as an index of root benefit/cost ratio analysis (Ostonen et al. 2007). Long and thin roots (high SRL) are believed to be the belowground equivalent of thin leaves, which are less expensive to produce (Withington et al. 2006; Ostonen et al. 2007). Water uptake may stimulate the production of finer roots, which results in a relatively greater length per unit mass thereby leading to an increase in SRL under drier conditions (Metcalf et al. 2008). Thus, a decline in soil moisture in some species may induce changes in the diameter of the root population (Ostonen et al. 2007).

Much less is known about the belowground components than about the aboveground components of ecosystems (Vogt et al. 1996; Jackson et al. 1997; Norby and Jackson 2000; Trumbore and Gaudinski 2003). Finér et al. (2011) in a recent review underlined how the responses of fine roots to temperature and soil moisture are still today more difficult to demonstrate and explain at global level. This is mainly due to (1) the small datasets of the various studies and the inconsistency among reports, and (2) results obtained by different methodologies.

Data on the fine roots of tree species growing in the Mediterranean Basin are also scarce and their changes in biomass have been generally ignored (Finer et al. 2007, 2011a; Jackson et al. 1997). Oaks (*Quercus* spp.) are major components of European temperate vegetation types (Bradshaw and Lindbladh 2005; Bolte and Löf 2010). However, very little is known about this species. Under field conditions, López et al. (1998, 2001) widely investigated fine-root characteristics of a *Quercus ilex*

stand in Mediterranean area located in NE Spain. In particular, López et al. (1998, 2001) investigated the effect on fine-root dynamics of soil water content in relation to thinning practices, and concluded that thick and long-lived roots contribute to the long-term development of the root system. Claus and George (2005) investigated *Quercus cerris* fine-root mass in central Italy in relation to chronosequence focusing on the fine-root biomass in relation to stand development. Manes et al. (2006) investigated the fine-root growth of 3-year-old *Quercus cerris* (turkey oak) seedlings under controlled pot conditions in relation to water stress compared with *Q. ilex*. They found a significantly greater reduction of fine-root length after 6 weeks of progressive soil drying in *Q. cerris* than in *Q. ilex*. Chiatante et al. (2005, 2006) and Di Iorio et al. (2011) reported a considerable rearrangement of fine roots after the onset of soil drying in 2-year-old *Quercus pubescens* seedlings subjected to water stress and fire disturbance. Differently, there is a lack of data on the fine-root mass and morphology in forest stands growing under natural conditions and in relation to seasonal variation in soil moisture. This lack of data hinders attempts to model accurately the behavior of terrestrial ecosystems, and their potential responses to climate change.

The overall objective of this study was to identify adaptive responses of fine-root systems to changes in soil water availability in a mature Turkey oak stand throughout an entire vegetative season. The specific objectives were to: (1) quantify the seasonal variation of (a) live and dead fine-root mass as a dynamic adaptation of primary production to soil moisture changes, (b) length, and (c) SRL; (2) estimate the annual production and turnover rate of live fine roots; (3) quantify all these fine-root traits for four fine-root diameter classes (<0.5, 0.5–1, 1–1.5, 1.5–2 mm).

Materials and methods

Experimental site

The experimental site is located in the Trigno river basin near Trivento (Molise, Italy), on the east side of the southern Italian Apennine. The site is located on a north-facing hill slope, at an altitude of 600 m (latitude 41°43'N, longitude 14°33'E—shallow-slope conditions, 4°–5°). The climate is montane Mediterranean with summer drought spanning June, July, and August. Rainfall is usually concentrated between late autumn and early spring. The drought period was determined based on temperature and rainfall data according to Bagnouls and Gaussen (1953). The mean yearly precipitation is 656 mm, falling mostly as rain (data from 1975 to 2006 from the Trivento weather station, Regione Molise).

The area under investigation is subject to seasonal and yearly variations in terms of drought and cold stress

Table 1 Vegetation and soil features of the survey site

		Soil					
Layer depth (cm)	Texture	pH H ₂ O	C/N	N (g kg ⁻¹)	P (ppm)	K (ppm)	Organic matter (g kg ⁻¹)
A (0–7)	Clay	8.4	8.2	0.9	2.9	180.4	13.0
C1 (7–30)	Silty clay	8.6	7.5	0.4	2.3	124.8	5.1
		Vegetation					
Tree number (stem per ha ⁻¹)			Mean dbh ^a (cm)		Mean tree height (m)		
1735 ± 106			9.4 ± 0.6		8.35 ± 0.4		

