New Phytol. (1998), **139**, 733–739

Temporal variation in temperature and rainfall differentially affects ectomycorrhizal colonization at two contrasting sites

BY RANDY L. SWATY*, CATHERINE A. GEHRING, MATT VAN ERT, TAD C. THEIMER, PAUL KEIM AND THOMAS G. WHITHAM

Department of Biological Sciences, Northern Arizona University, Box 5640, Flagstaff, AZ, 86011, USA

(*Received 9 December 1997; accepted 6 May 1998*)

SUMMARY

We examined the roles that seasonal shifts in precipitation and temperature played in the ectomycorrhizal (ECM) colonization of pinyon pine (*Pinus edulis* Engelm.) at two contrasting sites in northern Arizona. Pinyons growing in ash and cinder soils experienced much greater water and nutrient stress than pinyons growing nearby in sandy-loam soils. Over a one year period, we obtained monthly measurements of ECM colonization, root zone soil moisture and temperature, and air temperature and precipitation. Four major patterns emerged. Firstly, although climate as measured by ambient temperature and precipitation did not vary between the two sites, soil temperature was significantly higher and soil moisture significantly lower at the cinder site than at the sandy-loam site. Secondly, ECM colonization was significantly higher at the cinder site for 5 of 12 months. Thirdly, although nearly 70 % of the variation in ECM colonization of pinyons growing in cinder soil was predicted by a combination of soil moisture and soil temperature, these same variables had little predictive power for pinyons growing in sandy-loam soils. Air temperature and precipitation were also significantly correlated with ECM colonization at the cinder site but not the sandy-loam site. Fourthly, a watering experiment showed that ECM colonization significantly increased with supplemental water at the cinder site, but not at the sandy-loam site. Thus, in two sites that did not differ in plant community or climate, ectomycorrhizas in cinder soils were far more sensitive to changes in moisture and temperature than ectomycorrhizas in sandy-loam soils.

Key words: Ectomycorrhizal fungi, ectomycorrhizal colonization, temporal variation, environmental stress, cinder-ash soils.

INTRODUCTION

The extent of root colonization by ECM fungi can be influenced by features of the host plant, such as root physiology and morphology (Wilcox, 1968), by mycorrhizal fungal hyphal structure and phenology (Brundrett, 1991), and by soil conditions and climatic factors (Brundrett, 1991; Bowen, 1994). Soil moisture and soil temperature can have significant effects on ectomycorrhizal colonization (Hacskaylo, Palmer & Vozzo, 1965; Harvey, Jurgensen & Larsen, 1978; Parke, Linderman & Trappe, 1983; Ingleby, Last & Mason, 1985; Samson & Fortin, 1986; Rastin *et al*., 1990; Blasius, Kotte & Oberwinkler, 1989) and this sensitivity of ectomycorrhiza to changes in temperature and soil moisture could lead to significant seasonal variation in colonization. However, few studies have examined seasonal variation in ECM colonization, and the results of these studies have been mixed. Seasonal variation in ECM colonization has been reported in studies of a spruce (*Abies* spp.) stand in Poland (Twarowski, 1963), a Douglas fir and larch stand (*Pseudotsuga menziesii* and *Larix* spp.) in Montana (Harvey *et al*., 1978), two Pacific silver fir (*Abies amabilis*) stands in Oregon (Vogt *et al*., 1980) and a Norway spruce stand (*Picea abies*) in Germany (Blasius *et al*., 1989). No significant seasonal variation in mycorrhizal inoculum levels was reported in a jarrah forest in Australia (Brundrett & Abbott, 1994) or in total ECM fragments in a Douglas-fir stand in western Oregon (Fogel & Hunt, 1979).

