

Seasonal and Site Effects on Oak Fine Root Production and Ectomycorrhizal Colonization in California Oak Woodland¹

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Abstract

At three sites in a blue oak woodland in northeast California, we studied seasonal patterns of blue oak (*Quercus douglasii* Hook and Arn.) fine root (< 2 mm diameter) production and ectomycorrhizal (ECM) colonization using root ingrowth cores. In a short-term study, ingrowth cores were installed and harvested in 3-month intervals for one year. Oak fine root production was lower in fall and winter, higher in spring, and intermediate in summer. ECM roots were found only in spring and fall. In a long-term study, ingrowth cores were installed in January 1998 and harvested after 6, 9, and 12 months, respectively. ECM colonization was higher after the 6-month (winter, spring) interval, lower after the 9-month (winter, spring, summer) interval and intermediate after the 12-month (winter, spring, summer, fall) interval. Both long-term and short-term studies demonstrated that ECM fungi were active in spring and fall seasons. ECM colonization was much higher in an undisturbed six-month interval (winter + spring, long-term study) than in a disturbed 6-month interval (winter + spring, short-term study), suggesting that disturbance decreased mycorrhizal colonization.

Introduction

In northern California blue oak woodlands, plant growth is affected by the typical Mediterranean climate—cool, wet winters and hot, dry summers. Aboveground, oak leaves usually emerge in late March and senesce in October, while annual grasses begin to grow in November after first fall rains and senesce in early May. However, there is little information about belowground root growth. Three studies have quantified the biomass and spatial distribution of oak roots (Callaway and others 1991, Millikin and Bledsoe 1999, Millikin and others 1997), but information about oak fine root production and temporal distribution in California oak woodlands is lacking.

The importance of ectomycorrhizas (ECM) to ecosystem processes has been well documented. However there is little information about the timing of ECM occurrence and the longevity of ECM roots. In a Norway spruce stand in Sweden, there were seasonal effects on ECM formation; the average lifespan of ECM roots was 300-1,000 days, depending on soil characteristics and root branch order (Majdi

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and others 2001). In addition, about 45 percent ECM roots were dead after 200 days (Majdi and Nylund 1996).

In this study, using root ingrowth cores, we measured oak fine root production and ECM colonization at three sites in the Sierra Nevada foothills. The purpose of our study was to examine seasonal effects on oak and grass fine root production and ECM colonization in both short-term and long-term studies. This paper focuses on oak fine root production and ECM colonization; grass root production was reported elsewhere (Cheng and Bledsoe [In press]).

Methods

A short-term and a long-term study were conducted at three sites at the University of California Sierra Foothill Research and Extension Center (near Browns Valley, California) in 1998. For the 4-year period 1996-2000, mean annual temperature was 18°C (summer 24°C, winter 11°C) and mean annual precipitation was 90 cm. In 1998 the temperature was 16°C, while precipitation was 124 cm. In general, precipitation begins in October or November and ends in May. Soils are classified as fine, mixed, thermic Typic Haploxeralfs (Dahlgren and Singer 1991). The dominant trees include winter-deciduous blue oaks (*Quercus douglasii*) and foothill pines (*Pinus sabiniana*). Common annual grasses include *Bromus* spp. and *Avena barbata*. Additional characteristics are found in Cheng and Bledsoe [In press].

The three sites (River, Upland and Hilltop) we selected for this experiment were very similar in vegetation and soil but differed slightly in elevation. At each site, we randomly selected three open-grown blue oak trees. Around each tree, we installed ingrowth cores under the oak canopy and in the open area. Ingrowth cores (40 cm long and 7.5 cm diameter) were made of 3 mm nylon mesh and filled with sieved (2 mm) root-free soil from each site by horizon (A: 0-5 cm; B: 5-40 cm). Before filling cores, soils were lightly moistened with water so that soils remained within the ingrowth cores.

