

Fine root seasonal dynamics, plasticity, and mycorrhization in 2 coexisting Mediterranean oaks with contrasting aboveground phenology¹

Lluís COLL², Forest Sciences Center of Catalonia (CTFC), Solsona, 25280 Catalonia, Spain, and CREAF, Cerdanyola del Vallès,

08193 Catalonia, Spain, e-mail: lluis.coll@ctfc.cat

Jesús Julio CAMARERO, ARAID, Instituto Pirenaico de Ecología (CSIC), Avda, Montañana 1005, 50192 Zaragoza, Spain.

Juan MARTÍNEZ DE ARAGÓN, Forest Sciences Center of Catalonia (CTFC), Solsona, 25280 Catalonia, Spain.

Abstract: To advance understanding of the mechanisms underpinning the coexistence of Mediterranean oak species, we conducted a year-long analysis of the production, architecture, and mycorrhization status of the fine roots of a mixed evergreen (*Quercus ilex*) and winter deciduous (*Quercus faginea*) oak stand. We used the ingrowth bag technique to sample the fine roots produced by each species in spring, summer, and winter. For each season, root architecture traits (specific root length, root diameter, root tips) and variables associated to root ectomycorrhizal status were measured in the laboratory. Results showed a marked seasonality in the fine root architecture, including more fine root tips and longer roots per unit of weight formed in spring and summer, revealing a capacity in Mediterranean oak species to modify root architecture in spring and suggesting the possibility of increased resource capture in summer. Fine root ectomycorrhizal status was comparable between species and also showed marked seasonality: we found a high percentage of roots colonized by dead ectomycorrhizas in winter but low ectomycorrhizal colonization rates in summer. *Quercus ilex* produced greater amounts of fine roots than *Q. faginea* (particularly during spring), suggesting greater competitive ability in the former species for belowground resources.

Keywords: ectomycorrhizae, fine roots, phenology, *Quercus faginea*, *Quercus ilex*, root traits.

Résumé: Pour accroître notre compréhension des mécanismes supportant la coexistence d'espèces méditerranéennes de chênes, nous avons analysé sur une année la production, l'architecture et le statut mycorrhizien des racelles d'un peuplement mixte de chênes à feuilles persistantes (*Quercus ilex*) et caduques (*Quercus faginea*). Nous avons utilisé la technique du sac de croissance pour échantillonner les racelles produites par chaque espèce au printemps, à l'été et en hiver. Pour chaque saison, différents traits architecturaux des racines (longueur spécifique de la racine, diamètre de la racine, apex racinaire) et des variables associées au statut ectomycorhizien des racines ont été mesurés en laboratoire. Les résultats ont démontré une saisonnalité marquée dans l'architecture des racelles. Au printemps et à l'été, une plus grande quantité d'apex racinaires et des racines plus longues par unité de poids étaient formées, révélant ainsi la capacité de ces espèces méditerranéennes de chênes à modifier l'architecture racinaire au printemps et suggérant une meilleure acquisition des ressources en été. Le statut ectomycorhizien des racelles était comparable entre les espèces et montrait également une saisonnalité marquée puisque nous avons trouvé un pourcentage élevé de racines colonisées par des ectomycorhizes mortes en hiver, mais en été les taux de colonisation par des ectomycorhizes étaient faibles. *Q. ilex* a produit plus de racelles que *Q. faginea* (particulièrement au printemps) ce qui suggère une plus grande compétitivité de la première pour les ressources souterraines.

Mots-clés: ectomycorhize, phénologie, *Quercus faginea*, *Quercus ilex*, racelles, traits racinaires.

Nomenclature: Ruiz de la Torre, 2006.

Introduction

In the western Mediterranean Basin, mixed woodlands dominated by the evergreen holm oak (*Quercus ilex*) and other deciduous oaks (e.g., *Q. faginea* and *Q. pubescens*) are widespread (Quézel & Médail, 2003) and constitute unique and diverse forest ecosystems. There has been a wealth of research into the mechanisms underpinning the coexistence of these tree species (e.g., Bonfil *et al.*, 2004; Espelta *et al.*, 2005; Juárez-López, Escudero & Mediavilla, 2008). In a recent study of aboveground phenology, Montserrat-Martí *et al.* (2009) concluded that *Q. ilex* was better adapted to drought than *Q. faginea* as it started shoot

growth and leaf development later, thus suggesting higher tolerance to summer drought. These results suggested potential changes in the composition of these woodlands, as climate change-driven increases in temperature and alterations to seasonal precipitation regimes (e.g., a reduction in spring precipitation) could favour the replacement of *Q. faginea* by *Q. ilex*, at least in the most xeric sites. To get a deeper understanding of the coexistence mechanisms of these mixed oak woodlands, better comprehension of the belowground dynamics in these forests is needed. However, in Mediterranean areas (as in many other regions), comparative root studies based on sympatric woody species have rarely been carried out.