Vegetation data from all stems over 5-cm diameter in July 2008. All values are the mean of 7 plot (size ca. 314 m² each) ± 1 SE
^aStem diameter at breast height, 1.3 m. Soil features data from Di Iorio et al. 2008

periods. Evapotranspiration is high during summer when rainfall is low thereby resulting in a considerable moisture deficit (Van Beek et al. 2001). The mean summer and winter temperatures are estimated to be 22 and 7 °C, respectively. Soil type is the widespread Typic Eutrochrepts fine loamy mixed mesic (USDA 1998) (see Table 1 for soil site features from Di Iorio et al. 2008) that reacts to the montane Mediterranean climate with high shrinkage and cracks forming to a maximum depth of 1.0 m in the summer. This soil type frequently becomes waterlogged during the winter months (Barij et al. 2007). Vegetation over-storey at the study site is dominated by European Turkey-oak (*Quercus cerris* L.) (50–75 % cover). Turkey oak extends from southeast Europe to southwest Asia. In Italy, it is distributed over all the territory, preferring clay, and deep sub-acid soils. In the Apennines, this species forms pure or mixed forests together with other broadleaved species (i.e., *Quercus pubescens* Willd.) (Pignatti 1982).

The main understorey species at the study site are *Crataegus monogyna* Jacq. (land cover percentage: 25–50 %), *Euonymus europaeus* L. (<25 %), *Ligustrum vulgare* L. (25–50 %), *Ruscus aculeatus* L. (25–50 %), *Asparagus acutifolius* L. (<25 %), *Lonicera caprifolium* L. (<25 %), *Rosa canina* L. (<25 %), *Cornus mas* L. (<5 %) and *Prunus spinosa* L. (<5 %). The stand investigated is managed as coppice with standards, and the trees are felled at an average rate of once every 15–20 years. The mean age of the trees is between 28 and 30 years old with bigger seed origin trees almost 55 years old. To determine the above ground stand characteristics such as tree stocking density (no. trees ha⁻¹), mean stem diameter at breast height (dbh, cm) and mean tree height (m), seven sampling plots circular-shaped (diameter of 20 m) were surveyed along a transect within an area of 1 ha (Table 1).

Soil moisture

ThetaProbe type ML2 Delta-T Devices were used to record the volumetric soil moisture content (m³ m⁻³) by the well-established method of responding to changes in the apparent dielectric constant. On each sampling date, at the soil core sampling point four measurements (one

each plot) were taken at three soil depths (10, 20, and 30 cm; hereafter reported as mean 30-cm depth).

Fine-root measurements

The soil core sampling method (Vogt and Persson 1991) was used to quantify fine-root mass (<2 mm in diameter) during the 2008 growing season. At the study site four plots for stand measurements (see “Experimental site”) were selected and within each of them a 10-m² square-shaped plot was set up. Sudmeyer et al. (2004) found that maximum lateral root spread is roughly 1.5–2.5 times the tree height. Although this value refers to an agroforestry system, we considered it valid for our oak stands. Therefore, we set-up plots at a mean distance of 40 m each other, equal to 4.8 times the mean stand tree height and each plot was considered an independent replicate. At each sampling date, two soil cores (4-cm diameter × 30 cm deep) were randomly collected in each plot using a motor-driven portable core sampler (adapted from Ponder and Alley 1997). To investigate the kinetics of biomass and necromass, we collected soil samples on 12 dates between April 4 and November 27. Samples were collected at an interval of not less than 15 days and not more than 26 days; eight cores were collected on each sampling date for a total of 96 cores. We did not sample in winter because we assumed that during this season fine-root production and decomposition are low. 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 using a washing machine (adapted by Benjamin and Nielsen 2004). The fine roots were examined at the microscope and were divided into two groups: oak and other understorey species. Fine roots from oak trees were classified “live” [hereafter termed fine-root biomass (FRB)] or “dead” [fine-root necromass (FRN)] depending on their color, texture and shape (Vogt and Persson 1991). After selection, oak root fragments were first roughly grouped by caliper method in half-millimeter-diameter classes and scanned at a resolution of 400 dpi with a calibrated flatbed scanner coupled to a lighting system for image acquisition (Epson Expression 10000 XL). Successively, images were analyzed by WinRhizo Pro V. 2007d

(Regent Instruments Inc. Quebec) in order to group with higher accuracy the different fine-root fragments in four diameter classes (<0.5, 0.5–1.0, 1.0–1.5, and 1.5–2.0 mm). After fine-root length (FRL) measurement, oak live and dead fine-root samples were oven-dried separately by diameter classes and weighed. Understory fine roots were also dried and weighed.

Oak fine-root annual production (FRP) was estimated using the Decision Matrix method of Fairley and Alexander (1985), considering only significant biomass and necromass difference between two sampling dates. Rates of fine-root turnover (FRT) were calculated as FRP divided by maximum standing biomass (Gill and Jackson 2000).

