Interaction effects of vegetation type and Pacific madrone soil inocula on survival, growth, and mycorrhiza formation of Douglas-fir[1]

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Douglas-fir seedlings were planted in cleared blocks within three adjacent vegetation types, whiteleaf manzanita, annual grass meadow, and an open stand of Oregon white oak, in southwest Oregon. Within subplots in each block, either pasteurized or unpasteurized soil from a nearby Pacific madrone stand was transferred to the planting holes of the seedlings; control seedlings received no madrone soil. Second-year survival averaged 92, 43, and 12% for seedlings planted on the manzanita, meadow, and oak sites, respectively. Growth differences generally paralleled survival differences. Added madrone soil, whether pasteurized or unpasteurized, did not influence survival, but growth of seedlings on the manzanita site was substantially increased by the addition of unpasteurized madrone soil. Unpasteurized madrone soil did not influence growth of seedlings in the meadow and the oak stand. Pasteurized madrone soil did not affect growth in any of the vegetation types. When added to the manzanita site, unpasteurized madrone soil nearly tripled the number of mycorrhizal root tips forming on seedlings and resulted in formation of a new mycorrhiza type not seen otherwise. As with growth, unpasteurized madrone soil had little or no effect in the other vegetation types. These results suggest that manzanita and madrone impose on soils a biological pattern that stimulates Douglas-fir growth and survival, and they add to the growing body of literature showing that root symbionts and rhizosphere organisms mediate interactions among plant species.

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Des semis de Sapin de Douglas ont été plantés dans des surfaces dégagées à l'intérieur de trois types de végétation adjacents, de la Manzanite à feuilles blanches, une prairie à herbes annuelles et un peuplement clairiéré de Chêne blanc d'Orégon, au sud-ouest de l'Orégon. Dans chacune des placettes d'une surface, des sols pasteurisés ou non provenant d'un peuplement de Madrone du Pacifique ont été placés dans les trous de plantation des semis; les semis témoins n'ont reçu aucun sol de madrone. La survie à la fin de la 2^{e} année était en moyenne de 92, 43 et 12% pour les semis plantés dans le type à manzanite, la prairie et la chênaie, respectivement. Les variations de la croissance étaient en général semblables à celles caractérisant la survie. L'ajout du sol de madrone, pasteurisé ou non, n'a pas influencé la survie, mais la croissance des semis dans le type à manzanite a été accrue substantiellement par l'addition de sol de madrone non pasteurisé. Ce dernier sol non pasteurisé n'a eu aucun effet sur la croissance des semis dans la prairie et la chênaie. Le sol de madrone pasteurisé n'a affecté la croissance dans aucun des types de végétation. Lorsqu'on l'ajoutait au type à manzanite, le sol de madrone non pasteurisé a eu pour effet de presque tripler le nombre d'extrémités racinaires mycorhizées formées sur les semis et a eu pour résultat la formation d'un nouveau type de mycorhize encore jamais vu. Tout comme pour la croissance, le sol de madrone non pasteurisé a eu peu ou prou d'effet dans les autres types de végétation. Ces résultats montrent que la manzanite et le madrone imposent aux sols un modèle biologique qui stimule la croissance et la survie du Sapin de Douglas, et ils ajoutent aux connaissances actuelles qui montrent que les symbionts racinaires et les organismes de la rhizosphère produisent des interactions parmi les espèces végétales.

[Traduit par la revue]

Introduction

Numerous researchers have suggested that mycorrhizal fungi, which are mutualists with roughly 90% of plant species, play key mediative and integrative roles in plant communities (Bowen 1980; Janos 1980, 1983; Malloch *et al.* 1980; Pirozynski 1981; St. John and Coleman 1983; Harley and Smith 1983; Brownlee *et al.* 1983; Read *et al.* 1985; Perry *et al.* 1987). Mycorrhizal fungi may allow trees to compete successfully with grasses and herbs for resources (Bowen 1980) and perhaps detoxify allelochemicals produced by those competitors (Perry and Choquette 1987). The results of pot tests suggest that mycorrhizae can decrease competition between plant species (Perry *et al.*)[4] and increase the productivity of species mixtures, especially in soils where available phosphorus is limited (Puga 1985). Mycorrhizal hyphae can connect plants of different species and facilitate the transfer of carbon and nutrients (Bjorkman 1960; Reid and Woods 1969; Heap and Newman 1980; Francis and Read 1984; Finlay and Read 1986*a*, 1986*b*; Chiarello *et al.* 1982; Francis *et al.* 1986). However, the existence and implications of these and other integrative roles of mycorrhizal fungi remain largely unexplored outside the laboratory.