In the short-term study, 18 ingrowth cores (3 sites $\times$ 3 trees $\times$ 2 replicates) were installed every 3 months beginning in January 1998 and harvested 3 months later. The short-term study lasted one year, thus there were four seasonal sampling periods: winter, spring, summer and fall. In the long-term study, we installed 54 cores in January 1998 and harvested 18 cores after 6, 9, 12 months, respectively. In both studies, oak fine root production and ECM colonization were evaluated.

At harvest, each ingrowth core was removed from the soil and divided into four segments (0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm). In each segment, roots were separated from soil using a root elutriator (Gillison's Variety Fabrication, Inc., Benzonia, MI).³ Roots were stored in water at 4°C and sorted within one month. Dead oak roots, defined as desiccated, dark brown, shrunken and highly fragile, were separated from live oak fine roots. After sorting, ECM oak root colonization was examined under a dissecting microscope using the grid-line intersect method (Brundrett and others 1996). Colonization was calculated as ECM tips per meter of total root length. Root samples were dried at 70°C and weighed. Fine root production was estimated by measuring new fine root growth into ingrowth cores.

³ Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Results

There were no significant differences in oak fine root production between cores located under the canopy and in the open area, so data were combined. At all three sites, seasonal effects were significant (*fig. 1*). Oak fine root production was lower in fall and winter than in spring. Surprisingly, there was significant oak fine root growth in summer, even though soils were very dry during that time.

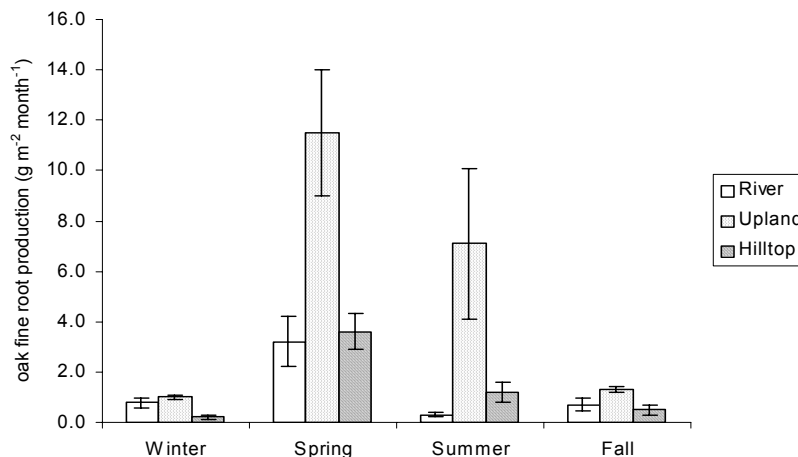


Figure 1—Seasonal effects on oak fine root production at three blue oak woodland sites. Values are means of four to six cores for each season: winter (Jan–Mar 1998), spring (Apr–Jun 1998), summer (Jul–Sep 1998), and fall (Oct–Dec 1998). For each core, data from all four soil depths were combined. Bars are standard errors of means. Data were modified from Cheng and Bledsoe [In press].

Site effects on oak fine root production were also significant. Overall oak fine root production was greater at the Upland site than at the River and Hilltop sites (*fig. 1*). Annual oak fine root production, which was estimated by adding total root production from each season, was highest at the Upland site ($63 \text{ g m}^{-2} \text{ y}^{-1}$), and less at the River ($15 \text{ g m}^{-2} \text{ y}^{-1}$) and Hilltop ($16 \text{ g m}^{-2} \text{ y}^{-1}$) sites.

Oak fine root production did not differ significantly with soil depth, but did differ with site and season (*fig. 2*). At the River site, root production was greater in spring than in other seasons at all soil depths (0–40 cm). At the Upland and Hilltop sites, root production was significantly greater in spring than in other seasons in the upper soil (0–20 cm), but was similar in spring and summer in the lower soil depths (20–40 cm).