Statistical analysis

Statistical analysis was carried out with the statistical software package SPSS 17.0 (SPSS Inc, Chicago IL, USA). The data were not normally distributed neither did they meet the assumption of homoscedasticity. They were square-root transformed or log-transformed to ensure normal distributions and equal variances to allow the use of parametric statistics. Analysis of variance (one-way ANOVA) for effect of time on fine-root traits (FRB, FRN, FRL, and SRL) irrespective of diameter classes (<2 mm in diameter) and by four diameter classes was carried out with time as fixed effect and sampling plot as random effect. Therefore, each pair of soil cores was pooled and treated as one replication ($n = 4$). The effect of soil moisture on FRB, FRL and SRL was assessed using a power regression function. To test the significance of each peak in the seasonal pattern, the Dunnett's test (unilateral alternative, $p < 0.05$) was applied to differences among the peak (reference mean) and both prior and subsequent first minimum values. Independent-samples t test was applied to test the significance of biomass and necromass differences between two sampling date for FRP estimation.

Results

Soil moisture

As a result of spring rainfall events (Fig. 1a), the highest soil water content was recorded between April (40.3 %) and June (38.9 %) (Fig. 1b). It decreased to almost 30 % at the beginning of July and to almost 18 % in August. In fact, rainfall events were very rare in summer (five events in July and two events in August), and the quantity of rain precipitated during these events was very scarce (in July one rain event produced 10.4 mm and one produced 3 mm; the other three rain events produced less than 1 mm). Soil moisture increased from the beginning of September to the beginning of October

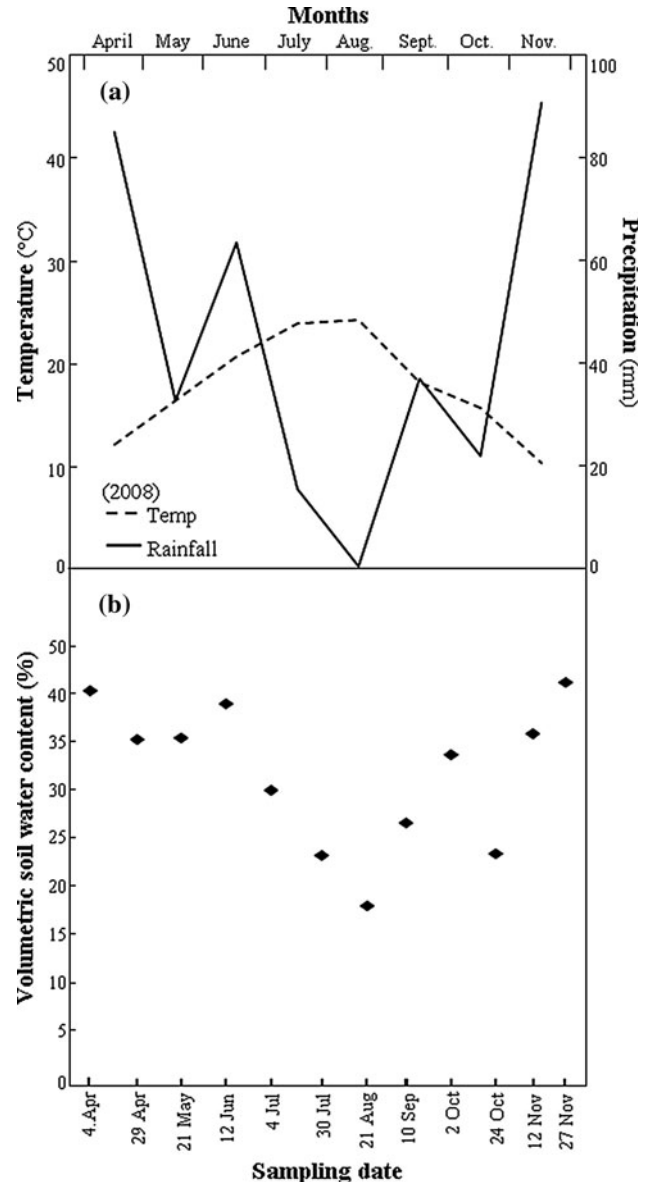


Fig. 1 Monthly average temperature and rainfall from April to November 2008 (a). Seasonal variation of soil moisture (b). Soil-moisture data are means \pm 1 SE (SE not visible because smaller than symbols)

as a result of early autumn rainfall. It decreased at the end of October in conjunction with a decrease in rainfall, and then increased up to the end of November.