In southwest Oregon and northern California, species in the families Ericaceae, Fagaceae, Pinaceae, Pyrolaceae, Rosaceae, and Betulaceae form ectomycorrhizae and share at least some fungal species (Largent *et al.* 1980; Molina and

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Trappe 1982). Ericaceous manzanitas (*Arctostaphylos* spp.) and Pacific madrone (*Arbutus menziesii* Pursh) are early pioneers after fire, and regenerating conifer seedlings often associate with them. In the hot, droughty environments that are common in this area, conifer seedlings establishing beneath the cover of other vegetation can benefit from the shade. More importantly, however, seedlings may "plug into" the network of compatible mycorrhizal hyphae supported by the surrounding ericoids, thereby gaining the opportunity for early mycorrhiza formation. In some habitats, the timing of mycorrhiza formation is critical to seedling survival (Amaranthus and Perry 1987; Perry *et al.* 1987). On the other hand, conifers in this area regenerate poorly beneath Oregon white oak (*Quercus garryana* Dougl. ex Hook.) (Atzet and Wheeler 1984), apparently benefiting from neither its shade nor its ectomycorrhizae.

The objective of this study was to determine whether growth, survival, and mycorrhiza formation differed (*i*) among Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings planted in cleared areas within three adjacent but different vegetative communities, and (*ii*) between seedlings within each community that were planted with or without small amounts of soil from a nearby madrone stand. We hypothesized that conifers would form the greatest numbers of mycorrhizae, and would grow and survive best on soils previously occupied by manzanita, and that madrone soil, acting as mycorrhizal inoculum, would improve conifer seedling performance in the meadow and the oak stand.

Methods

Site description

The study site is in a small valley at 385 m elevation in the Siskiyou Mountains of southwest Oregon. Annual precipitation averages 65 cm, less than 10% of which falls from mid-May through mid-September. Soils are fine loamy, mixed mesic Ultic Haploxeralfs, 60–100 cm deep, formed in granitic colluvium and underlain by weathered granitic bedrock. Three distinct vegetation types occur within the valley: annual grass meadow (an old homestead), oak savannah, and a conifer–ericoid community. In the last, a fire in 1938 created a mosaic of differing ages and mixtures of Douglas-fir, ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.), whiteleaf manzanita (*Arctostaphylos viscida* Parry), and Pacific madrone.

Our study area was on a southwest-facing, gentle (< 10%) toe slope just above the valley bottom, and it included portions of the meadow, the oak stand, and a dense, virtually pure stand of whiteleaf manzanita. The meadow was stocked primarily with hedgehog dogtail (*Cynosursas echinatus* L.), catchweed bedstraw (*Galium aparine* L.), roughstalk bluegrass (*Poa trivialis* L.), and *Anthricus* sp. Tree height in the open oak stand averaged 10–12 m, and the sparse understory consisted of various grasses and herbs.

Soils in all three vegetation types are classified in the Holland series (Soil Conservation Service 1979). Surface layers (to 18 cm) are dark greyish brown to brown sandy loams. Percentages of sand, silt, and clay were 52, 24, 24 in the manzanita stand, 54, 24, 22 in the meadow, and 40, 31, 29 in the oak stand, respectively.

Field procedure

One-year-old nonmycorrhizal Douglas-fir seedlings were planted in spring 1985, when soil moisture was at field capacity on each site (vegetation type). No more than 3 days before planting, five blocks were prepared within each site. In all blocks manzanita were felled with a chainsaw, oaks were left standing, and low vegetation and surface organic layers were removed with hoes. Three plots were planted 1 m apart within each block, each plot consisting of nine seedlings at 40-cm spacing in a 3 × 3 array. Seedling diameter 1 cm above the soil surface was recorded at the time of planting.