Most studies examining temporal variation in ECM colonization have been conducted only during the growing season, or have sampled ECM populations infrequently. In this study we measured ECM colonization of pinyon pines (*Pinus edulis* Engelm.) along with soil moisture, soil temperature, ambient temperature and precipitation for 1 yr at two field sites differing in soil type. The two sites

* To whom correspondence should be addressed.
E-mail: rls6@dana.ucc.nau.edu

Table 1. *A comparison of the cinder and the sandy-loam site*

Parameter	Cinder site	Sandy-loam site
Mean ambient temperature (°C)[a]	20·3	20·8
Mean daily precipitation (mm)[a]	1·56	1·66
Soil moisture (% water)[a]*	3·2	5·6
Soil temperature (°C)[a]*	17·2	13·8
Extractable phosphate (μg g^{-1} soil)[b]*	4·45	12·20
Soil NO_3 mineralization (μg g^{-1} soil d^{-1})[b]*	0·015	0·147
Soil NH_4 mineralization (μg g^{-1} soil d^{-1})[b]*	−0·021	0·062
Cone production (mean no. female cones per tree per site)[c]*	185·00	300·00
Water stress (xylem pressure; MPa)[d]*	−2·830	−2·380
Growth (stem length in mm)[e]*	33·36	46·32

[a] Data from current study; daily ambient temperature and precipitation obtained from National Park Service.
[b] Adapted from Gehring & Whitham (1994).
[c] Mean number of total conelet production per tree in 1988 based on a minimum of nine trees per site (extrapolated from Christensen & Whitham (1991): Fig. 1).
[d] Mean water stress for pinyons growing in one cinder and one sandy-loam site (extrapolated from Mopper *et al.* (1991): Fig. 2).
[e] Mean stem length data over an 11-year period from one cinder site and one sandy-loam site, (Cobb, unpublished).
* Comparisons significant at $P < 0.05$.

were similar in elevation, mean annual precipitation and mean annual temperature, but one site had ash and cinder soils low in nutrients and moisture whereas the other site had sandy loam soils significantly higher in nutrients and moisture (Christensen & Whitham, 1991; Mopper *et al.*, 1991; Gehring & Whitham, 1994, 1995; Cobb *et al.*, 1997) (Table 1). Plant performance parameters such as water stress and shoot growth were lower in pinyons growing in cinder soils than pinyons growing in sandy-loam soils (Table 1). Ectomycorrhizal colonization also varied between these two environments at one period of the year (Gehring & Whitham, 1994, 1995), but responses of ectomycorrhiza to temporal variation in soil moisture and soil temperature were not addressed. By utilizing this system, in which edaphic factors varied significantly but climate was similar, we hoped to understand better the role of soil factors in influencing changes in ECM colonization through time.

We addressed the following questions: (1) does ECM colonization change significantly over time at either the cinder site or the sandy-loam site and are there differences between the sites in the magnitude of this change?; (2) do temporal changes in ECM colonization correlate with soil moisture and/or soil temperature changes and are the responses similar in the two environments?; (3) are soil parameters, measured at the time of collection better predictors of ECM colonization than monthly means of air temperature and rainfall collected at a nearby weather station?; (4) Can we alter ECM colonization by manipulating soil water?

MATERIALS AND METHODS

Study site descriptions

The cinder soil site we studied was located south of Sunset Crater National Monument, Coconino County, AZ, USA (elevation 1859 m). The soils at this site were composed of ash, lava and cinders (Hendricks, 1985). The sandy-loam study site was 22 km away near Walnut Canyon National Monument, Coconino County, AZ, USA (elevation 1950 m) and was made up of sandstone and limestone-derived soils (Hendricks, 1985). Plant communities at both sites were dominated by pinyon pine (*P. edulis*), one-seed juniper (*Juniperus monosperma* Engelm.) and ponderosa pine (*Pinus ponderosa* Lawson). Grasses were rare at the cinder site, and Gambel's (*Quercus gambellii* Nutt.) oak was absent. At the sandy-loam site, grasses were more common and there were a few clones of Gambel's oak. The ECM tree species present at one or both sites were pinyon pine, ponderosa pine, and Gambel's oak.