Fine-root mass, length, and SRL

The annual mean FRB (<2 mm in diameter) was slightly (17 %) lower than the annual mean FRN (Table 2). FRB was almost equal for all diameter classes with the 0.5–1.0 mm class showing the highest fraction (30 %); this was particularly evident in the case of FRN (36 %). In contrast, the finer diameter class (<0.5 mm)

constituted 79 % of live FRL (Table 2), and only 21 % of FRB. The mean annual FR mass of the understory was $121.2 \pm 8.5 \text{ g m}^{-2}$ with an estimated mean annual FRL of $2,039 \pm 82 \text{ m m}^{-2}$ (data not shown).

Time significantly ($p < 0.05$) affected FRB, FRL, and SRL for all diameter classes considered, which showed three distinct peaks during the growing season. The random effect of sampling plot was not significant ($p > 0.05$). In fact, both FRB and FRL progressively increased from the beginning of April to mid-June, and then slightly decreased at the beginning of July. In both cases, this first small peak was not statistically significant for all the four diameter classes considered (Fig. 2). Subsequently, FRB and FRL showed a second, significant peak ($p < 0.05$) at the end of July in the case of the fractions smaller than 1 mm (0–0.5 and 0.5–1 mm) (Fig. 2a, b, d, e), and at the end of August in the case of the larger fractions (1–1.5 and 1.5–2 mm) (Fig. 2g–k). Both peaks occurred during the transition from the wet to dry season.

Both the FRB and FRL of all diameter classes decreased until September–October but increased again at the end of October. This third peak was significant ($p < 0.05$) only for the smaller diameter classes (0–0.5 and 0.5–1 mm) (Fig. 2a, d) in terms of FRB, and for 0–0.5 and 1–1.5 mm diameter classes (Fig. 2b, h) in terms of FRL. Both FRB and FRL continued to decrease after this third peak up to the end of the sampling period (27th November).

The seasonal pattern of FRN differed depending on diameter class. A time effect was significant ($p < 0.05$) only for the smaller (<0.5 mm) and the largest (1.5–2.0 mm) diameter classes (Table 3). The two smaller diameter classes (<0.5 and 0.5–1.0 mm) increased continuously during the study period. In contrast, the larger diameter classes (1.0–1.5 and 1.5–2.0 mm) showed three main peaks, at the beginning of July, beginning of October and end of November respectively. All three peaks occurred almost 1 month after the FRB peaks (Fig. 2g, j).

No remarkable seasonal variation occurred as regards SRL. However, there was a summer peak on 21st August that was significant for the very fine-root diameter class (<0.5 mm) (Fig. 2). In this period, when

soil moisture was lowest (Fig. 1b), the growth rate of FRL was higher than that of FRB (Fig. 2). As SRL is inversely related to the square of the fine-root diameter (Ostonen et al. 2011), we investigated the seasonal variation of the mean diameter within each diameter class. What we found was a significant decrease only in the case of the finest-root class ($p < 0.001$) on 21st August (data not shown).

FRB and FRL showed a significant inverse power relationship ($p < 0.001$) with the soil moisture for all diameter classes (Fig. 3). The coefficient of determination (R^2) decreased with increasing root diameter; in fact, it decreased from 0.43 and 0.49 in the very fine roots (<0.5 mm; Fig. 3a, b) to 0.13 and 0.15 in the larger fine roots (1.5–2 mm; Fig. 3j, k) in the case of FRB and FRL, respectively. SRL showed the same inverse power relationship with soil moisture only in the case of the finest roots (<0.5 mm) (Fig. 3c). In fact, the proportion of the latter in total fine-root biomass and length increased from 13.3 % (4 April) to 29.2 % (30 July) and to 22.6 % (21 August), from 73.8 % (4 April) to 85.9 % (30 July) and to 83.4 % (21 August), respectively (data not shown).

Fine-root production and turnover rate

Table 2 shows the FRP and turnover rate calculated irrespective of diameter classes (<2 mm in diameter) and with respect to the four different diameter classes. The two smaller classes (<0.5 and 0.5–1.0 mm) showed similar FRP values higher than the two larger classes (1–1.5 and 1.5–2 mm), and accounted for 60 % of the total annual FRP. FRT values were highest in the case of the finest root fractions (<0.5 and 0.5–1.0 mm), and decreased as root diameter increased.