Seedlings within each plot received one of three soil-transfer treatments when planted: UM (unpasteurized madrone soil), PM (pasteurized madrone soil), or NT (no soil transfer). Soil for the UM and PM treatments was collected in the Pacific madrone stand from the feeder-root zones of 12 trees that had no conifers nearby. PM soil was pasteurized with steam at 70°C for 3 h and kept in a sealed container until planting. Treatment consisted of transferring 100–120 mL of madrone soil into the excavated planting holes of the Douglas-fir seedlings within 24 h of soil collection.

Seedling survival was monitored at 4-week intervals throughout the study period. Stem diameter (again at 1 cm height) and leader growth were measured for all surviving seedlings at the end of the first and second growing seasons. In November 1985, after fall rains and soil-moisture recharge, 45 live seedlings on each site were excavated, placed on ice, and transported to the laboratory, where they were stored at 2°C for no more than 14 days before root examination.

To monitor soil water content, soil samples to 35 cm depth were collected from all sites at 2- to 3-week intervals throughout the first growing season. Samples were packed in airtight containers and taken to the laboratory, where they were weighed, oven-dried for 24 h at 105°C, and then reweighed.

The percentage of the day's potential solar radiation received was measured with a Solar Pathfinder® (Amaranthus 1984) at the center of each block and calculated for each month during the monitoring period.

In June 1986, four soil samples to 15 cm depth were collected at random spacing along each of three transects in each of the three vegetation types where seedlings were planted and in the Pacific madrone stand from which transfer soils were collected (12 samples per site). All samples were analyzed for pH (50:50 soil : distilled H_2O), total N and P (Kjeldahl digest with ammonia and orthophosphate read on an autoanalyzer), and extractable K, Ca, and Mg.

Analysis

Soil and extraneous material were gently washed from roots, and roots were subsampled from three cross sections 1.5 cm thick (upper, middle, and lower positions) of the entire root system. All active root tips in each section were tallied and identified as mycorrhizal or nonmycorrhizal, and many cross sections were examined for the presence of a Hartig net to aid in determination of ectomycorrhizal root colonization.

Mycorrhizal tips were separated by type according to characteristics observable through a binocular microscope (2× to 5× magnification). Information gathered for each ectomycorrhiza type included color, surface appearance, branching, morphology, degree of swelling, length, and characteristics of rhizomorphs. Two mycorrhiza types were dominant on the 1st-year outplanted seedlings at each site. Types that occurred less frequently were grouped into a "minor" category. Where short roots were colonized by more than one fungal type, the type nearest the root apex was tallied as the mycorrhiza.

Data were subjected to analysis of variance. Before analysis, root-tip counts (mycorrhizal and nonmycorrhizal) were logarithmically transformed to compensate for log-normally distributed values (Steel and Torrie 1980), percentage survival data were converted to an inverse sine, and stem-diameter measurements were transformed to basal area. Differences in seedling survival, height, basal area, and mycorrhizal colonization were examined with Tukey's multiple range test.

Results

Soil pH did not differ significantly among sites (including the madrone stand from which soil was transferred), nor did nutrients, except for potassium, which was higher in oak