A number of studies conducted in boreal, temperate, and tropical forests have shown how plants belonging to

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²Author for correspondence.

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different functional groups develop diverse rooting patterns to coexist (Bauhus & Messier, 1999; Comas & Eissenstat, 2004; Coll *et al.*, 2008). In addition to different rooting patterns, important differences in the mycorrhization status of roots may also be found between species with different ecological and functional strategies. Oaks, for example, are known to be critically dependent on ectomycorrhizal fungi (EM) to improve their capacity for absorption of water and nutrients (Morris *et al.*, 2008a; Richard, Selosse & Gardes, 2009). In general, this genus presents a high EM species richness (*e.g.*, Richard *et al.*, 2011), but differences in EM community composition could be found between sympatric species, *e.g.*, evergreen *versus* deciduous oaks (Morris *et al.*, 2008b).

In the current global climate-change context, the composition and dynamics of Mediterranean plant communities are expected to be conditioned by the capacity of each species to adjust its phenological phases in response to climate warming, and in particular to summer drought (Castro-Díez & Montserrat-Martí, 1998; Montserrat-Martí, Palacio-Blasco & Milla Gutiérrez, 2004). Although there is a general consensus that understanding root phenology is critical for the prediction of plant dynamics (Lyr & Hoffmann, 1967), field studies focusing on the seasonal variation of root plasticity are scarce. Root phenology can indeed have direct consequences for the amount of mycorrhizal colonization, particularly in drought-prone areas (Swaty *et al.*, 1998). At present, little among-season variation in the composition of EM communities has been found in Mediterranean forests (Richard *et al.*, 2011). However, predicted drought increases related to climate warming are expected to modulate future fungi composition and colonization of tree roots (Cavender-Bares *et al.*, 2009; Querejeta, Egerton-Warburton & Allen, 2009; Richard *et al.*, 2011) and thus affect tree performance (*e.g.*, Morte *et al.*, 2001).

Here, we report a 12-month tracking study following fine root dynamics in a mixed forest dominated by evergreen holm oak (*Quercus ilex* subsp. *ballota*) and deciduous Portuguese oak (*Quercus faginea*). Our initial hypothesis was that both species would present differences in their belowground phenological activity that followed the patterns found aboveground in a previous study (Montserrat-Martí *et al.*, 2009) that suggested a higher capacity of *Q. ilex* to cope with summer drought compared to *Q. faginea*. We also expected important seasonal variations of root architecture and mycorrhization rates oriented to increase the capture of belowground resources.

Methods

STUDY SITE AND SPECIES

The study site was located near Agüero (Huesca) in northeast Spain (42°18'N, 0°47'W, 750 m asl). In this area, the soil is calcareous and the vegetation is dominated by low trees (mainly *Q. ilex*, *Q. faginea*, *Arbutus unedo*, *Pinus halepensis*, and *Juniperus oxycedrus*) and scrubs (mainly *Viburnum tinus*, *Pistacia lentiscus*). Climate is continental Mediterranean, with an annual average rainfall of 750 mm, mean minimum temperature of the coldest month (January) of 4.3 °C, and mean maximum temperature of the warmest month (July) of 28.4 °C.

A homogenous flat 8-ha area including both *Q. ilex* and *Q. faginea* adults growing together was delimited. These species are widely distributed in the Iberian Peninsula and frequently coexist, preferentially inland and in continental areas. In the study site, aboveground phenology, bud development, shoot length, and radial growth of 10 marked individuals per species were monitored from January 2006 to January 2011 (see Montserrat-Martí *et al.*, 2009 for details). In the study site, budburst of *Q. faginea* and *Q. ilex* trees occurred in April and May, respectively, whereas shoot elongation and leaf expansion took place from May to June. Volumetric soil water content (SWC, %) in the upper soil layer (10 cm) and around each adult tree base was also measured monthly from March 2007 to June 2008 using a TDR probe (ThetaProbe Soil Moisture Sensor, Delta-T, Cambridge, UK), taking 3 measurements below each tree canopy at 0.5, 1, and 2 m from the main stem of each individual (Figure 1).