In both short-term and long-term studies, we examined oak fine roots and determined ECM colonization. No ECM oak roots were found at the Hilltop sites in two studies (*table 1*). In the short-term study, ECM oak roots were found only in spring and fall. The colonization rates were similar between the River and Upland sites. In the long-term study, ECM roots were found at all time intervals. The

colonization rate was higher in 6-month interval (75 and 53 tips/meter, respectively) than in 9-month (21 and 9 tips/meter) and 12-month intervals (42 and 24 tips/meter).

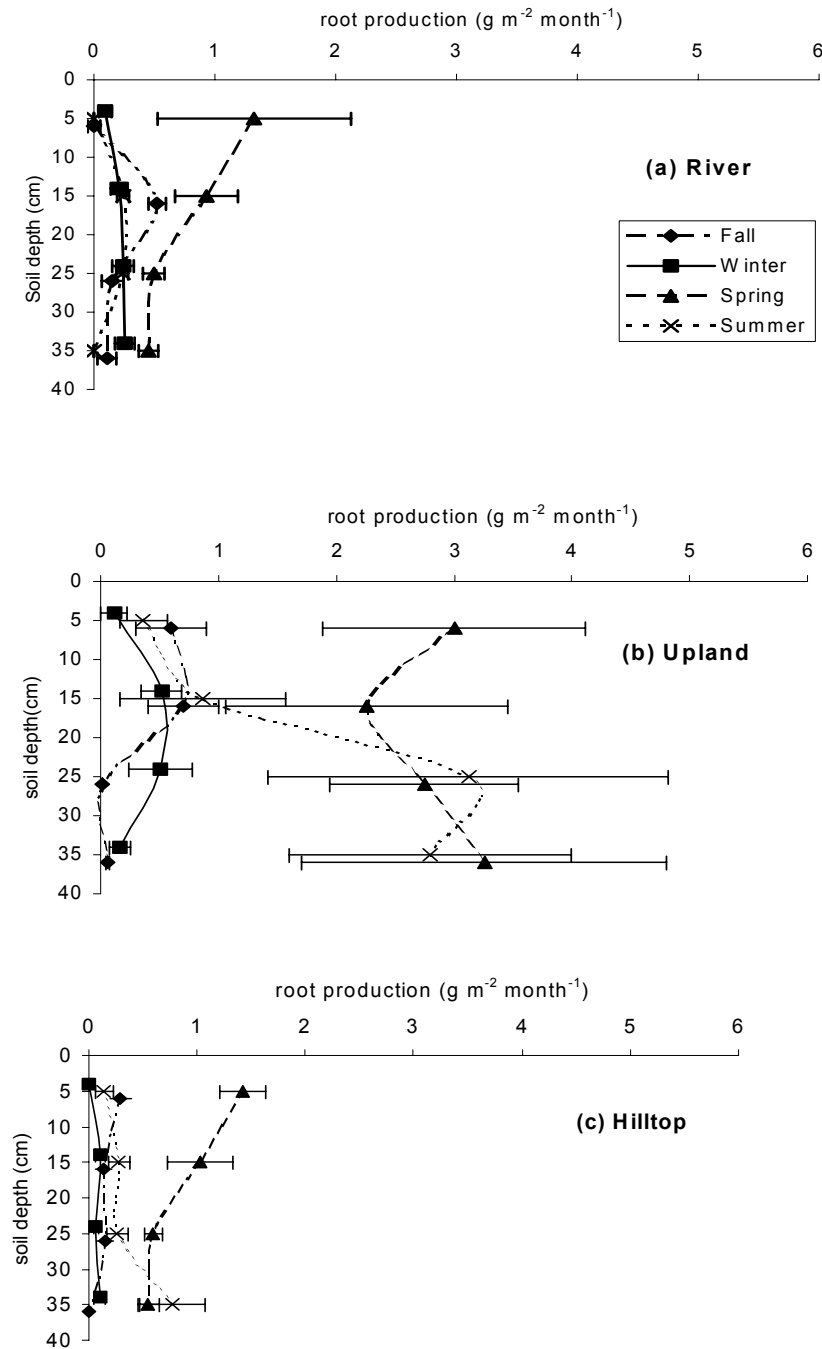


Figure 2—Effects of soil depth on oak fine root production at three blue oak woodland sites: a) River, b) Upland, c) Hilltop. For each season and soil depth, values are means of four to six cores. Bars are standard errors of means. Data from the Upland sites were modified from Cheng and Bledsoe [In press].