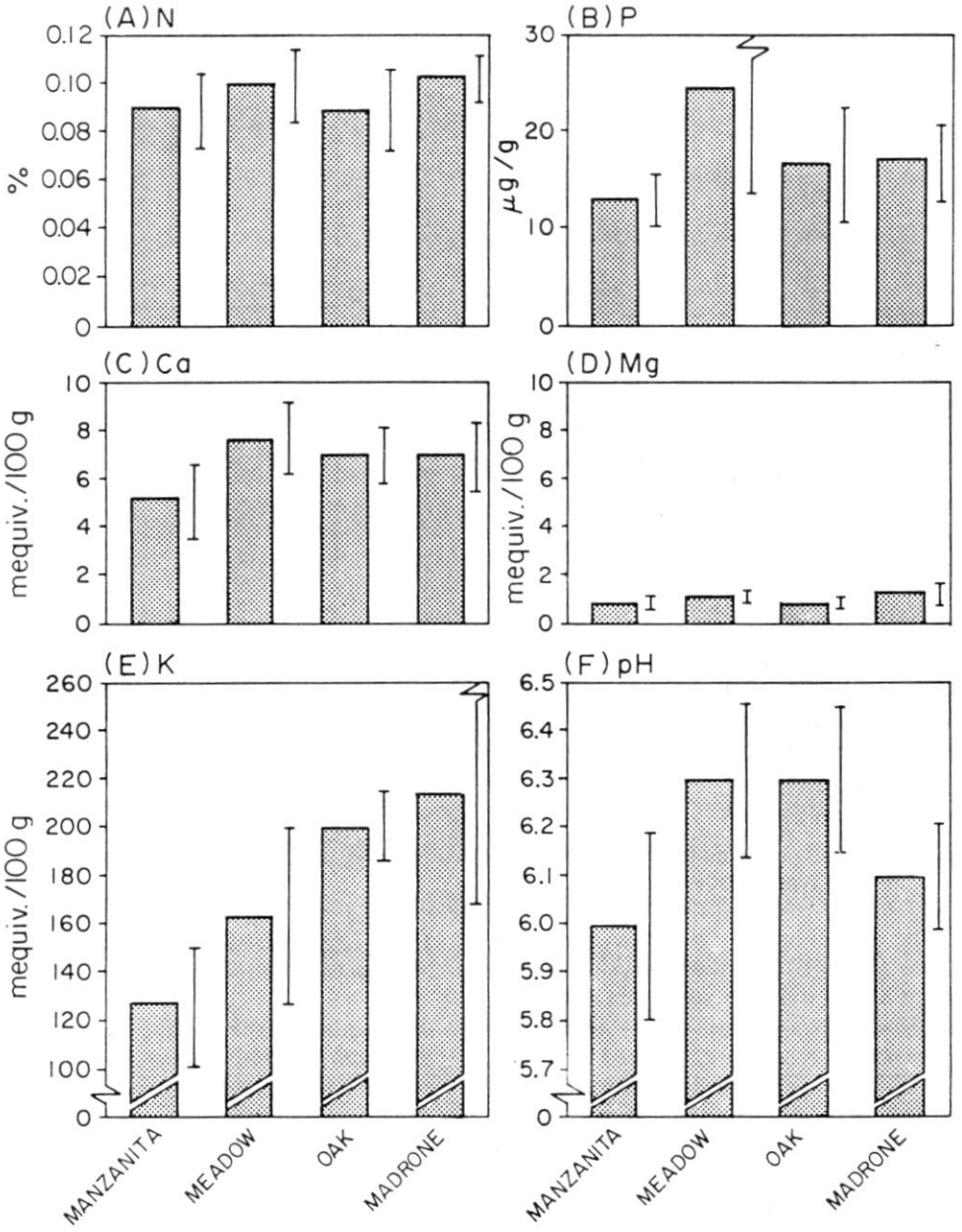

FIG. 1. Soil nutrients (A–E) and pH (F) for the four study sites. Seedlings were planted on the manzanita, meadow, and oak sites; soil was transferred from the madrone site. Vertical lines indicate standard error.

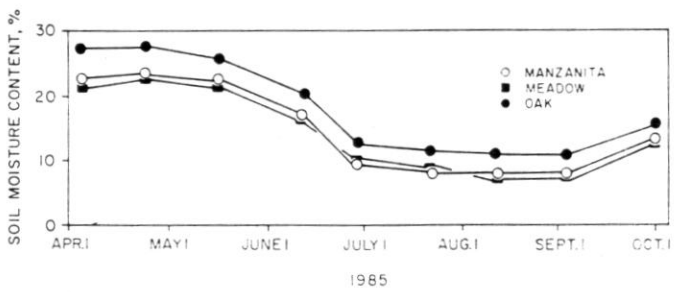

FIG. 2. Soil moisture levels during the 1985 growing season (year 1) on the manzanita, meadow, and oak sites.

and madrone than in manzanita soils (Fig. 1). Soil moisture content (based on ovendry weight) was also similar among sites throughout the growing season, although the higher clay content in oak soils apparently held slightly more moisture than did soils on the other two sites (Fig. 2). Beginning about May 17, all sites exhibited a rapid reduction in available soil moisture, and by July 1 soil moisture was below 15% on all sites. Some replenishment was evident by the end of September. Solar radiation was somewhat lower under the shade of the oaks, averaging 74.8% of mean total potential; solar radiation on the manzanita and meadow sites averaged 89.6 and 88.4%, respectively.