Discussion

The mean total (live and dead) fine-root mass in our Turkey-oak stand in the Southern Apennines of Italy (oak fine roots 321 g m^{-2} ; understory fine roots 122 g m^{-2}) was consistent with the values reported for the

Table 2 Annual mean fine-root traits (FRB, FRN, FRL, and SRL) per diameter class

Diameter class (mm)	FRB		FRN		FRL		SRL (m g^{-1})	FRP ($\text{g m}^{-2} \text{ year}^{-1}$)	FRT (year^{-1})
	(g m^{-2})	%	(g m^{-2})	%	(m m^{-2})	%			
0–2	145 ± 8	100	176 ± 8.4	100	1142 ± 77	100	8.3 ± 0.63	287.61	1.17
0–0.5	32.3 ± 2.1	21.2 ± 1.4	32.0 ± 1.7	18.2 ± 1	920.2 ± 71.4	79.0 ± 6.1	27.5 ± 0.84	87.46	1.22
0.5–1	44.9 ± 2.6	29.4 ± 1.7	63.2 ± 2.6	35.9 ± 1.5	173.8 ± 9.7	14.9 ± 0.8	3.9 ± 0.06	87.65	1.20
1–1.5	39.9 ± 3.0	26.2 ± 2.0	47.9 ± 2.3	27.2 ± 1.3	49.2 ± 3.6	4.2 ± 0.3	1.2 ± 0.16	64.36	1.07
1.5–2	35.2 ± 3.0	23.2 ± 2.0	32.9 ± 2.3	18.7 ± 1.3	21.3 ± 1.8	1.8 ± 0.2	0.6 ± 0.01	48.14	0.85

Values are the mean \pm 1 SE; $n = 48$

FRB fine-root biomass, FRN fine-root necromass, FRL fine-root length, SRL specific root length, FRP fine-root production (Decision Matrix method), FRT fine-root turnover rate (FRP/maximum standing biomass)

