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Drought effects on fine-root and ectomycorrhizal-root biomass in managed *Pinus oaxacana* Mirov stands in Oaxaca, Mexico

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Abstract The effects of a severe drought on fine-root and ectomycorrhizal biomass were investigated in a forest ecosystem dominated by *Pinus oaxacana* located in Oaxaca, Mexico. Root cores were collected during both the wet and dry seasons of 1998 and 1999 from three sites subjected to different forest management treatments in 1990 and assessed for total fine-root biomass and ectomycorrhizal-root biomass. Additionally, a bioassay experiment with *P. oaxacana* seedlings was conducted to assess the ectomycorrhizal inoculum potential of the soil for each of the three stands. Results indicated that biomasses of both fine roots and ectomycorrhizal roots were reduced by almost 60% in the drought year compared to the nondrought year. There were no significant differences in ectomycorrhizal and fine-root biomass between the wet and dry seasons. Further, the proportion of total root biomass consisting of ectomycorrhizal roots did not vary between years or seasons. These results suggest that both total fine-root biomass and ectomycorrhizal-root biomass are strongly affected by severe drought in these high-elevation tropical pine forests, and that these responses outweigh seasonal effects. Forest management practices in these tropical pine forests should consider the effects of drought on the capacity of *P. oaxacana* to maintain sufficient levels of ectomycorrhizae especially when there is a potential for synergistic interactions between multiple disturbances that may lead to more severe stress in the host plant and subsequent reductions in ectomycorrhizal colonization.

Keywords Ectomycorrhizae · *Pinus oaxacana* · Prescribed burning · Harvesting · Drought

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Introduction

Mycorrhizal fungi function as an interface between plants and the soil (Bethlenfalvay 1992), and most tree seedlings without these associations grow poorly because of a reduced capacity to acquire the soil resources needed for growth (Perry et al. 1987). Research has shown that many factors can reduce the presence of mycorrhizal fungi needed to form these symbiotic associations (Vogt et al. 1993), including timber harvesting (Jones et al. 2002), fire (Dahlberg 2002; Smith et al. 2004), and drought (Swaty et al. 1998). Further, ecosystems dominated by plants obligately dependent on ectomycorrhizal associations tend to be high-stress environments—with stresses ranging from drought, fire, low temperatures, and flooding (Harley and Smith 1983). As a genus, *Pinus* is considered to be obligately dependent on ectomycorrhizal fungal associations for their growth and survival (Trappe 1962; Read 1998). Pine forest ecosystems are typically impacted by periodic drought and fire, and the high stress tolerance of *Pinus* species is a critical physiological trait enabling pine trees to maintain competitiveness in stressful environments (Smith and Hinckley 1995).

Although ectomycorrhizal fungal associations have been implicated in maintaining positive water balance in plants in general (e.g., Bowen 1973) and in the genus *Pinus* in particular (Parke et al. 1983), few studies have explicitly and simultaneously considered the effects of moisture stress on the dynamics of fine-root biomass production and ectomycorrhizal-root biomass and colonization rates. Most studies that have examined interactions between mycorrhizae and moisture availability have focused on assessing the positive and negative changes in the percent of ectomycorrhizal colonization of root tips. For example,

Meier et al. (1990) and Davies et al. (1996) reported increases in the proportion of root tips colonized by mycorrhizal fungi in response to moisture stress, while Becker et al. (1987) and Lansac and Martin (1995) reported decreases in colonization rates. Variable patterns of mycorrhizal colonization have been suggested to result from changes in plant–fungal associations in response to inherent differences in site conditions related to soil type and moisture availability (Swaty et al. 1998, 2004). However, we are aware of no studies that have quantified changes in total fine-root and ectomycorrhizal-root biomasses in response to moisture stress caused by severe drought.

Both harvesting and prescribed burning are important forest management practices integral to the management of pine forests (Smith et al. 1996). Although a relatively extensive body of literature exists on the effects of these management activities on ectomycorrhizal-root colonization rates and soil inoculum potentials (see Jones et al. 2002 for a review), the study results have been highly variable, with some reporting negative and others reporting stimulatory effects on mycorrhizal-root colonization. Further, few studies have quantified changes in ectomycorrhizal-root biomass in forest ecosystems under field conditions (Vogt et al. 1982a,b; Dahlberg et al. 1997; Stendell et al. 1999).