First-year survival on NT plots averaged 100, 72, and 73% on the manzanita, meadow, and oak sites, respectively (Fig. 3A). By the end of the second growing season, survival had dropped to 42% in the meadow and 12% in the oak stand but remained high (92%) in the manzanita (Fig. 3B). Soil transfer from the madrone stand did not significantly influence seedling survival in any community type.

At the end of the 1st year, basal-area increment of NT seedlings on the manzanita site averaged more than twice that of NT seedlings in the meadow and four times that of

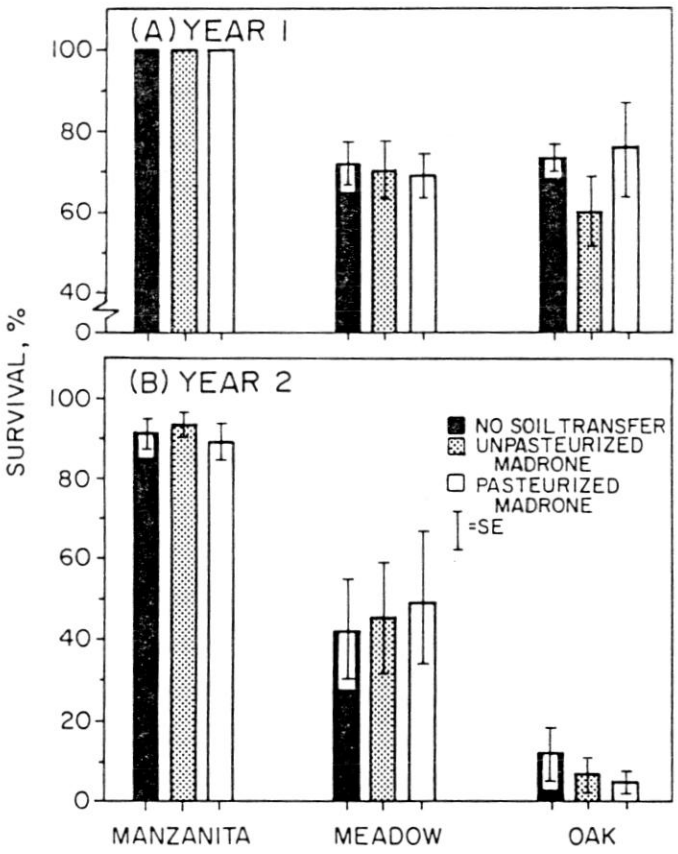

FIG. 3. Percentage of seedlings surviving in years 1 and 2, by vegetation type and within each type, by soil transfer treatment.

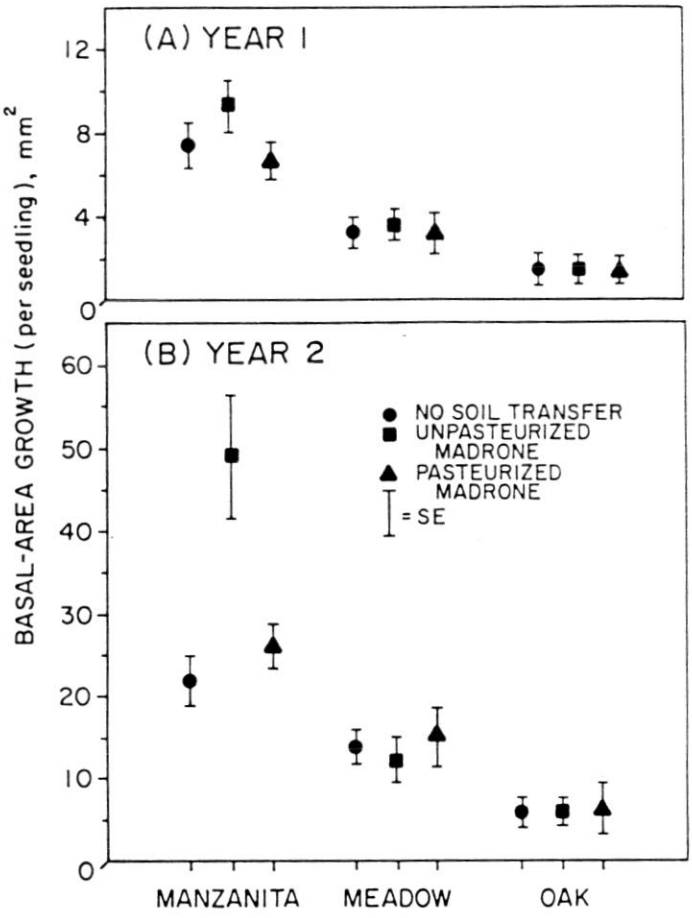

FIG. 4. Average basal-area growth per seedling in years 1 and 2, by vegetation type and within each type, by soil transfer treatment.