FINE ROOT SAMPLING

Fine root sampling started in mid-May 2007 and ended in late May 2008. Eight trees per oak species were selected and tagged, and their size (diameter at 1.3 m, total height) and number of stems per tree were recorded (Table I). All sampled trees were formerly coppiced and presented a multi-stemmed growth form. Based on wood cores taken at 1.3 m above the soil the mean (\pm SE) tree-ring number of stems was 33 ± 2 (*Q. faginea*) and 25 ± 3 (*Q. ilex*). The individuals were probably much older. The mean (\pm SE) distance between nearest neighbour conspecific sampled trees was 43.3 ± 9.3 m (*Q. faginea*, minimum tree-to-tree distance 23.0 m) and 37.6 ± 10.1 m (*Q. ilex*, minimum tree-to-tree distance 13.3 m).

Three soil cores were randomly excavated around each tree at about 50 cm from the main stem of each tree and near (25–50 cm apart) the soil water measurement points. The minimum distance between cores was about 50 cm. The cores had a diameter of 9 cm and were excavated to a depth of 15–20 cm using a steel corer. A 20-cm long 8-mm mesh bag was then installed in each hole. The bags were filled with mineral soil taken from a nearby pit and passed through a 2-mm mesh sieve to remove all roots. All the bags were sampled and refilled with sieved soil 3 times during the year, in October 2007 (May–October sampling period, summer hereafter), in February 2008 (October–February period, winter hereafter), and again in May 2008 (February–May period, spring hereafter).

Samples were frozen until processed. In the laboratory, fine roots were carefully separated from the soil using a 2-mm mesh sieve and tap water. Species were identified by comparing harvested roots with samples and, in cases of doubt, using a microscope. Once the fine roots were separated from the soil and adequately identified, they were placed in a large Petri dish with distilled water and placed in cool storage.

FINE ROOT TRAITS AND ANALYSIS OF ECTOMYCORRHIZATION STATUS

Root samples were placed in a glass Petri dish with water, and EM colonization was analyzed using a