Ectomycorrhizal colonization

Monthly, from September 1995 to August 1996, root samples were taken from 25 previously unsampled, mature trees (i.e. those that produced female cones) with trunk diameters 15–25 cm at 20 cm aboveground at each study site. Roots were sorted from soil samples obtained with a shovel from inside the canopy, on the west side of each tree at a depth of

Table 2. *Results of two-way* ANOVA *of data from the cinder and the sandy-loam site*

	Site (d.f. = 1)		Time (d.f. = 11)		Interaction (d.f. = 11)	
Parameter	*F*	*P*	*F*	*P*	*F*	*P*
Air temperature	2·730	0·099	204·910	< 0·001	0·290	0·998
Precipitation	0·177	0·674	4·739	< 0·001	0·163	0·998
Soil temperature	208·560	< 0·001	403·876	< 0·001	66·933	< 0·001
Soil moisture	274·500	< 0·001	33·559	< 0·001	60·505	< 0·001
Ectomycorrhizal colonization	74·443	< 0·001	18·614	< 0·001	9·916	< 0·001

10–30 cm. The majority of pinyon fine roots occurred in the top 20 cm of the soil at both sites. An average of 85 short roots were scored from each tree at each time. Gehring (unpublished) has found that scoring 80–100 root tips per tree provided similar estimates of ECM colonization to scoring 3–5 times that number. The techniques of Gehring & Whitham (1991) were used to distinguish ECM from non-ECM and living from non-living roots. Percentage ECM colonization was calculated as the number of active ECM root tips divided by the total number of short roots (Gehring & Whitham, 1994). To determine if there were site differences and/or temporal variation in ECM colonization, we used a two-way ANOVA with time and site as treatment factors. We used a Levene's test to determine if the degree of temporal variation differed between the sites. These and all subsequent statistical analyses were performed using SPSS for Windows®, release 6·0.

Soil and climate parameters

We made monthly measurements of soil moisture and soil temperature to determine whether ECM colonization was predicted by environmental parameters. In the cavity dug to obtain root samples of each sample tree, soil temperature was measured with a VSR soil thermometer that was positioned next to the roots that were sampled for analysis of ECM colonization. Approximately 100 ml of soil was collected from this same cavity near the roots and stored in plastic bags until gravimetric soil analysis was performed. Daily air temperature and precipitation measurements were obtained from the Visitor Centers at Sunset Crater and Walnut Canyon National Monuments (each within 10 km of the study sites). Multiple regression analysis was used to examine the relationships between ECM colonization and environmental parameters.

Watering experiment

In order to test experimentally the hypothesis that additional water affected ECM colonization, five control pinyons were paired for size and location with five treatment pinyons at each site. The control and treatment trees had trunk diameters ranging from 10 to 15 cm at 20 cm from the ground and were given 10 gallons of water every 4 d for three weeks at each site. Because of the drought conditions of the summer of 1996, the watering experiment was conducted in early July, when monsoonal rainfall was significantly less than normal. Three weeks after the watering treatment began, soil moisture, and ECM colonization were measured at each tree as described above. Paired *t*-tests were used to compare ECM colonization and soil moisture between watered and control trees.

RESULTS

Climate data

We found no significant differences in ambient air temperature between the cinder and sandy-loam sites but did find significant changes in ambient temperature over time (Table 2, Fig. 1*a*). There were no significant site × time interactions. The mean daily ambient temperature at the cinder soil site was 20·3 °C, with a minimum temperature of −3·3 °C and a maximum temperature of 36·7 °C. The mean daily ambient temperature at the sandy-loam site was 20·8 °C with a minimum temperature of −17·8 °C and a maximum temperature of 37·2 °C.

We also found no significant differences in precipitation between the sites although rates of precipitation changed significantly over time at both sites (Table 2, Fig. 1*b*). There was no site × time interaction. The total annual precipitation at the cinder site was 59·7 cm whereas the total precipitation for the sandy-loam site was 59·5 cm. For both sites, the periods with the highest levels of precipitation occurred during the winter months and during the late summer and early autumn.