Pine forests dominated by *Pinus oaxacana* Mirov are an important component of the Sierra Norte mountains of Oaxaca, Mexico, encompassing a total area of approximately 12,000 ha (Perry 1991). These forests occur primarily on communal lands that are managed by local people for timber production. Clear-cutting was the traditional silvicultural practice for these forests, although prescribed fire is being increasingly used following harvesting operations to facilitate pine regeneration by exposing the mineral soil and reducing understory competition (Keeley and Zedler 1998). Previous studies in these forests have focused on assessing the effectiveness of different silvicultural treatments (Becerra et al. 1993); however, little is known about the response of mycorrhizal fungal associations to these anthropogenic disturbances or to the periodic droughts that commonly occur during the growing season in this region.

Understanding how disturbances caused by both anthropogenic activities and naturally occurring extreme climatic events influence mycorrhizal dynamics and soil inoculum potential in these tropical pine ecosystems is needed for developing sustainable management practices for timber production that ensure the maintenance of symbiotic associations required for healthy ecosystem functioning. This study examined changes in nonmycorrhizal fine-root biomass and ectomycorrhizal-root biomass in *P. oaxacana* forests during a drought and nondrought year. Responses were assessed within three forest stands having different forest management histories (tree harvesting, tree harvesting and burning, and a control with no treatment). We hypothesized that the drought would reduce ectomycorrhizal-root biomass. Although lack of repetition of silvicultural treatments precluded inferring general patterns about treatment effects on mycorrhizal-root colonization, we expected that stands with cumulative disturbances (i.e., drought, harvesting, and burning) would have greater reductions in ectomycorrhizal-root biomass compared to the control stand that was only exposed to drought.

Materials and methods

Description of the study site

The study site is a secondary pine–oak forest located in the Sierra Norte region of Oaxaca, Mexico, on lands communally owned by Ixtlán de Juárez. The study plots were located between 17°18′16″ latitude and 17°34′00″N, and 96°31′38″ and 96°20′00″W longitude. Elevation ranged between 2,190 and 2,400 m above sea level (masl), and slopes averaged 40% (Gómez-Cárdenas et al. 1994). Parent material consists of igneous, sedimentary, and metamorphic rocks, and the predominant soils in the region are Vertisols, Regosols, and Litosols (INEGI 1984). Both subhumid temperate and humid temperate climatic zones are represented in the region (García 1981). Mean annual average temperature ranges 12–17°C, and mean annual precipitation ranges 1,000–1,300 mm, mostly falling in the wet summer season. However, during the El Niño Southern Oscillation event of 1997–1998, a severe drought occurred throughout southern Mexico (Román-Cuesta et al. 2004).

Three forest stands, each approximately 100 ha in size and originally supporting 76–85 pine trees per hectare and 14–19 oak trees per hectare, were used in this study. Each stand had been subjected to different silvicultural treatments in 1990: (1) seed tree (ST) harvesting, in which 17–27 trees per hectare were left on the site following harvesting to provide a seed source for regeneration; (2) ST harvesting (also reducing stand density to 17–27 trees per hectare) with prescribed burning (STB) applied following the harvesting treatment; and (3) a control site (C) that did not receive any treatment. Prior to the treatments, the ST and STB stands supported 76 pine trees per hectare and 19 oak trees per hectare; the control stand had 85 pine trees per hectare and 14 oak trees per hectare. These forests regenerated on agricultural lands after abandonment by local farmers approximately 50 years earlier. The three stands had comparable land-use histories and biophysical conditions, as indicated by local written and oral accounts and

Table 1 Biomasses of total roots, fine roots, and ectomycorrhizal roots (g m^{-2}) and proportion of total root biomass composed of ectomycorrhizal-root biomass for a drought year (YR1, 1998) and a nondrought year (YR2, 1999)

Year	Total root biomass	Fine-root biomass	Ectomycorrhizal biomass root	Proportion (EM/total)
YR1	26.1 (2.8)[a]	18.1 (2.4)[a]	8.9 (0.7)[a]	53.4 (4.5) NS
YR2	59.4 (3.2)[b]	38.4 (2.7)[b]	21.1 (0.8)[b]	58.0 (5.3) NS