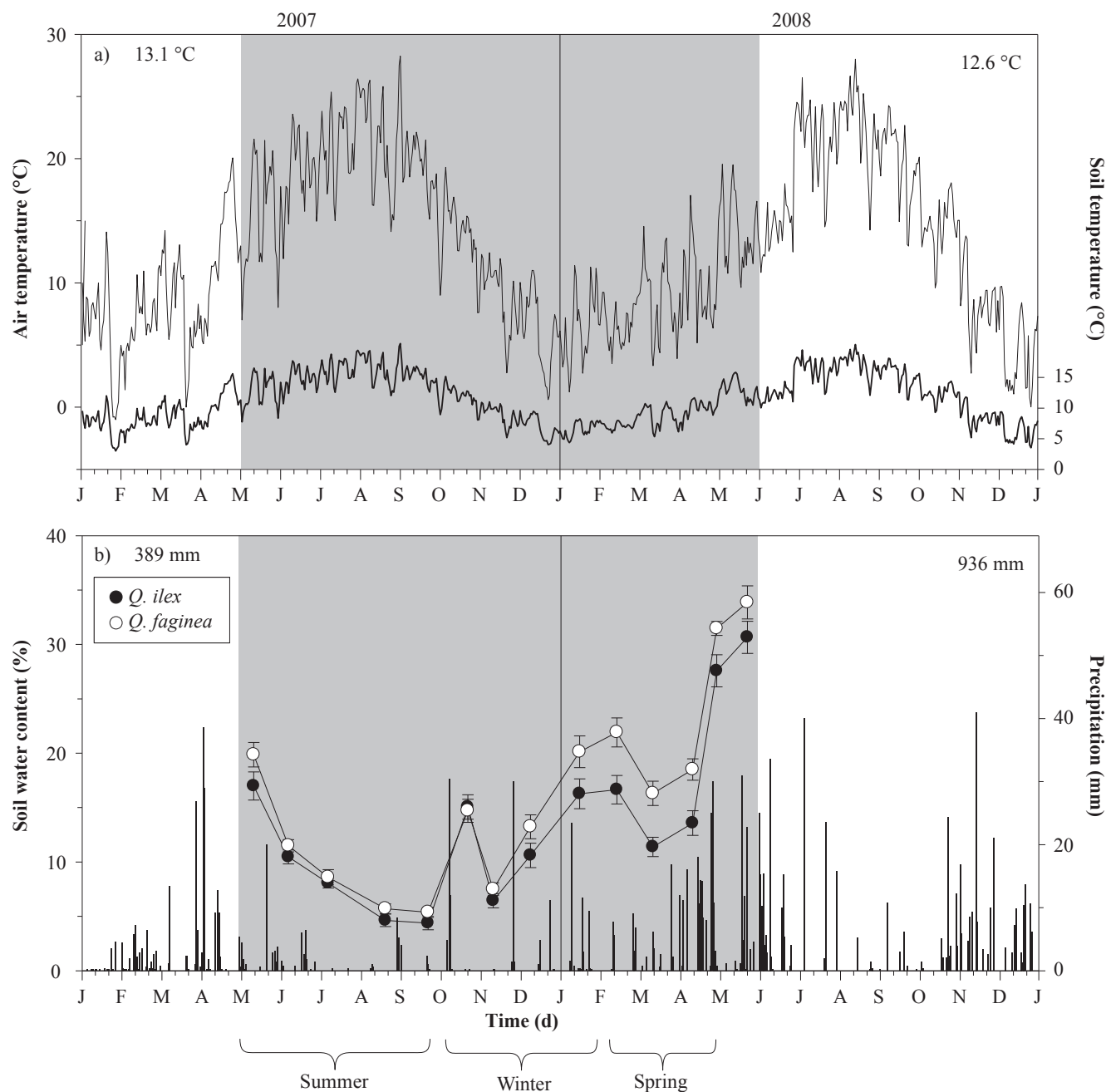


FIGURE 1. a) Daily air (thin line) and soil (thick line) temperatures (°C) and b) daily precipitation (mm, bars) and monthly mean volumetric soil water content (%) (line with symbols) of *Quercus ilex* (black circles) and *Quercus faginea* (white circles) during the study period. The grey area indicates the sampled period. The 3 sampling seasons are indicated at the bottom: May to October 2007 (summer), October 2007 to February 2008 (winter), and February to May 2008 (spring). Values at the top of each panel indicate a) mean annual temperatures and b) total annual precipitation.

Leica MS5 dissecting microscope (magnification 50–100×). In cases of doubt, microscopic samples were prepared with water and KOH and a compound Leica DMRB microscope (magnification 100–1000×) was used. The root tips were then counted and divided into 3 groups: 1) non-ectomycorrhized root tips (Non_EM), 2) root tips with dead ectomycorrhizas (Dead_EM), and 3) root tips colonized by living ectomycorrhizas (EM). Root tips were assessed as presenting dead EM when we observed a collapsed periderm or when any microstructural or macroscopic

TABLE I. Size (diameter at 1.3 m, height), number of stems per tree, and volumetric soil water content below the tree (means \pm SE) for the 8 individuals of each species that were monitored in this study. Different letters indicate significant differences between species at $P < 0.05$ based on Mann-Whitney U tests.

	<i>Quercus ilex</i>	<i>Quercus faginea</i>
Diameter (cm)	9.8 \pm 0.8a	12.6 \pm 1.4a
Height (m)	3.5 \pm 0.2a	5.6 \pm 0.6b
No. stems per tree	8 \pm 1a	5 \pm 1b
Soil water content (%)	14.7 \pm 0.8a	17.3 \pm 0.9b

characteristics were visible. Once the EM status was assessed, the roots were scanned and their diameter and length were estimated using WinRHIZO software (Régent Instruments, Québec, Québec, Canada). Specific root length (SRL, $\text{cm} \cdot \text{g}^{-1}$) was calculated once the analyzed roots were dried and weighed.