Soil parameters

Although the climates at the two sites were similar, we found significant differences in the temperature of the soil at the two sites. Soil temperature changed significantly over time and there was a significant site × time interaction indicating that the soil temperature differences between the two sites varied with time (Table 2, Fig. 2*a*). Statistical analysis of

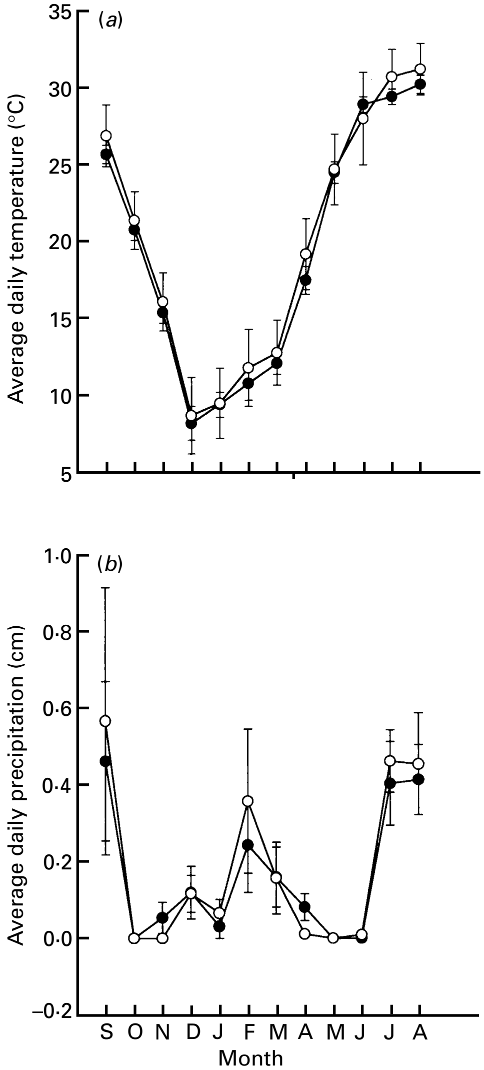

Figure 1. Mean daily ambient temperature (*a*) and precipitation (*b*) data obtained from Sunset Crater National Monument (●, cinder site) and Walnut Canyon National Monument (○, sandy-loam site) from September, 1995 to August, 1996 (mean ± 1 SE).

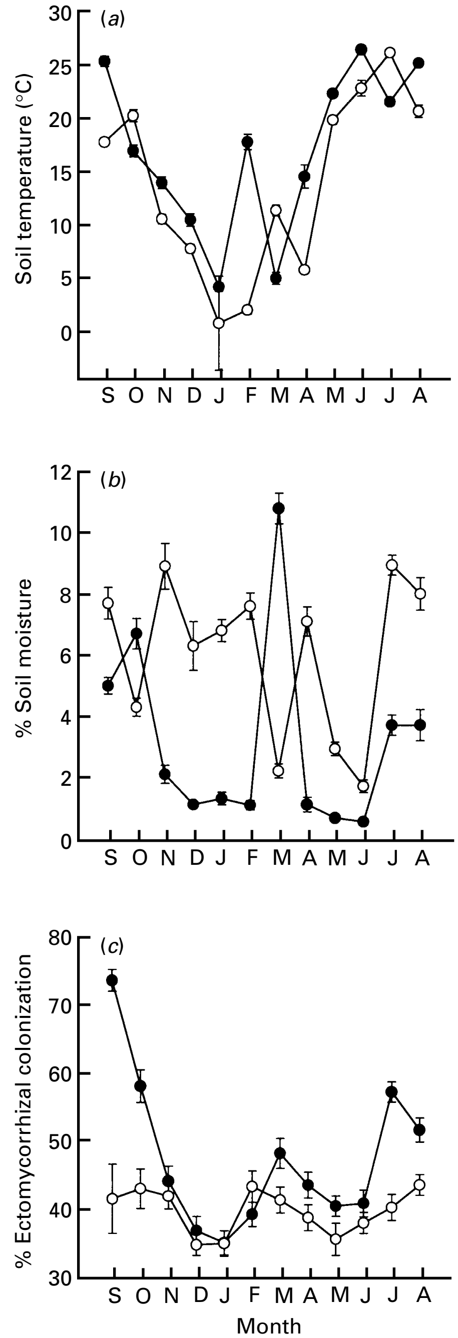

Figure 2. Temporal variation in soil temperature (*a*), % soil moisture (*b*), and % ectomycorrhizal colonization (*c*) for September, 1995 through August, 1996 (mean ± 1 SE). All values were obtained from the root zone at the cinder (●) and the sandy-loam (○) sites.