NT seedlings under the oaks (Fig. 4A), a pattern that continued in the 2nd year (Fig. 4B). By the 2nd year, height growth (which was not affected by any treatment in the 1st year) for NT seedlings was also greatest on the manzanita site (Fig. 5). On an area basis (roughly calculated as 2-year basal-area growth of the average NT seedling multiplied by the number of NT survivors), Douglas-fir in the NT treatment grew 0.017, 0.004, and 0.0006 m^2/m^2 on the manzanita, meadow, and oak sites, respectively.

Madrone soil transfer did not affect seedling growth in the meadow or the oak stand. On the manzanita site, however, 2nd-year basal-area growth of UM seedlings was nearly twice that of either PM or NT seedlings (Fig. 4B), and 2nd-year height growth of UM seedlings was 40% greater (Fig. 5B). During the second growing season, UM seedlings in manzanita averaged roughly 4 times more basal-area growth per seedling than those in pasture and 8 times more than those under oaks. On an area basis (calculated as described earlier), UM seedlings grew 0.034 m^2/m^2 net basal area over 2 years on the manzanita site and only 0.004 and 0.0004 m^2/m^2 on the meadow and oak sites, respectively. Height growth also differed significantly, though less dramatically (Fig. 5B).

Seedlings on the manzanita and meadow sites formed equal numbers of mycorrhizae; those on the oak site formed fewer (Fig. 6). However, mycorrhiza types differed between manzanita on the one hand and meadow and oak on the other. Type A (whose color, structure, and rhizomorph development suggested that it was *Rhizopogon vinicolor*) dominated on seedlings from the manzanita site, whereas type B (tentatively identified as *Pisolithus tinctorius*) dominated on the meadow and oak sites. Fruiting bodies of *Pisolithus tinctorius* were observed in the meadow, and probably originated from mycorrhizae on bordering trees or shrubs.

On the manzanita site, unpasteurized madrone soil greatly enhanced total mycorrhiza formation. This resulted from the greater abundance of *R. vinicolor* and also from the appearance of an unidentified yellow mycorrhiza which we designated type C (Fig. 6). Although small numbers of type C formed on UM seedlings in the meadow, overall mycorrhiza formation on those seedlings was not enhanced. UM and PM seedlings on the oak site, though they formed no type C mycorrhizae, formed a greater proportion of *R. vinicolor*.

Discussion

Douglas-fir seedlings, when planted in soils previously occupied by whiteleaf manzanita, grew and survived better than seedlings planted either in an adjacent cleared meadow or beneath open stands of Oregon white oak which were cleared of surface vegetation. Small amounts of unpasteurized soil from a nearby Pacific madrone stand improved seedling growth on the manzanita site but not on the other sites. Taking into account both mortality and basal-area growth of surviving individuals over the 2 years, Douglas-fir inoculated with UM soil occupied space within the manzanita site at a rate roughly 10 times greater than in the meadow and 100 times greater than under the oaks.