STATISTICAL ANALYSES

Between-species and between-period differences in fine root production, traits, and ectomycorrhizal status were analyzed using linear mixed models with JMP 6.0 (SAS Institute, Cary, North Carolina, USA). The soil holes were incorporated into the model as random effects, whereas species and sampling period (and its interaction) were considered fixed effects. If a significant effect of the sampling period was detected, a multiple *post hoc* comparison of the means was performed using the Tukey HSD test. As the sampling periods did not have the same length, the variables weight, length, and density were divided by the number of days within each sampling period. When heteroscedasticity and non-normality of regression residuals were observed, we applied log- (length, weight, and density variables) and arcsine square root transformations (ectomycorrhizal colonization rates). Between-species and between-period differences were considered significant at $P < 0.05$. Finally, we used Spearman's correlation coefficients to assess the relationships between the different fine root variables and soil water content at tree level and for selected seasons.

Results

The studied period was characterized by a dry winter season in 2007 followed by a very wet spring in 2008; the lowest SWC values below trees were recorded in late summer 2007, whereas SWC reached maximum values during spring 2008 (Figure 1b). Mean SWC was significantly higher under *Q. faginea* than under *Q. ilex* trees (Table I).

The 2 studied species showed marked differences in the colonization dynamics of the ingrowth bags. Overall, *Q. ilex* developed more numerous and longer fine roots than *Q. faginea*, particularly in spring, when the sampled root density was highest (Table II; Figure 2a). In contrast, *Q. faginea* demonstrated fairly constant fine root regrowth throughout the year. The differences between spring and winter fine root proliferation into the bags were not significant when estimated in terms of weight. This was due to the low specific root length (around $15 \text{ m} \cdot \text{g}^{-1}$) found in the roots sampled in winter (Figure 2b).

Morphologically, the fine roots of both species presented similar traits and phenological patterns (Table II), being wider and less branched (lowest values for specific root length [SRL] and number of root tips) in winter than in the other seasons (Figure 2b). The highest SRL values for both species were found in fine roots sampled in summer, which for a given weight were almost twice as long as those sampled in winter. There was equally marked seasonality in the degree of fine root ectomycorrhizal status. The maximum percentage of non-ectomycorrhizal root tips (*ca* 25%) was found in summer (Figure 3a), whereas in winter both

TABLE II. Statistics (F , P) of linear mixed models testing the effect of species and sampling season on different fine root variables related to root production and traits, and ectomycorrhizal fungi (in bold, P values < 0.05)

Root parameter	Variables (units)	Factor	F -ratio	P
Regrowth	Biomass ($\text{mg} \cdot \text{day}^{-1}$)	Season	8.9385	0.0003
		Species	7.0965	0.0106
		Season * Species	1.3264	0.2705
	Length ($\text{cm} \cdot \text{day}^{-1}$)	Season	7.1345	0.0013
		Species	8.5442	0.0054
		Season * Species	2.2732	0.1088
	Density ($\text{cm} \cdot \text{m}^{-3} \cdot \text{day}^{-1}$)	Season	7.7307	0.0008
		Species	7.8924	0.0073
		Season * Species	2.1454	0.1230
Traits	Diameter (cm)	Season	9.4431	0.0002
		Species	0.0333	0.8561
		Season * Species	0.2072	0.8132
	SRL ($\text{m} \cdot \text{g}^{-1}$)	Season	16.0111	< 0.0001
		Species	0.6443	0.4262
		Season * Species	0.0005	0.9995
	No. root tips	Season	4.3267	0.0161
		Species	3.9655	0.0526
		Season * Species	1.2502	0.2914
Ectomycorrhizal fungi	EM (%)	Season	12.2673	< 0.0001
		Species	1.6982	0.1990
		Season * Species	0.1854	0.8311
	Dead_EM (%)	Season	67.5031	< 0.0001
		Species	0.5476	0.4630
		Season * Species	0.3880	0.6795
	Non_EM (%)	Season	10.4995	< 0.0001
		Species	0.5394	0.4664
		Season * Species	0.2983	0.7428

Abbreviations: SRL, specific root length; EM, root tips colonized by living ectomycorrhizas; Dead_EM, root tips with dead ectomycorrhizas; Non_EM, non-ectomycorrhized root tips.

species showed the highest percentage of root tips presenting dead ectomycorrhizas (*ca* 40%) (Figure 3b). The frequency of root tips showing no signs of ectomycorrhizal status was low and fluctuated between 5–10% in winter and 20–30% in summer. Both species presented similar ectomycorrhizal composition (Table II). Mycorrhizal diversity in sampled roots was relatively low at just 1 to 3 species, with the genus *Cenococcum* being the dominant species during summer (data not shown).