each month individually indicated that soil temperature differed significantly between the sites during all months of the year, with the cinder site having the higher value in nine of the 12 months (Fig. 2*a*). The mean soil temperatures were 17·2 °C for the cinder soil and 13·8 °C for the sandy-loam soil.

The two sites also differed significantly in soil moisture which changed significantly over time. Again there was a significant site × time interaction, indicating that soil moisture responses with time varied between the sites (Table 2, Fig. 2*b*). Statistical analysis of each month separately showed that soil moisture was significantly lower 10 out of 12 months at the cinder soil sites, with the two exceptions occurring when the sample date immediately followed a period of rain. The annual mean gravimetric soil moisture was 3·3 % for the cinder soil site and 5·6 % for the sandy-loam site.

Temporal variation in ectomycorrhizal colonization

Both soil type and month of sampling had a significant effect on ectomycorrhizal colonization (Table 2, Fig. 2*c*). There was also a significant time × site interaction, indicating that the relationships between the sites changed with time. Separate analyses for each month indicated that ECM colonization was significantly higher at the cinder site than the sandy-loam site during 5 months of the year (Sept., Oct., Mar., July and Aug.). Furthermore, the magnitude of the change in ectomycorrhizal colonization with time was significantly greater (4 times) at the cinder site than at the sandy-loam site ($t = -2{\cdot}350$, d.f. = 11, $P = 0{\cdot}038$). Ectomycorrhizal colonization ranged from 35·3 to 74·1 % (38·8 % difference) at the cinder site and from 35·1 to 44·4 %, (9·3 % difference) at the sandy-loam site.

Relationship between ectomycorrhizal colonization and soil and air parameters

A multiple regression analysis demonstrated that soil moisture and soil temperature combined significantly correlated with ECM colonization at the cinder site ($r^2 = 0{\cdot}675$, $F = 10{\cdot}381$, $P = 0{\cdot}004$). Partial regression results indicated that soil moisture and soil temperature both had significant effect on ECM colonization at the cinder site ($\beta = 0{\cdot}647$, $t = 3{\cdot}450$, $P = 0{\cdot}006$ for soil moisture and $\beta = 0{\cdot}715$, $t = 3{\cdot}812$, $P = 0{\cdot}003$ for soil temperature). This result contrasted with the pattern at the sandy-loam site, where soil moisture and soil temperature did not have a significant effect on ECM colonization ($r^2 = 0{\cdot}008$, $F = 1{\cdot}094$, $P = 0{\cdot}336$).

Similarly, a combination of mean ambient temperature and mean precipitation for the month before sampling was an excellent predictor of ectomycorrhizal colonization at the cinder site ($r^2 = 0{\cdot}941$, $F = 38{\cdot}705$, $P < 0{\cdot}001$). Both precipitation and temperature contributed significantly to the regression ($\beta = 0{\cdot}740$, $t = 6{\cdot}402$, $P < 0{\cdot}001$ for precipitation, $\beta = 0{\cdot}392$, $t = 3{\cdot}391$, $P < 0{\cdot}001$ for temperature). Again, trees at the sandy-loam site showed a different pattern, with no significant relationship between ambient temperature combined with precipitation and ECM colonization ($r^2 = 0{\cdot}097$, $F = 0{\cdot}324$, $P = 0{\cdot}735$). At the cinder site, the combination of ambient temperature and mean monthly precipitation gave higher regression values for ECM colonization than the combination of soil temperature and soil moisture.