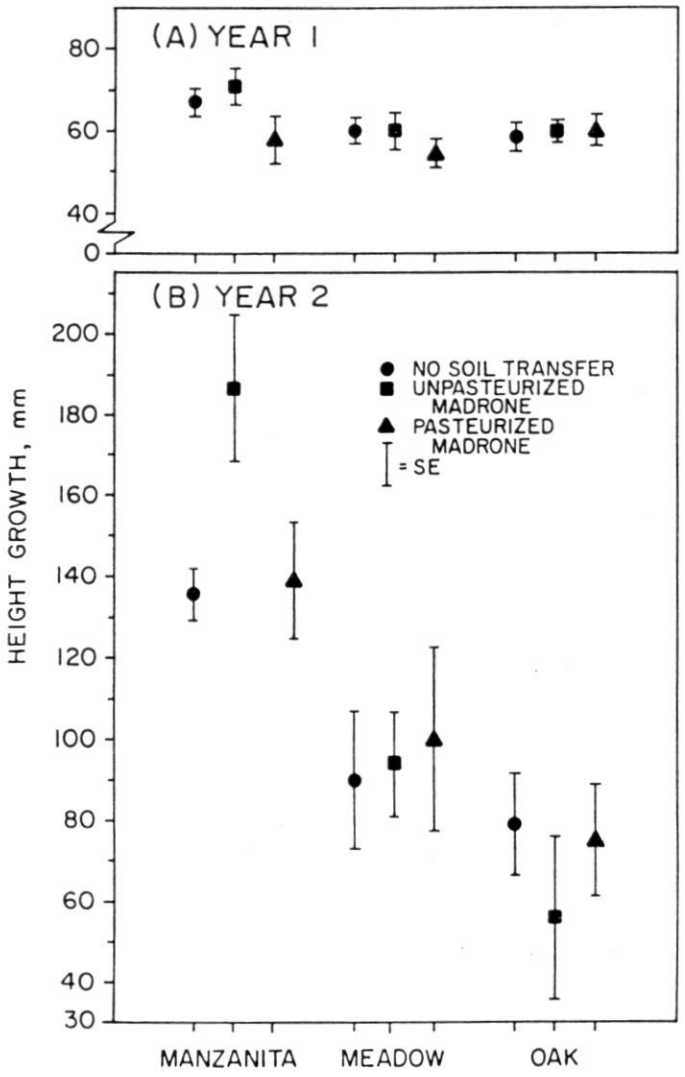

FIG. 5. Average seedling height growth in years 1 and 2, by vegetation type and within each type, by soil transfer treatment.

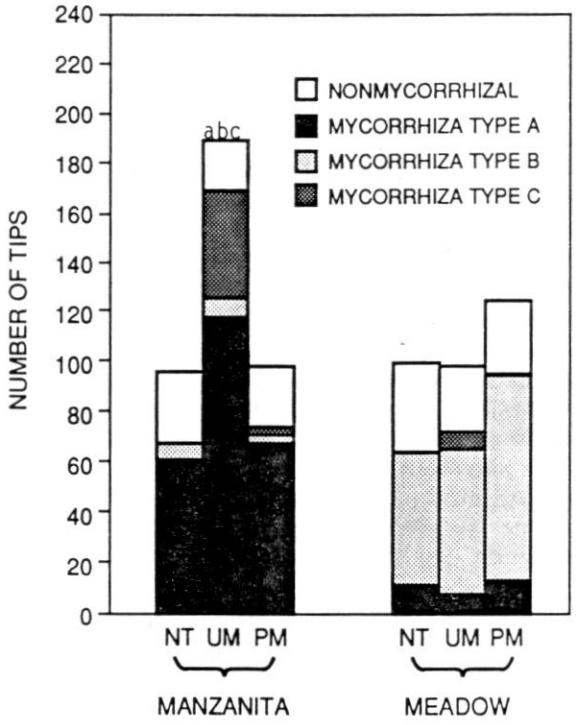

FIG. 6. Average seedling mycorrhiza formation at the end of the 1985 growing season (year 1), by vegetation type and, within each type, by soil transfer treatment. Within a given vegetation type, lower case letters indicate statistically significant differences ($p < 0.05$) from the NT treatment: (*a*) for total root tips, (*b*) for type A mycorrhizae, (*c*) for type C mycorrhizae. Type B mycorrhizae differed significantly among vegetation types but were not influenced by soil transfers. NT, no soil transfer; UM, unpasteurized madrone soil; PM, pasteurized madrone soil.

We detected no differences in soil physical structure, water content, or macronutrients that could explain these results. In this droughty environment, the moderate shade of the oaks should benefit rather than inhibit seedlings. Undetected variation in micronutrients or other inherent site factors cannot be ruled out.