SWC significantly affected fine root production (Table III). During the spring, the 2 variables were negatively correlated when all sampled trees were considered, but any significant trend disappeared when the analysis was conducted by individual species (Table III). In contrast, during the summer, the 2 species showed marked differences in terms of the role played by SWC in fine root production. In summer *Q. ilex* tended to increase fine root production in response to SWC decreases, whereas we found no response of *Q. faginea* to SWC variations. We did not find any effect of SWC on root ectomycorrhizal patterns (data not shown).

Discussion

We postulated that the different aboveground phenological patterns in crown development of the 2 co-occurring

oak species (Montserrat-Martí *et al.*, 2009) would translate to contrasting belowground fine root activity. Overall, we found *Q. ilex* to present higher root recolonization rates than *Q. faginea*. Between-species differences in fine root density were particularly marked in spring, which as a rule is the most significant period of root growth (Lyr & Hoffmann, 1967; Pregitzer *et al.*, 2000) and canopy development (Montserrat-Martí *et al.*, 2009). Although caution is needed in the interpretation of these patterns since we only followed 1 y of growth and we did not assess exploration strategies of EM fungi, our results suggest that *Q. ilex* plants present in general a greater soil exploitation potential than *Q. faginea* ones (Oppelt, 2003) and thus a greater competitive ability to capture water during the periods in which it is available in the soil, *i.e.*, just before the onset of the summer drought that characterizes Mediterranean climates.

The study provided information on the seasonal variation of root traits and ectomycorrhizal colonization rates. In spring and summer, both species formed more fine root tips and longer fine roots per unit of weight than in winter. This reflects the capacity of both species to increase the volume of soil exploited per unit of carbon used for root construction. This may help the plants to exploit water and nutrients in small volumes of favourable soil (Eissenstat, 1991; Bausch & Messier, 1999; Curt *et al.*, 2005) and thus supply themselves with the resources needed to complete the different aboveground phenological phases of growth. In our study, we could not adequately evaluate annual fine root production because both 1) sampling during the year was done in the same hole (surrounding roots were cut several times) and 2) fine root turnover was not considered. However, seasonal samplings of fine root regrowth and