Ectomycorrhizal responses to added water

Based on our observation that soil moisture affected ECM colonization (Fig. 1*a*) we predicted that adding water would have a significant effect on ECM colonization at the cinder site, but no impact on ECM colonization at the sandy-loam site. Watering significantly increased soil moisture at both sites (cinder, $t = 5{\cdot}39$, $P = 0{\cdot}003$; sandy-loam, $t = 3{\cdot}30$, $P = 0{\cdot}014$) (Fig. 3*a*). We found significant differences in ECM colonization between the watered and control trees at the cinder site ($t = 3{\cdot}08$, $P = 0{\cdot}02$), where watered trees had 19·2 % higher levels of ECM colonization than controls. However, there were no significant differences in ECM colonization between watered and control trees at the sandy-loam site ($t = 1{\cdot}62$, $P = 0{\cdot}09$) (Fig. 3*b*). Therefore, in both observational and experimental studies, we found that ECM colonization was more responsive to changes in environmental parameters at the cinder soil site than at the sandy-loam site.

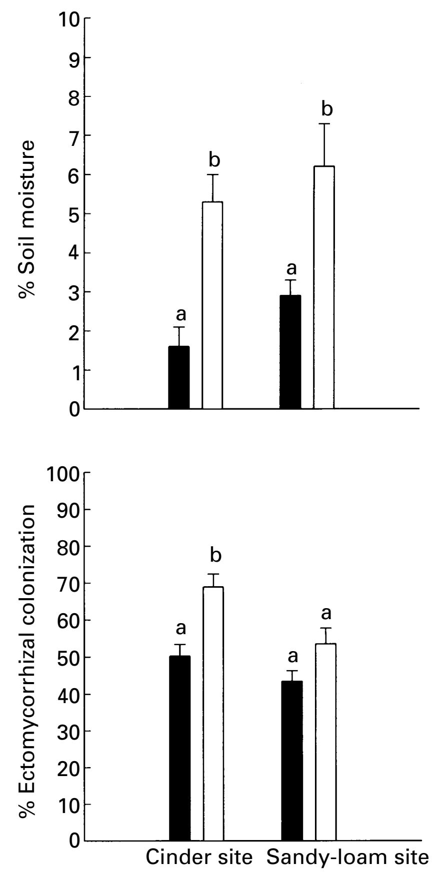

Figure 3. Mean percentage soil moisture (*a*) and mean percentage ectomycorrhizal colonization (*b*) for watered (□) and control (■) groups at the cinder and sandy-loam sites. Different letters above histograms indicate significant differences ($P \leqslant 0{\cdot}05$). Bars represent means ± 1 SE.

DISCUSSION

Variable responsiveness of ectomycorrhizal colonization to soil and climate parameters

Although the cinder and sandy-loam sites studied here experienced the same climate, we observed three major differences in ECM colonization between pinyons growing in the two sites. First, ECM colonization was significantly higher at the cinder site than the sandy-loam site during 5 months of the year. This corroborates previous findings that were limited to spring and fall sampling (Gehring & Whitham, 1994, 1995). Second, the temporal variation in ECM colonization was 4 times greater at the cinder site than at the sandy-loam site. Third, the degree of responsiveness to environmental parameters differed between the two sites, with ECM colonization at the cinder site varying significantly with climate and soil parameters whereas no significant relationship between the same parameters was observed at the sandy-loam site. The difference in responsiveness was also observed following supplemental watering which resulted in changes in ECM colonization at the cinder site but not at the sandy-loam site.

Fluctuations in ECM colonization with seasonal fluctuations in temperature and moisture could be advantageous to plants, particularly those growing in nutrient-poor soils or drought situations. Ectomycorrhiza have been hypothesized to be most important in soils where the need for enhanced nutrient and water uptake is the greatest (Meyer, 1973), and increased numbers of ECM roots during moist times might allow plants to maximize water and nutrient uptake. Furthermore, in arid environments, photosynthetic rates can be suppressed during dry times of the year (Lajtha & Getz, 1993), potentially reducing the ability of plants to support ECM fungal mutualists. Giovaninni *et al.* (unpublished) have shown that the photosynthetic rates of pinyons growing in cinder soils are highly sensitive to moisture with peaks in photosynthetic activity occurring in the spring and following the summer monsoon rains. These data suggest that increased photosynthetic rates could coincide with increased ECM colonization in pinyons at the cinder site.