Data reported as least square mean values, X (±SE)
NS Nonsignificant
[a]Indicates statistical differences between years ($p<0.01$)
[b]Indicates statistical differences between years ($p<0.01$)

Table 2 Biomasses of total roots, fine roots, and ectomycorrhizal roots (g m^{-2}) and proportion of total root biomass comprised of ectomycorrhizal-root biomass for two seasons (dry and wet) occurring during a drought year (YR1, 1998) and a normal year (YR2, 1999)

Year	Season	Total root biomass	Fine-root biomass	Ectomycorrhizal-root biomass	Proportion (EM/total)
YR1	Dry 1	25.0 (4.4)[a]	17.1 (3.8)[a]	8.4 (1.1)[a]	47.4 (5.9) NS
YR1	Wet 1	26.7 (5.1)[a]	18.8 (4.4)[a]	9.1 (1.2)[a]	60.8 (6.6) NS
YR2	Dry 2	60.0 (5.4)[b]	37.9 (4.6)[b]	20.8 (1.2)[b]	57.9 (7.6) NS
YR2	Wet 2	58.9 (5.2)[b]	38.9 (4.5)[b]	21.4 (1.3)[b]	58.1 (7.1) NS

Data reported as least square mean values, *X* (±SE)

NS Nonsignificant

[a]Indicates statistical differences between years ($p<0.01$)

[b]Indicates statistical differences between years ($p<0.01$)

previous research (Valdés et al. 2003). At the time of this study, the overstory tree canopy in the forest stands consisted of approximately 80% *P. oaxacana* Mirov, with associated species including *Pinus lawsonii* Roezl, *Pinus leiophylla* Schl. et Cham, *Pinus teocote* Schl. et Cham, *Quercus castanea* Née, *Quercus crassifolia* Humb. et Bonpl, *Quercus obtusata* Humb. et Bonpl, *Quercus peduncularis* Née, *Quercus rugosa* Née, and *Quercus scytophylla* Liebm. The *Quercus* species comprised 14–19% of the total number of tree stems present in these plots.

Fine-root and ectomycorrhizal-root biomass

A 30×30-m plot was established in each stand for sampling purposes. Root cores were collected from each plot with polyvinyl chloride (PVC) cylinders (5 cm inside diameter) to a depth of 20 cm following Vogt et al. (1982a,b) for nine sampling times over a 2-year period between October 1997 and November 1999 (10/97, 3/98, 8/98, 9/98, 11/98, 1/99, 3/99, 9/99, and 11/99). For each sampling period, five soil cores were collected at random locations from each plot. Cores were stored at 4°C until processed.

In the laboratory, fine roots (<2 mm diameter) of pine trees only were removed from the cores by rinsing with water to remove soil particles using a 2-mm mesh sieve, and the subsamples were further processed under a stereoscope using forceps. Only the organic A horizon (including the upper humus layer) of the soil cores were processed (approximately 10–15 cm in depth), since visual examination indicated that very few fine roots were present in the mineral soil horizon. Fine roots belonging to nonpine species (primarily oak and understory plant species) were removed from the sample based on their distinctive morphologies and coloration. Only live pine roots were considered (recognized by their turgidity and light-colored cortex and stele), and were separated into two categories: fine nonmycorrhizal root tips and ectomycorrhizal root tips (distinguished by the presence of an ectomycorrhizal sheath of fungal tissue). To verify the accuracy of the visual classification, root tips (>900 per sampling period) were randomly selected from the samples, stained with cotton blue, and examined under a compound microscope to confirm the presence of a Hartig net. Once sorted, each sample was air-dried to a constant weight (oven-drying was not possible because roots were later used for DNA extraction and analysis). A conversion factor for converting air-dried fractions to oven-dried weights was produced by oven-drying subsamples of processed root cores at 70°C.