Table 1—Ectomycorrhizal colonization (short-term and long-term studies) at three blue oak woodland sites. In the short-term study, cores were harvested 4 times: winter (Jan 199–Mar 1998); spring (Apr 1999–Jun 1998); summer (Jul 1999–Sep 1998); fall (Oct 1998–Dec 1998). In the long-term study, cores were harvested after 6 months (Jan–Jun 1998); 9 months (Jan–Sep 1998) and 12 months (Jan–Dec 1998).

Study	Interval	Sites			Mean
		River	Upland	Hilltop	
		ectomycorrhizal tips/m root length			
Short-term	Winter	0	0	0	0
	Spring	26	15	0	14
	Summer	0	0	0	0
	Fall	32	19	0	17
Long-term	6 months	75	53	0	43
	9 months	21	9	0	10
	12 months	42	24	0	22

Discussion

Oak fine root production occurred year around (*fig. 1*), but more than half of the production occurred in spring (58 percent of total). About 28 percent of the production occurred in summer and only 15 percent occurred in fall and winter. We suggest three possible reasons to explain these seasonal patterns. First, soil temperature and moisture are critical factors affecting root growth. Spring is a favorable season for root growth in term of soil temperature and moisture, so it is not surprising that oak fine root production was greater in spring than in other seasons. In summer when soils are very dry, oaks exhibit hydraulic lift and can use subsoil water to extend the growing season of oak fine roots (Huang 1997, Ishikawa and Bledsoe 2000). In our study, we found significant oak fine root production in summer. Similarly, López and others (1998, 2001) also reported that new fine root production of holm oak occurred in summer in Spain. Second, oak fine root production was affected by grass root growth due to competition for soil resources, such as water (Gordon and others 1989) and nitrogen (Welker and others 1991). Increased grass root production may decrease oak fine root production. In fall, after the first rains, grass seeds germinated and grew rapidly. In spring, annual grass flowered and set seed, but grass roots grew very little. In summer, when soils were very dry, annual grasses were dead. Cheng and Bledsoe [In press] reported that grass root production was the greatest in fall and winter; in contrast, oak fine root production was the greatest in spring and summer. Third, timing of root production may be affected by aboveground events (Burke and Raynal 1994, Fahey and Hughes 1994, Hendrick and Pregitzer 1996). In summer, high demand for water and nutrients by the expanding oak canopy stimulated oak fine root growth; while during winter dormancy, oak fine root production was low.

Unlike grass roots, oak fine root production did not show significant differences with soil depth (Cheng and Bledsoe [In press]). In summer, oak fine root production was greater in lower soil depth at both Upland and Hilltop sites, which suggest that oak trees use subsoil water to extend root growth in the dry summer period. Oak fine

root production was higher at the Upland site than at the River and Hilltop sites. In contrast, grass root production was higher at the River and Hilltop site than at the Upland site (Cheng and Bledsoe [In press]). There may be both spatial and temporal factors, which differentially affect oak and grass roots production, allowing oak and grass roots to dominate in different seasons and at different sites. Why was oak fine root production so different at the three sites?