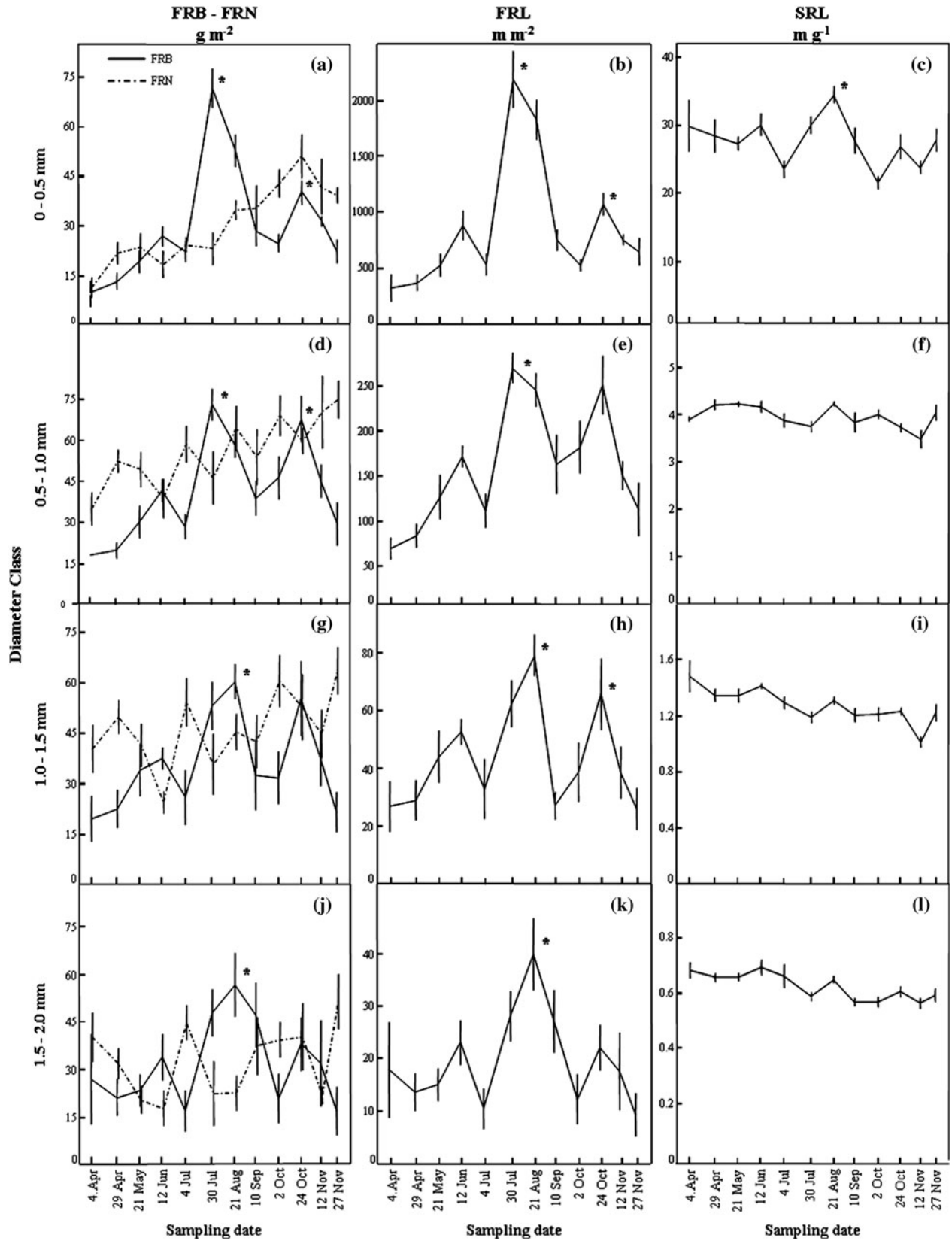


Fig. 2 Seasonal variation of fine-root biomass (FRB, solid line), necromass (FRN, dotted line), length (FRL) and specific root length (SRL) (columns) according to diameter class (rows). Data refer to each sampling date represented as means ($n = 4$) \pm 1 SE. Asterisks indicate statistically significant peaks ($p < 0.05$)

Table 3 Split-plot design one-way ANOVA for the effects of time on fine-root traits (FRB, FRN, FRL, and SRL) irrespectively of diameter classes (roots with diameter <2 mm) and by different diameter classes

Parameter	Diameter class (mm)	Source of variation		
		Time		
		df	F	p value
FRB	0–2	11	12.7	0.000
	0–0.5	11	22.8	0.000
	0.5–1	11	8.8	0.000
	1–1.5	11	3.3	0.003
	1.5–2	11	2.8	0.010
FRN	0–2	11	2.4	0.023
	0–0.5	11	4.6	0.000
	0.5–1	11	1.4	0.207
	1–1.5	11	1.6	0.139
	1.5–2	11	2.4	0.021
FRL	0–2	11	15.5	0.000
	0–0.5	11	13.3	0.000
	0.5–1	11	8.1	0.000
	1–1.5	11	3.3	0.004
	1.5–2	11	3.2	0.004
SRL	0–2	11	2.1	0.040
	0–0.5	11	3.5	0.002
	0.5–1	11	3.1	0.005
	1–1.5	11	4.1	0.001
	1.5–2	11	4.7	0.000

same or similar species. For example, it was 395–398 g m⁻² for the older stands of *Q. cerris* in central Italy (Claus and George 2005), 298 g m⁻² for a *Q. alba* stand in Missouri, USA (Joslin and Henderson 1987), and 536–654 g m⁻² young and old *Q. robur* stand in the Netherlands (Bakker 1998). Moreover, our results were of the same order of magnitude as those reported for temperate deciduous forests in Jackson et al. (1997) and Finér et al. (2011a, b). In particular, Jackson et al. (1997) reported a mean live and total fine-root mass of 440 and 780 g m⁻², respectively, 63 % of which in the upper 30 cm. More recently, Finér et al. (2011) reported a mean fine-root total mass of 362 g m⁻² at a mean sampling depth of 47.2 cm.

Data regarding fine-root length are scarce. In a study of temperate deciduous forests, Jackson et al. (1997) predicted a mean standing crop root length of 3.4 km m⁻² (calculated for the upper 30 cm of soil), which is similar to the values measured in our study site if oak fine roots plus understory fine roots are considered (respectively 1.2 and 2.0 km m⁻²). Jackson et al. (1997) noted that there is a need for more field estimations of fine-root length to obtain an accurate biome prediction.

Concerning SRL, in a meta-analysis, Ostonen et al. (2007) reported a fine-root SRL (<2 mm in diameter) ranging between 1.4 and 25 m g⁻¹ depending on tree species. Our result (8.3 m g⁻¹) falls within this range, and is similar to the value reported for *Q. robur* (4.1–21.3 m g⁻¹; Bakker 1998) and for *Q. cerris* (4.10–6.80 m g⁻¹; Claus and George 2005).

In our *Q. cerris* stand, both fine-root mass and length showed a complex seasonal growth pattern. Our obser-

vations are similar to Brassard et al.'s (2010) finding that fine-root biomass generally peaks in mid to late summer and is minimal in late fall to early winter. It has been suggested that this seasonal variation could reflect seasonal variations of water and consequent nutrient availability (Coners and Leuschner 2005; Vanguelova et al. 2005; Mainiero and Kazda 2006) as well as an ontogenic response to local conditions (Chiatante et al. 2005).