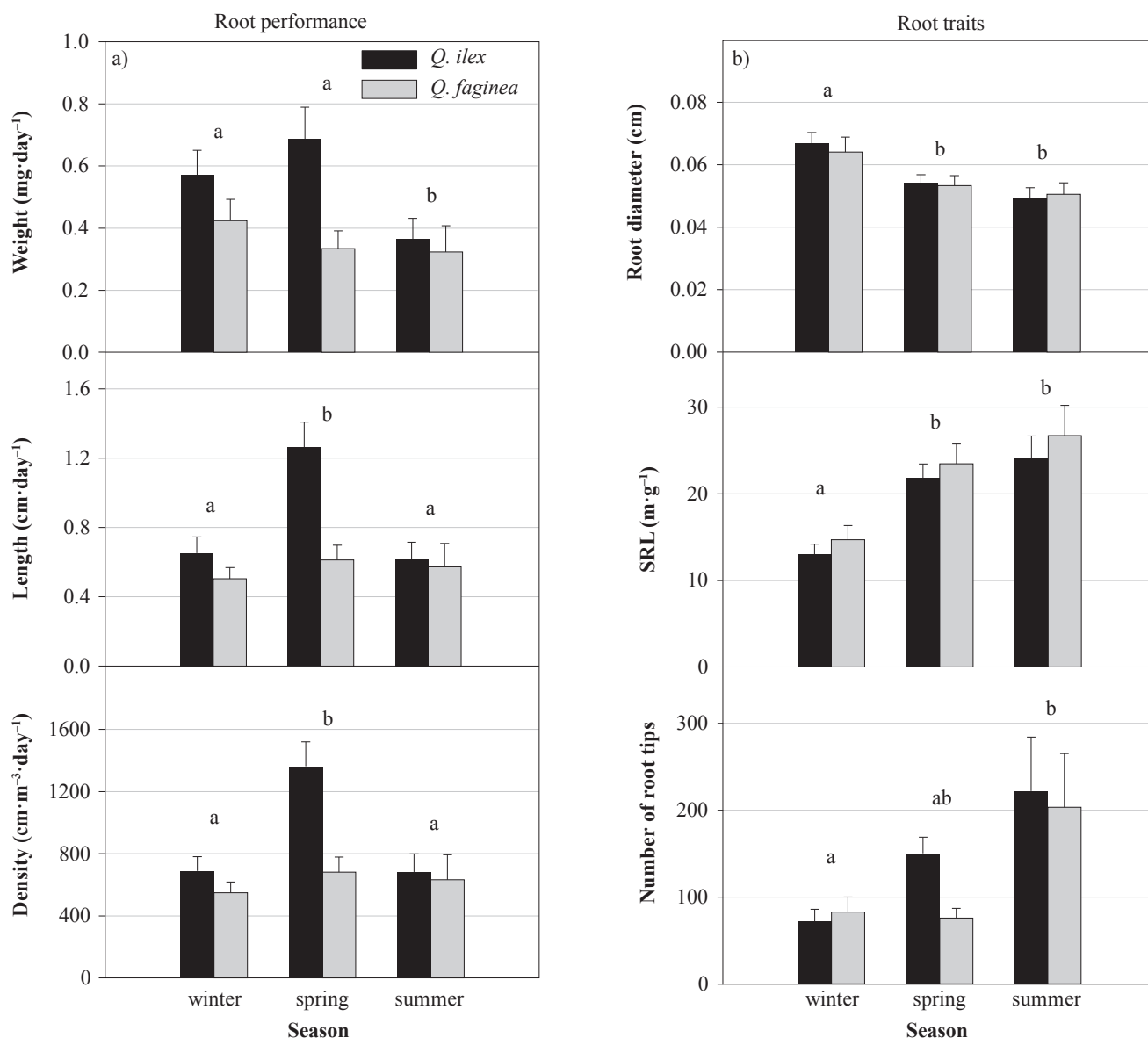


FIGURE 2. a) Parameters of fine root productivity (weight, length, density) and b) related fine root traits (diameter, specific root length [SRL], number of root tips) for *Quercus ilex* (black bars) and *Quercus faginea* (grey bars) over 3 seasons. Values are means plus SE. Different letters indicate significant differences ($P < 0.05$) between sampling periods.

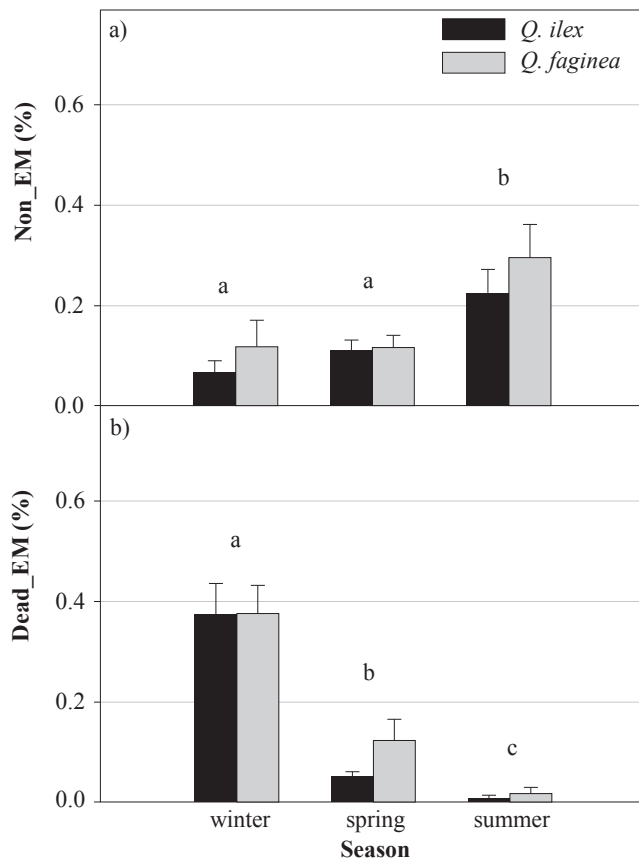


FIGURE 3. a) Percentage of non-ectomycorrhized (Non_EM) root tips and b) percentage of root tips with dead ectomycorrhizas (Dead_EM) in the fine roots of *Quercus ilex* (black bars) and *Quercus faginea* (grey bars) plants sampled at different periods of the year. Values are means plus SE. Different letters indicate significant differences ($P < 0.05$) between sampling periods.