Perhaps more surprising was the lack of effect of variation in air or soil temperature or moisture on ECM colonization at the sandy-loam site. Several researchers have found significant relationships between air and/or soil climate and ECM colonization (Harvey *et al.*, 1978; Vogt *et al.*, 1980; Blasius *et al.*, 1989; Rastin *et al.*, 1990; Antibus & Linkins, 1992). For example, seasonal variation in Douglas fir and larch ECM root tip counts in western Montana were partly attributed to changes in soil temperature and soil moisture (Harvey *et al.*, 1978). Additionally, temporal variation in number of living ectomycorrhiza of Norway spruce trees in Germany was reported in two studies (Blasius *et al.*, 1989; Rastin *et al.*, 1990). By contrast, in bioassay experiments, no temporal variation or correlation between climate and ECM fungal inoculum levels was found in a jarrah forest of Australia (Brundrett & Abbott, 1994).

Although we expected that soil parameters would have the highest correlation with ECM colonization, the best predictor of ECM colonization at Sunset Crater proved to be a combination of ambient temperature and precipitation. We hypothesize that this apparent contradiction was due to the sampling methods employed. The soil parameters were measured once per month on the day of ECM sampling whereas ambient temperature and precipitation values were monthly means of daily measurements. The soil values might not have been an accurate representation of the range of conditions experienced by the ECM roots between sampling periods. For example, in March, 1996, soil moisture was 10 times greater (11 % compared with 1 %) than the previous month. This abnormally high reading was due to rainfall the day before sampling. However, mean monthly precipitation for February and March varied only twofold, 50 mm in February and 25 mm in March. More frequent soil sampling would probably have improved the relationship between soil parameters and ECM colonization at the cinder site.

Implications

Ectomycorrhizal colonization varied with time at both cinder and sandy-loam sites, but to a markedly different degree at the two sites. Our data were consistent with the hypothesis that ectomycorrhiza at one site responded to environmental changes differently than at the other site. We were surprised to observe such different patterns of response in the same plant species growing in two areas of nearly identical climate. Our findings argue for more studies on the dynamics of ECM associations through time in a variety of environments.

One of the potential reasons for the differences we observed between the sites is that the community of ECM fungal associates of pinyon pines at cinder and sandy-loam sites can differ markedly (Gehring *et al.*, 1997). These community differences might have contributed to the differential responses to climate we observed at the two sites. The data of Gehring *et al.* (1997) combined with our results argue for further research on the functional attributes of different fungal species under a variety of environmental conditions.

ACKNOWLEDGEMENTS

We thank the United States Forest Service for their cooperation, K. Ogle, R. St. Laurent and N. Cobb for statistical and computer advice, and G. Wimp, J. White and two anonymous reviewers for commenting on the manuscript. This research was supported by DOE grant DE-FG03-94ER61849, USDA grant 95-37302-1801 and NSF grant DEB-9408009.

REFERENCES

Antibus RK, Linkins AE III. 1992. Effects of liming a Red Pine forest floor on mycorrhizal numbers and mycorrhizal and soil acid phosphatase activities. *Soil Biology and Biochemistry* **24**: 479–487.

Blasius D, Kottke I, Oberwinkler F. 1989. Spatial and seasonal dynamics of ectomycorrhizae of *Picea abies* (L.) Karst. In the Black Forest. *Agriculture, Ecosystems and Environment* **28**: 27–30.

Bowen GD. 1994. The ecology of ectomycorrhizal formation and functioning. *Plant and Soil* **159**: 61–67.

Brundrett M. 1991. Mycorrhizas in natural ecosystems. *Advances in Ecological Research* **21**: 171–311.

Brundrett MC, Abbott LK. 1994. Mycorrhizal fungus propagules in the jarrah forest. I. Seasonal study of inoculum levels. *New Phytologist* **127**: 539–546.