In our study, from the beginning of April to the beginning of June with high soil water conditions content and progressive increment of air temperature, fine-root mass and length increased. In summer FRB and FRL peaks lasted only few weeks, during which the mean air temperature exceeded 20 °C and soil water content was decreasing. When the drought period was prolonged and soil water content reached very low values (end of August), both fine-root traits decreased for all diameter classes considered. We found that there was a close, inverse relation between both FRB and FRL and soil water content. Teskey and Hinckley (1981) observed that temperature was the dominant factor for oak root growth at low temperatures, but soil water content was the most important factor when temperatures increased above 17 °C. As found by Cudlin et al. (2007) in a recent meta-analysis, the fact that root growth stops and several roots die (decrease in root length and biomass) might indicate that an overall reduction of the root production becomes more functional when water shortage exceeds a certain limit in terms of content and time. Therefore, a higher biomass allocation to belowground organs is a frequent occurrence during a mild drought, but when water stress continues, root growth usually decreases (Joslin et al. 2000; Chiatante et al. 2005, 2006; Di Iorio et al. 2011). We suggest that our fine-root production flushes during the driest period could be a strategy to overcome the unfavorable environmental conditions. The finest root fractions (<0.5 and 0.5–1.0 mm) showed the highest inverse relationship with soil water content as regards both FRB and FRL. These findings indicate that the soil moisture deficit at the beginning of July led to an increase mainly in very fine-root biomass and length.

Third fine-root mass and length peaks occurred after September and October rainfall events when the soil water content began to increase. According to Edwards and Harris (1977) these third peaks were significant only in the case of roots belonging to the smaller diameter classes (<0.5 and 0.5–1.0 mm). In line with previous studies (Chiatante et al. 2005, 2006; Di Iorio et al. 2011), we suggest that this second flush of fine-root production is a recovery mechanism whereby the plants can 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.

Joslin et al. (2006) hypothesized that a tree fine-root system consists of pools of fine roots of different ages. One pool is very dynamic and has a life span <1 year