Although there were some differences in soil chemical characteristics among three sites (*table 2*), these soil chemical differences were small and not sufficient to explain why oak and grass root growth patterns were so different among the sites. At the Hilltop site, oak trees were large and widely distributed (*table 2*), and grass fine root production was high (Cheng and Bledsoe [In press]), reducing oak fine root production by competition for water and nutrients. This may explain why oak fine root production was low at this site. We also hypothesize that smaller oak trees are more active and produce more fine roots. Millikin and others (1997) demonstrated there was linear relationship between the log of DBH and the log of oak large woody root biomass. However there was no information about the relationship between oak DBH and root fine root biomass. At the Upland site, where oak fine root production was highest, some oak trees have double-trunks. Perhaps growth of these trees was vigorous and caused the high production of oak fine roots. Future work is needed to explore why oak root production can vary among sites in the same ecosystem.

Table 2—Differences in soil (B horizon, 5-40cm) chemical and site characteristics among three blue oak woodland sites. For each soil chemical characteristic, values with same letter were not significantly different ($p > 0.05$). Data were modified from Cheng and Bledsoe [In press].¹

Characteristics	River	Upland	Hilltop
Soil CEC (umol g ⁻¹)	308.0ab	346.0a	281.0b
X ^a -K (umol g ⁻¹)	8.8a	3.3c	6.0b
X ^a -Mg (umol g ⁻¹)	14.8c	72.8a	31.3b
Avail-P (ug g ⁻¹)	34.2a	8.4b	15.7b
Site Elevation (m)	137.0	183.0	404.0
Stems (per ha)	216.0	205.3	108.9
Average DBH (m)	0.3	0.3	0.5
Canopy area (m ² m ⁻²)	0.6	0.4	0.3

¹ X^a = exchangeable.

In the short-term study, ECM infection occurred in different seasons (*table 1*). In winter and summer, the colonization rate was zero, suggesting that environmental factors played important roles in ECM formation. Soil may have been too dry in summer, too cold and moist in winter for ECM fungi activity. In the long-term study, ECM colonization was highest in the 6-month interval (winter + spring), then decreased after the 9-month interval (winter + spring + summer), and then increased after the 12-month interval (harvested in fall). Both short-term and long-term data showed similar seasonal ECM colonization patterns (*table 1*). Spring and fall were better seasons for ECM formation than winter and summer. ECM colonization was significantly higher in the 6-month interval of long-term study than in the spring season of short-term study, which suggested that less disturbance (long-term study) increased both oak fine root production and ECM colonization rate. Compared with

data from the 6-month interval, the colonization rate in the 9-month interval was 70–80 percent less, probably due to decomposition of roots. Thus, in this California oak woodland, the estimated ECM root lifespan was less than 6 months. Longevity of mycorrhizal roots depends on several environmental factors, such as soil temperature, moisture, nutrient availability, as well as root branching order (Majdi and others 2001). In our study, dry and hot summers adversely affected ECM root longevity, which was much lower than that reported by other researchers (Majdi and others 2001, Majdi and Nylund 1996). The survival and vitality of ECM roots over the summer may enhance water and nutrient efficiency of blue oaks. After one year, ECM colonization rate increased due to formation of new ECM roots in the fall. Surprisingly, no ECM roots were found at the Hilltop site, where grass root production was the highest among three sites (Cheng and Bledsoe [In press]). We assume that soil resources were depleted by grass roots, reducing ECM to zero.

El Niño effects were apparent in 1998, a relatively wet year. Total precipitation in 1998 was 124 cm, which was 40 percent higher than the average level in the adjacent 5 years. In spring the precipitation was 23 cm, much greater than that in 1997 (5 cm) or 1999 (5 cm). Thus, soil moisture may have been higher in 1998 than in other years, perhaps explaining the significant oak fine root growth in the summer of 1998. Long-term observations are needed to study root dynamics in oak woodlands.

Summary

This study reported that oak fine root production was higher in spring with lower, but significant summer growth. ECM colonization occurred mostly in spring and fall. In the long-term study, less disturbance associated with installing ingrowth cores in the long-term study significantly increased ECM colonization. Oak fine root production and ECM colonization were different among three sites, perhaps due to the interacting effects of grass root production and site characteristics. Future work is needed to study root dynamics in different sites and to study competition between blue oak and annual grass roots.

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