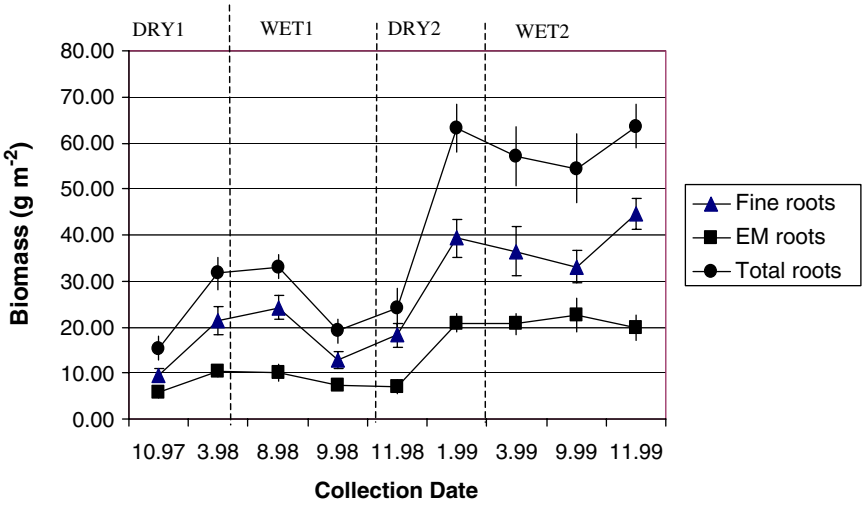

Fig. 1 Biomass of fine roots (*FR*), ectomycorrhizal roots (*EM*), and total roots (*TR*) for each sampling date, divided into seasons (two dry seasons and two wet seasons) in *P. oaxacana* forest ecosystems (mean±SE)

Table 3 Biomasses of total roots, fibrous roots, and ectomycorrhizal roots (g m^{-2}) and proportion of total root biomass comprised of ectomycorrhizal root biomass for three treatments (ST: Seed Tree; STB: Seed Tree with Prescribed Burning; C: Control)

Treatment	Total root biomas	Fibrous root biomass	Ectomycorrhizal root biomass	Proportion (EM:total)
ST	45.5 (3.7)[a]	19.7 (3.4) NS	17.6 (1.5)[a]	62.3 (6.9) NS
STB	34.8 (3.5)[b]	16.8 (3.4) NS	10.9 (1.4)[b]	42.6 (6.6) NS
C	50.1 (3.7)[a]	18.4 (3.3) NS	17.2 (1.5)[a]	54.7 (6.6) NS

Data reported as least square mean values, *X* (±SE)
NS Nonsignificant
[a]Indicates statistical differences between years ($p<0.01$)
[b]Indicates statistical differences between years ($p<0.01$)

Ectomycorrhizal soil inoculum potential

The intact soil core bioassay method (Brundrett et al. 1996) was used to determine ectomycorrhizal inoculum potential of soil in the three stands. Five soil cores per plot were collected with PVC cylinders (5 cm inside diameter) to a depth of 15 cm for 6 sampling periods (9/98, 11/98, 1/99, 3/99, 9/99, 11/99) and utilized as the growth media into which pine seedlings were transplanted. Seedlings were grown for 8 weeks (the minimal time considered necessary for mycorrhizal formation to occur while reducing potential confounding effects from soil core conditions; Brundrett et al. 1996) in a growth chamber maintained at a photoperiod of 14/10 h (light/dark) at 28/25°C and received equal amounts of distilled water. At 8 weeks, each seedling was harvested, and its root system was washed gently to remove soil and organic debris. The entire root system was placed in a petri dish filled with water, examined under a dissecting microscope (×60), and the number of root tips colonized by ectomycorrhizal fungi was determined.

Data analysis

Data collected for the different sampling times were stratified by year and season (dry 1, October 1997–April 1998; wet 1, May 1998–November 1998; dry 2, December 1999–April 1999; and wet 2, May 1999–November 1999) to make statistical comparisons on the data collected during this study. Significant differences between seasons and treatments were tested using analysis of variance (ANOVA)