Christensen KM, Whitham TG. 1991. *Indirect herbivore mediation of avian seed dispersal in pinyon pine*. *Ecology* **72**: 534–542.

Cobb NS, Mopper S, Gehring CA, Caouette M, Christensen KM, Whitham TG. 1997. Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. *Oecologia* **109**: 389–397.

Fogel R, Hunt G. 1979. Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. *Canadian Journal of Forest Research* **9**: 245–256.

Gehring CA, Whitham TG. 1991. Herbivore-driven mycorrhizal mutualism in insect susceptible pinyon pine. *Nature* (London) **353**: 556–557.

Gehring CA, Whitham TG. 1994. Comparisons of ectomycorrhizae across extremes of soil type and herbivory. *American Journal of Botany* **81**: 1509–1516.

Gehring CA, Whitham TG. 1995. Duration of herbivore removal and environmental stress affect the ectomycorrhiza of pinyon pines. *Ecology* **76**: 2118–2123.

Gehring CA, Theimer TC, Whitham TG, Keim P. 1997. Ectomycorrhizal fungal community structure of pinyon pines growing in two environmental extremes. *Ecology*. (In press.)

Hacskaylo E, Palmer JG, Vozzo JA. 1965. Effect of temperature on growth and respiration of ectotrophic mycorrhizal fungi. *Mycologia* **57**: 749–756.

Harvey AE, Jurgensen MF, Larsen MJ. 1978. Seasonal distribution of ectomycorrhizae in a mature Douglas-fir/Larch forest soil in western Montana. *Forest Science* **24**: 203–208.

Hendricks DM. 1985. *Arizona soils*. Tucson, AZ, USA: University of Arizona Press.

Ingleby K, Last FT, Mason PA. 1985. Vertical distribution and temperature relations of *Betula* spp. growing on coal soil. *Forest Ecology and Management* **12**: 279–285.

Lajtha K, Getz J. 1993. Photosynthesis and water-use efficiency in pinyon juniper communities along an elevational gradient in northern New Mexico. *Oecologia* **94**: 95–101.

Meyer FH 1973. Distribution of ectomycorrhizae in native and man-made forests. In Marks JC and Kozlowski TT, eds. *Ectomycorrhizae: their Ecology and Physiology*. New York, NY, USA: Academic Press, 79–106.

Mopper S, Mitton JB, Whitham TG, Cobb NS, Christensen KM. 1991. Genetic differentiation and heterozygosity in pinyon pine associated with resistance to herbivory and environmental stress. *Evolution* **45**: 989–999.

Parke JL, Linderman RG, Trappe JM. 1983. Effect of root zone temperature on ectomycorrhizal and vesicular–arbuscular mycorrhiza formation in disturbed and undisturbed forest soils of southwest Oregon. *Canadian Journal of Forest Research* **13**: 657–665.

Rastin N, Schlechte G, Hüttermann A, Rosenplänter K. 1990. Seasonal fluctuation of some biological and biochemical soil factors and their dependence on certain soil factors on the upper and lower slope of a spruce forest. *Soil Biology and Biochemistry* **22**: 1049–1061.

Samson J, Fortin JA. 1986. Ectomycorrhizal fungi of *Larix laricina* and the interspecific and intraspecific variation in response to temperature. *Canadian Journal of Botany* **64**: 3020–3028.

Twarowski Z. 1963. Investigations on the annual development dynamics of mycorrhizae in 40-year-old spruce stands. *Prace Instytutu Badawczego Lesnictwa* **260**: 72–102.

Vogt KA, Edmonds RL, Grier CC, Piper SR. 1980. Seasonal changes in mycorrhizal and fibrous-textured root biomass in 23- and 180-year-Old Pacific silver fir stands in western Washington. *Canadian Journal of Forest Research* **10**: 523–529.

Wilcox HE. 1968. Morphological studies of the roots of red pine, *Pinus resinosa*. II. Fungal colonization of roots and the development of mycorrhizae. *American Journal of Botany* **55**: 686–700.