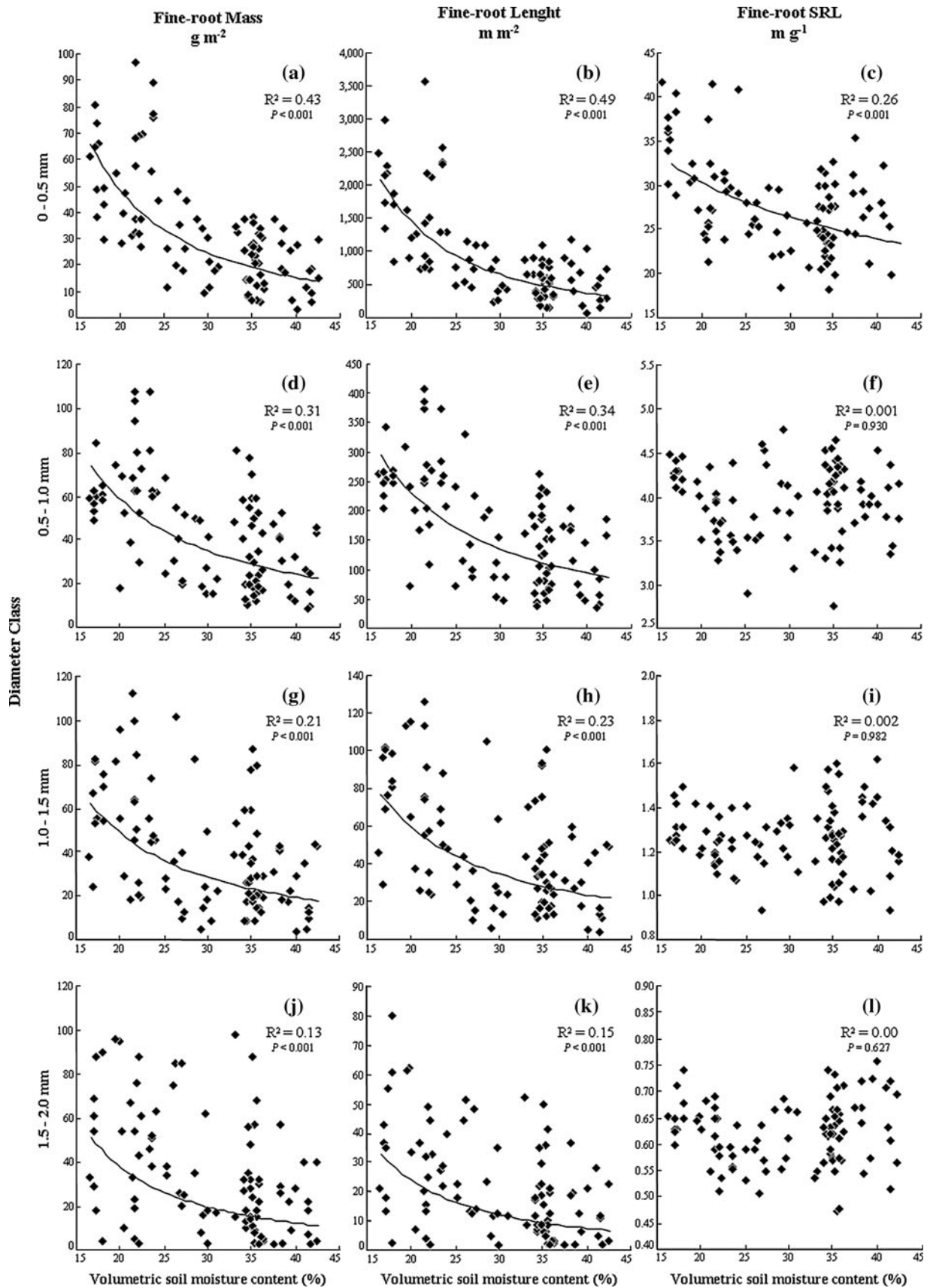


Fig. 3 The relationship between volumetric soil moisture and FRB, FRL, and SRL (*columns*) according to diameter class (*rows*). Data refer to the surface 30-cm soil layer between April and November 2008

(“short-lived”), and the other has a life span > 1 year (“long-lived”). It is feasible that the difference we found between the initial value of biomass and the peak values measured in July–August could be due mainly to the production (flush) of new fine roots. Moreover, the fact that the peak of fine roots measured in July–August lasts just a few weeks suggests that most of these new fine roots produced are of the “short-live” type. Furthermore, also the second flush measured in October, though less abundant than the first one, could be formed mainly by “short-lived” fine roots because also this second peak lasts only a few weeks. If this is the case, the amount of fine roots present at the beginning of the growing season (spring) and throughout the winter could represent the portion of the root system classifiable as “long-lived” fine roots. In our study, the difference in biomass between April and November was roughly 1 %. Thus, the peaks in fine-root mass and length observed may be attributed to the production and shedding of “short-lived” fine roots, thereby resulting in a very low net annual increment in total fine-root mass.

The life span of fine roots is controversial probably due to different species and growing environmental conditions. López et al. (2001) studying *Q. ilex* in Mediterranean climate conditions asserted that spring and autumn fine roots have a shorter life span than fine roots produced in summer and winter. On the contrary, our results, similar to those reported by Eissenstat and Yanai (1997) and Guo et al. (2008), show that roots born in spring and winter generally live longer than roots born in summer and autumn. Although their fine-root turnover rates were based 1-year data, our results are in agreement with Joslin et al. (2006). They found that very fine roots in the surface soil had a faster turnover than larger roots. Similarly, we found that very fine roots had a shorter life span (< 1 year) than larger roots (> 1 year). This finding confirmed the ephemeral nature of very fine roots produced during the growing season.

The only significant season-related peak in SRL occurred in fine-roots (< 0.5 mm) when their mean diameter was lowest and when soil was at driest, which demonstrates that warm and dry conditions increased the SRL of the finest-root. This is in accordance with Bjork et al. (2007) and Makita et al. (2011) who reported a morphological plasticity of roots especially in the finest fine-root fraction. Thus, in summer more root length per unit mass was produced than during the rest of the growing season. This observation is compatible with a high morphological plasticity of the finest-root class, which plays a main role in water and nutrient uptake at time of soil water shortage.

The mechanism occurring when water stress increase, which carbon gain is lowered consequent to the reduction in stomatal conductance, suggests that carbon is preferentially channeled into the fine-root production (Dickson and Tomlinson 1996; Thomas and Gausling 2000; in Di Iorio et al. 2011). We observed in our study that *Q. cerris* acted in the same way but seemed to optimize the investment of carbon by reducing the mean

diameter of very fine roots, which led to the production of more root length per unit dry mass. In fact, this response is easier to detect when evaluated also in terms of SRL rather than in terms of biomass and length considered separately. Thus, the variation of fine-root traits is mainly due to the pool of thinner roots that, in turn, results in a higher annual production and FRT rate. Our data on the responses of fine roots to soil water content have shed some light on the mechanisms that govern plant–water relationships. These mechanisms are important for forests growing under natural conditions because they enable plants to survive the typical dry summer in the Mediterranean area, which is likely to become drier and to last longer given the increase in temperature expected in this century.

Conclusions

We investigated, at stand level, how soil moisture deficit affects the characteristics of *Q. cerris* fine roots during the growing season. Both fine-root biomass and length were influenced by seasonal variations of soil water content and were consistently higher when the soil was drier. We found that peaks constituting the bimodal pattern of fine-root growth were characterized by an increase of the thinner fraction (< 0.5 mm in diameter) of the root population. In summer this pattern leads to an increase of the mean forest fine-root mass and length and an increase of fine-root SRL. While we found a significant relationship between some of the measured fine-root characteristics and soil moisture at our study site, we cannot exclude that other variables such as stand age could contribute to this variation. Therefore, a more comprehensive measurement program is required to elucidate the effects of other potentially important drivers of root growth patterns and processes.

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