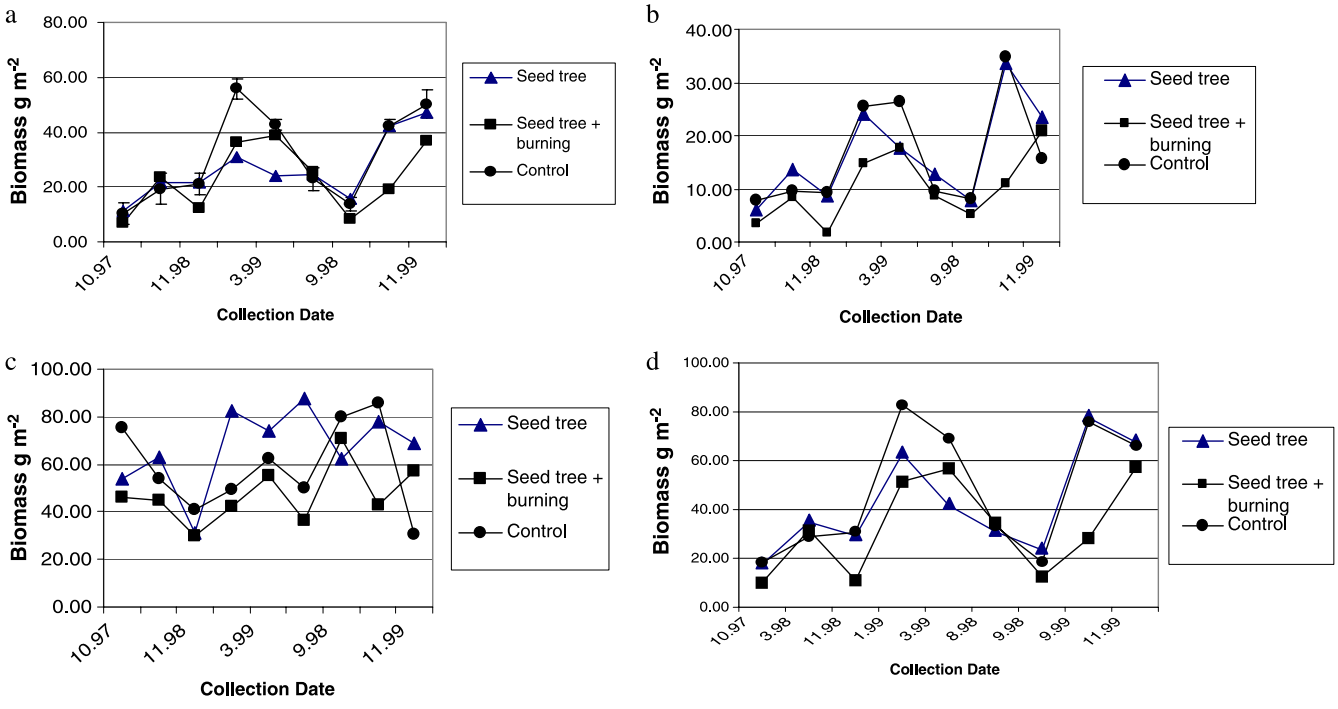

Fig. 2 Biomass of **a** fine roots, **b** ectomycorrhizal roots and **c** proportion of total root biomass comprised of ectomycorrhizal biomass, and (**d**) total roots for each sampling date by treatment (seed tree harvesting, seed tree harvesting with prescribed burning, and control) (mean±SE)

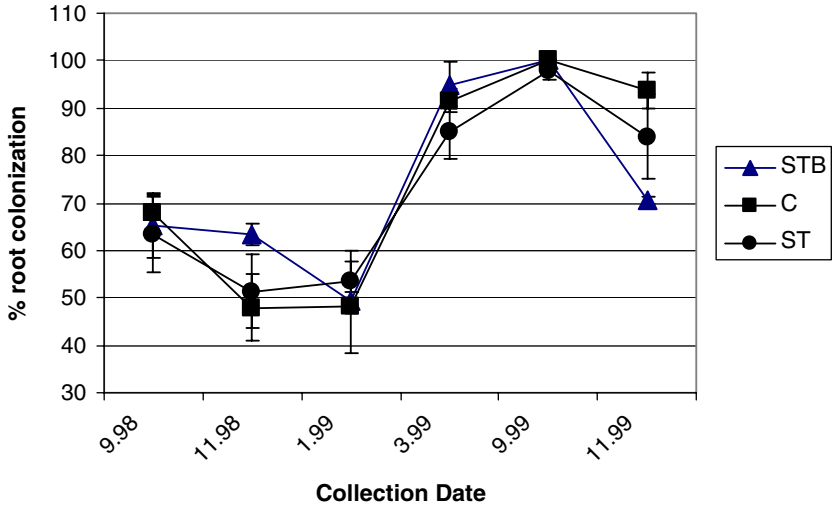

Fig. 3 Ectomycorrhizal inoculum potential of the soil for three treatments [seed tree (*ST*) harvesting, seed tree harvesting with prescribed burning (STB), and control (*C*)], determined by a greenhouse bioassay experiment with *Pinus oaxacana* seedlings, grown in soil cores collected from the three treatment sites during six different sampling periods (mean±SE)