The differing proportions of mycorrhiza types among treatments strongly suggest that the influence of manzanita is biological. However, numerous abiotic factors can affect the types of mycorrhizae that form on seedlings (Schoenberger and Perry 1982; Pilz and Perry 1984). The effect of madrone soil transferred to seedlings on the manzanita site was almost certainly biological; it induced a new mycorrhiza type, and pasteurization rendered it ineffective. Increased formation of *Rhizopogon* mycorrhizae and the appearance of the new mycorrhiza type on seedlings with added madrone soil could have resulted either from direct transfer of mycorrhizal inocula in madrone soils or from stimulation of mycorrhiza formation by bacteria or actinomycetes in madrone soil. Several studies have shown that rhizosphere bacteria influence mycorrhiza formation (Shemakhanova 1967; Bowen and Theodorou 1979; Perry and Rose 1983; Meyer and Linderman 1986; Garbaye and Bowen 1987). Elsewhere we report that rhizosphere nitrogenase activity was significantly greater for seedlings on the manzanita site than for those in the meadow (seedlings planted in the oak stand were not tested). That effect was greatly enhanced by addition of madrone soil and is related to the presence of *Azospirillum* sp. on or within mycorrhizae (Amaranthus *et al.* 1987).

On the other hand, the relative ineffectiveness of madrone inocula on the meadow and oak sites indicates that more is involved in Douglas-fir response than the simple presence or absence of the "right" organisms. Theodorou and Bowen (1971) showed that grasses inhibited mycorrhiza formation by *Rhizopogon luteolus* Fr. Nordh. on radiata pine (*Pinus radiata* D. Don), and suggested that this was due to lower soil P in the presence of grass. Stimulation of *Rhizopogon* formation in oak soils by both PM and UM soils may indicate nutrient limitation, although we detected no differences in macronutrients among any of the soils. Some organisms, particularly actinomycetes and other spore-forming bacteria, survive pasteurization (Shemakhanova 1967; R. Linderman, personal communication) and might influence mycorrhiza formation (Shemakhanova 1967; Perry and Rose 1983).

Our work in clearcuts of this area supports the findings of this study. In the field, the rate of Douglas-fir root-tip formation correlates positively with proximity to manzanita (M.P. Amaranthus and D.A. Perry, in preparation). In the greenhouse, small amounts of soil (100 mL) taken from the vicinity of the ectomycorrhizal hardwoods madrone, tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), and canyon live oak (*Quercus chrysolepsis* Liebm.) stimulate

growth of Douglas-fir (Borchers and Perry 1987). As in this study, increased growth is accompanied by a higher proportion of *Rhizopogon* mycorrhizae.

A wide variety of nonconiferous plant species may support conifer mycorrhizal fungi (Molina and Trappe 1982). In southwest Oregon and northern California, plants in six families are ectomycorrhizal. This does not mean that all of them harbor rhizosphere organisms that stimulate conifer growth, as demonstrated by our results with seedlings planted in Oregon white oak stands. However, of five broadleaved ectomycorrhizal plant species tested in this study and by Borchers and Perry (1987), soils collected from the root zones of four (madrone, manzanita, tanoak, and canyon live oak) have stimulated Douglas-fir growth. This phenomenon may extend to plant species that are not usually thought of as ectomycorrhizal. In Australia, ectomycorrhizal fungi have been shown to colonize the roots of various "non-ectomycorrhizal" plant species (Theodorou and Bowen 1971; Kope and Warcup 1986). Theodorou and Bowen (1971) suggest that this facilitates survival and spread of ectomycorrhizal fungi. In greenhouse bioassays of soil from the Oregon Cascade Mountains, the number of *Rhizopogon vinicolor* mycorrhizae formed by Douglas-fir seedlings correlates positively with the cover of vesicular–arbuscular mycorrhizal vine maple (*Acer circinatum* Pursh) and snowbrush (*Ceanothus velutinus* Dougl.) on plots where soils were collected (R. Brainerd and D.A. Perry, unpublished data). This could be a nutrient effect, as soil nitrogen and phosphorus concentrations also correlate positively with cover of these species.

Foresters frequently view noncrop plant species as undesirable competitors for light, water, and nutrients, and there is little doubt that such competition occurs. However, our results and those of others indicate that plant species may interact positively as well as negatively (Hunter and Aarsen 1988). Better understanding of ecological relationships within early successional communities may have much to offer forestry.

Acknowledgements

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