TABLE III. Spearman's correlation coefficients between soil water content and fine root production in spring and summer for all sampled individuals pooled together (*Quercus ilex* + *Quercus faginea*) and for each species separately (*Q. ilex*, *Q. faginea*). Significant ($P < 0.05$) correlations are indicated with an asterisk (*).

Season	<i>Q. ilex</i> + <i>Q. faginea</i> (<i>n</i> = 16)	<i>Q. ilex</i> (<i>n</i> = 8)	<i>Q. faginea</i> (<i>n</i> = 8)
Spring	-0.626*	0.001	-0.500
Summer	-0.426	-0.571	-0.381

plasticity give us a reliable approximation of the capacity of each species to recolonize new areas at different periods of the year and enable us to estimate their ability to compete for soil resources.

The relationship between fine root dynamics and SWC is under-researched compared to the relationship between root plasticity and exploitation of soil nutrient patches (Hodge, 2004). Overall, our results showed a general negative relationship between fine root density and SWC in spring, mostly in *Q. faginea* trees. Increasing carbon allocation to fine roots in response to drought may indicate a strategy of preferential allocation of carbon and nutrients to the organs responsible for capturing the most constraining resource in drought-prone forest ecosystems, namely soil

water (Bloom, Chapin & Mooney, 1985; Gower, Vogt & Grier, 1992). Such a strategy has already been reported for other Fagaceae species (Van Hess, 1997). However, drought also increases fine root mortality, which could counteract the enhancement of fine root production (Meier & Leuschner, 2008). Thus, increasing root turnover probably explains the lack of significant relationships between fine root production and soil water content during summer 2007, when a moderate drought affected the studied forest (Figure 1).

Fine root ectomycorrhizal colonization is expected to play a significant role in the adaptability of species to climate change (Eissenstat *et al.*, 2000). The mutualistic association between ectomycorrhizal fungi and vascular plants enables them to absorb a larger quantity of water and nutrients (Kropp & Langlois, 1990; Smith & Read, 1997; Reyna, 2007) because the hyphae enable plants to explore large volumes of soil. Our study did not find significant differences between *Q. ilex* and *Q. faginea* plants in any ectomycorrhizal-related variables, and in general, both species presented a relatively high rate of ectomycorrhization. We did, however, find clear seasonality in the ectomycorrhizal colonization of fine roots. Thus, the relative frequency of non-ectomycorrhized root tips increased in summer, a pattern that could be attributed to a drought-induced reduction in fungal development in the soil (Coleman, Bledsoe & Lopushinsky, 1989; Fitter, Heinemeyer & Staddon, 2000). A similar trend was also observed by Bonet, Fischer, and Colinas (2001), who found the lowest rates of truffle (*Tuber melanosporum*) colonization in *Q. ilex* roots from July to October. In contrast, in winter we found that almost 90% of root tips were colonized by ectomycorrhizal morphotypes, although around 40% of them were dead, revealing that the development of these fungi experiences some difficulties under low soil temperatures. Unfortunately, we recorded only a basic description of the EM status of the roots and did not assess the seasonal variation of the EM communities. However, a recent study conducted by Richard *et al.* (2011) in a *Q. ilex* coppice stand showed little seasonal variation of the EM communities. Although our data do not enable us to conclude this, the comparable patterns we found between *Q. ilex* and *Q. faginea* would suggest that the 2 species host EM communities that are relatively similar, at least in respect to their sensitivity to seasonal environmental conditions.

In summary, we detected a marked seasonality in the fine root architecture and production of coexisting *Q. ilex* and *Q. faginea*, demonstrating the ability of these species to modify their roots in spring and summer, possibly as a strategy to increase resource capture during the growing period. In general, *Q. ilex* showed greater fine root regrowth than *Q. faginea*, although this trend should be confirmed by studies over several growing seasons. Both species presented comparable ectomycorrhizal status, with spring marking the period in which there was the maximum percentage of root tips with living ectomycorrhizal fungi. Further research aimed at getting a better understanding of the effect of drought on the EM assemblages of the species constituting mixed forest would provide new insights for prediction of the future dynamics of these systems in a climate warming context.

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