ProcMixed procedures in SAS v.9 for Windows (SAS Institute, Cary, NC) based on a nested subsampling design with two sources of variation: collection time (within year) and sample (within collection time). Tukey post hoc multiple comparisons adjusted for all pairwise comparisons were used to determine mean differences ($P<0.05$). Assessment of drought effects was conducted by combining data across experimental plots to enable incorporation of both spatial and temporal variability. Lack of replication in treatment plots precluded analysis of differences between sites for individual collection times; therefore, only annual and seasonal patterns in response to experimental treatments were considered.

Results

Seasonal and annual comparisons of total fine-root and ectomycorrhizal-root biomass

Total fine-root biomass (nonectomycorrhizal and ectomycorrhizal roots) was significantly lower during the drought year compared to the nondrought year (26.1 and 59.4 g m^2, respectively; $P<0.0001$; Table 1). These data indicate a reduction in total fine-root biomass by 56% during the drought year compared to the nondrought year. Within each year, no significant seasonal differences were recorded for fine-root biomass ($P=0.77$; Table 2).

Similarly, the biomass of ectomycorrhizal roots was also significantly lower during the drought year compared to the nondrought year (8.9 and 21.1 g m^2, respectively), reflecting a 58% reduction ($P<0.0001$; Table 1; Fig. 1). Within a year, ectomycorrhizal-root biomass did not vary significantly when comparing between the wet and dry seasons ($P=0.60$; Table 2).

The proportion of total fine-root biomass composed of ectomycorrhizal roots did not differ significantly between years nor seasons, with yearly means ranging 55–61% ($P=0.65$) and seasonal means ranging 52–65% ($P=0.59$ and 0.36, respectively; Tables 1 and 2).

Variation in fine-root and mycorrhizal-root biomass across treatment stands

Comparing across treatments, total fine-root biomass was significantly lowest in stands with silvicultural treatments (ST, 45.5 g m^{-2}; STB, 24.6 g m^{-2}) compared to the stand without any treatment (50.1 g m^{-2}; Table 3). These patterns were most pronounced during the two wet seasons, while biomass values were more similar to each other during the dry seasons (Fig. 2). The STB treatment also had a lower proportion of root tips colonized by ectomycorrhizal fungi (42.6%) compared to the control and ST treatment (54.7 and 62.3%, respectively; Fig. 2).

Ectomycorrhizal inoculum potential of the soil

For the bioassay study, all assay seedlings growing in soils from the two silvicultural treatments and control plots had a relatively high proportion (47–98%) of the root tips colonized by ectomycorrhizal fungi, with root colonization being generally higher during the wet season compared to the dry season (Fig. 3). No distinctive patterns were observed for ectomycorrhizal inoculum potential of the soils when comparing between the treatment and control plots.

Discussion

The strongest pattern observed in this study was the sharp decrease (by nearly 60%) in the amount of total fine-root and ectomycorrhizal-root biomass maintained by *P. oaxacana* trees during the drought year compared to the nondrought year. These results suggest that biomass production of fine roots and mycorrhizal colonization of root tips may be strongly modulated by extreme drought events in these tropical mountain pine forests in southern Mexico. Other studies have shown that the development of fine roots is often reduced in response to drought (Meier et al. 1990;

Vogt and Bloomfield 1991; Lansac and Martin 1995). These patterns in fine-root production are not unexpected because moisture stress can lead to decreased carbohydrate production when stomatal conductance and net photosynthesis are reduced (Parke et al. 1983; Augé et al. 1987), thereby reducing allocation to belowground structures. This may, in turn, also reduce the amount of photosynthate translocated to roots to support mycorrhizal symbionts. However, the amount of ectomycorrhizal biomass that a plant continues to maintain during a drought is not well documented.

Previous studies that have measured changes in ectomycorrhizal colonization in response to drought have generally documented a decrease in the percent ectomycorrhizal colonization of root tips in response to moisture stress (Runion et al. 1997; Nilsen et al. 1998). For example, Runion et al. (1997) recorded higher percentages of *Pinus palustris* seedling root tips colonized by ectomycorrhizal fungi when growing under adequate water compared to conditions of high water stress. Similarly, Nilsen et al. (1998) reported that mycorrhizal colonization of *Picea abies* root tips decreased significantly during drought. The assumption could be made that changes in percent ectomycorrhizal colonization of root tips should respond in a similar manner to drought as the total amount of ectomycorrhizal biomass maintained by a plant; however, this relationship may not be linear for two main reasons: (1) total amount of fine-root biomass may fluctuate, which would lead to changes in the amount of fine roots available for mycorrhizal colonization and, potentially, total mycorrhizal biomass, and (2) individual plants are capable of physiologically regulating the colonization of their root systems by mycorrhizal symbionts in response to changing resource availability (Harley and Smith 1983). Therefore, the proportion of the root system supporting ectomycorrhizal associations may also fluctuate in response to changes in microclimate caused by drought. Simultaneous measurement of the percent colonization of root tips by mycorrhizal fungi and the proportion of total root biomass composed of ectomycorrhizal biomass may provide a more sensitive measure of plant response to a changing environment because these variables may be associated with different plant physiological responses to drought. In our study, no differences were recorded in the proportion of fine-root biomass supporting ectomycorrhizal fungi in response to drought. This suggests that in mature *P. oaxacana* trees, the predominant belowground response to drought is a reduction in the amount of carbon allocated to fine-root production but not in the proportion of photosynthate allocated by the host pine trees to supporting symbiotic fungi. Similarly, Meier et al. (1990) reported that soil water deficits caused a decrease in root biomass but did not affect the number or percentage of root tips colonized by fungi that form ectomycorrhizal associations on *Pinus taeda* seedlings. In contrast, Lansac and Martin (1995) reported decreases in both root biomass and in the percent of root tips colonized by ectomycorrhizal fungi on several Mediterranean shrubs exposed to drought after being transplanted from the field to greenhouse conditions.

The relationship between fine-root production and ectomycorrhizal colonization may be highly site-specific, varying with differences in efficiency of resource capture among fungal species and with changes in site resource availability over space and time (Harley and Smith 1983; Swaty et al. 1998). For example, Swaty et al. (1998) found that changes in the amount of ectomycorrhizal colonization of root tips varied greatly depending on local site conditions: on dry sites, the degree of colonization varied directly in response to seasonal changes in precipitation and temperature and increased significantly in response to supplemental moisture, while on moist sites, the amount of colonization was not sensitive to seasonal changes or to supplemental watering. This suggests that plant physiological adaptations to particular site conditions may strongly determine how plants regulate the amount of ectomycorrhizal colonization that can occur on root tips in response to fluctuations in microclimate. Thus, it is possible that growing conditions in the *P. oaxacana* forests at the Oaxaca study site were not sufficiently stressful to cause a shift in tree carbon allocation patterns since there were no changes in the proportion of ectomycorrhizal-root biomass maintained as part of the root system. Given the contrasting observations discussed above, more work is needed to better understand belowground plant response to drought by different species and under varying environmental conditions.

In contrast to the annual differences observed in ectomycorrhizal-root biomass, no significant seasonal differences were recorded in ectomycorrhizal-root biomass during either of the 2 study years. These findings are contrary to those reported for temperate ecosystems in the Pacific Northwest USA, where Vogt et al. (1980) found that ectomycorrhizal-root biomass was lowest during the summer months, which was attributed to greater allocation of carbohydrates to rapid shoot growth during the growing season. In temperate forests, the greatest mycorrhizal colonization of root tips generally occurs immediately before or after periods of aboveground growth by the host plant and at the beginning of the rainy season (Vogt and Bloomfield 1991). These time periods coincide with high amounts of photosynthate being present in the phloem that can be translocated to the roots (Vogt and Bloomfield 1991). However, in tropical regions where climatic conditions are more favorable for growth all year round, these seasonal differences may not be as pronounced so that ectomycorrhizal-root biomass may be maintained at more constant levels. Further, in our study, fluctuations in ectomycorrhizal-root biomass in response to annual differences in climatic conditions far outweighed seasonal differences, suggesting that the threshold in microclimate change required to elicit a significant change in plant–mycorrhizal interactions is greater than that normally experienced between seasons in any given year and may only be surpassed during extreme droughts or other major disturbance events.

Treatment effects in this study need to be interpreted with caution because replication of sites was not possible; however, our data from these pine forests in Oaxaca,

Mexico suggest patterns that warrant closer examination. The lower total fine-root and ectomycorrhizal-root biomass recorded for the STB treatment compared to the ST treatment or the control recorded in our study agrees with general findings reported in the literature, indicating that burning has a more severe and long-term inhibitory effect on mycorrhizal colonization compared to most other forest management practices (Jones et al. 2002). In bioassay studies using *Pseudotsuga menziessii* seedlings, clear-cutting with burning was found to reduce ectomycorrhizal colonization of root tips for 16 (Perry et al. 1982) and 20 (Schoenberger and Perry 1982) years following the application of the treatments. Studies assessing the impact of clear-cutting alone on the amount of ectomycorrhizal colonization of root tips have produced more contradictory results, with some studies reporting reductions in ectomycorrhizal colonization rates (Parke et al. 1984; Hagerman et al. 1999) and others indicating increases in these rates (Pilz and Perry 1984) or no significant effect of clear-cutting on mycorrhizal colonization rates (Perry et al. 1982; Torres and Honrubia 1997; Visser et al. 1998). Although these studies did not report changes in the amount of mycorrhizal colonization of root tips, the dominant fungi colonizing root tips changed significantly. Other studies have also shown that management activities may have a stimulatory effect on mycorrhizal colonization rates of fine roots, in particular, sod-cutting (Baar 1996), scalping (Harvey et al. 1996), and partial canopy removal (Zhou et al. 1997).

In contrast to changes in ectomycorrhizal colonization directly on the roots, measures of the ectomycorrhizal inoculum potential of the soil were not as sensitive to the disturbances examined in this study. The inoculum potential of the soils measured during this study did not display distinctly different patterns, with average colonization rate of seedlings root tips ranging between 47 and 98% across all treatments. Similarly, in a related study conducted at the same study site, Valdés et al. (2003) found that the number of fruiting bodies recorded was not affected by the silvicultural treatments, although the composition of genera varied significantly. Given the relatively high overall levels of ectomycorrhizal root colonization documented in this study, it is unlikely that these reductions are sufficient to significantly diminish the capacity of soil to provide fungal inoculum that can colonize root systems of regenerating seedlings. Nevertheless, natural regeneration of *P. oaxacana* seedlings in the STB treatment was about 50% lower than in the site with only ST treatment (Valdés et al. 2003). Thus, reduced seedling regeneration on these sites may have been due to other factors besides soil inoculum potential such as the direct influence of microclimate alteration on seedling survival or growth. Similarly, Parke et al. (1984) concluded that reductions in ectomycorrhizal inoculum potential following clear-cutting and burning were not the main causal factors for regeneration failures. It is notoriously difficult to separate direct effects of the treatments and the indirect effects of microclimate changes (e.g., temperature, light, moisture, etc.) caused by the treatments on the soil biota (Pilz and Perry 1984).

In summary, severe drought was found to significantly reduce both fine-root biomass and ectomycorrhizal-root biomass in these tropical mountain *P. oaxacana* forest stands in Oaxaca, Mexico. However, the proportion of photosynthate allocated by the host pine trees to supporting the fungal symbionts was not affected by the drought. Forest management treatments were found to have less pronounced effects on ectomycorrhizal- and fine-root biomass compared to drought at this site in southern Mexico, although observed patterns suggest that prescribed burns may have long-term effects on mycorrhizal colonization. Conversely, soil inoculum potential did not differ among stands, and these forests appeared to have sufficiently high inoculum potential to effectively colonize seedlings regenerating on the site. Forest management practices should consider the effects of drought on reducing the capacity of *P. oaxacana* to maintain sufficient levels of ectomycorrhizae and thereby enhancing vulnerability of forest stands to stress. For example, allowing adequate time following droughts to enable both total fine-root and ectomycorrhizal-root biomass to reestablish before conducting silvicultural treatments (especially prescribed burns) could help maintain greater forest health and resiliency. Additional research is required to further elucidate the effects of different natural and anthropogenic disturbance relationships on mycorrhizal–root interactions and the processes of recovery and resilience in these forests.

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