Effect of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, nonreforested clear-cuts

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Small amounts (150 mL) of soil from established conifer plantations and mature forest were transferred to planting holes on three clear-cuts in southwest Oregon and northern California to enhance mycorrihiza formation. The clear-cuts, 8–27 years old and unsuccessfully reforested, included a range of environmental conditions. At Cedar Camp, a high-elevation (1720 m) southerly slope with sandy soil, transfer of plantation soils increased 1st-year Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedling survival by 50%. Notably, soil from a plantation on a previously burned clear-cut doubled mycorrhiza formation and tripled seedling basal area growth. Soil from mature forest did not improve survival and growth. Less dramatic effects owing to soil transfer were evident on other sites, which were lower in elevation and had clayey soils with greater water-holding capacity, and where woody shrubs had apparently preserved mycorrhizal fungi. At Crazy Peak (1005 m), seedling survival was uniformly good, and soil from a previously burned plantation increased Douglas-fir mycorrhiza formation. At Wood Creek (500 m), soil from a plantation on a previously unburned clear-cut increased mycorrhizal branching on sugar pine (*Pinus lambertiana* Dougl.) seedlings, but there was no other effect. Results suggest that adequate mycorrhiza formation is critical to seedling growth and survival on cold, droughty sites. Populations of mycorrhizal fungi, and perhaps other beneficial soil biota, decline if reforestation is delayed or other host plants are absent. These declines can be offset by soil transfer from the proper source; in this study, soil from vigorous young plantations.

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Les auteurs ont placé de petites quantités de sol (150 mL) provenant de plantations de conifères bien établies et de forêts à maturité, dans les cavités de plantation lors du reboisement de stations coupées à blanc dans le sud-ouest de l'Oregon et le nord de la Californie, afin d'accélérer la formation des ectomycorhizes. Ces forêts coupées à blanc depuis 8 à 27 ans et où la reforestation est demeurée infructueuse, représentent toute une gamme de conditions environnementales. À Cedar Camp, une station de haute altitude (1720 m) sur sol sableux exposé au sud, le traitement à augmenté la survie de plantules de sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) de 50%. En particulier, il faut noter que l'apport de sol provenant d'une plantation établie sur un brûlé après coupe à blanc, a permis de doubler la formation des mycorhizes et de tripler la croissance en terme de surface basale. Les sols provenant de forêts à maturité n'ont pas permis d'augmenter la survie, ni la croissance. Des effets moins marqués liés au transfert de sol ont été observés sur d'autres sites qui se trouvaient à des élévations plus faibles sur des sols contenant de l'argile, pourvus d'une meilleure capacité de rétention en eau et où des arbustes ont apparemment préservé les champignons ectomycorhiziens. A Crazy Peak (1005 m), la survie des plants était généralement bonne et l'addition de sol venant d'une plantation préalablement brûlée a permis d'augmenter la formation des mycorhizes. A Wood Creek (500 m), l'addition de sol provenant d'une plantation sur coupe à blanc non brûlée à augmenté la ramification des mycorhizes du *Pinus lambertiana* Dougl., sans plus. Les résultats suggèrent qu'une formation adéquate de mycorhizes est nécessaire pour la survie et la croissance des plants sur les sites froids et secs. Les populations de champignons mycorhiziens, et peut-être d'autres organismes utiles du sol, diminuent si la reforestation retarde ou s'il n'y à pas d'autres plantes hôtes. Ces déficiences peuvent être comblées par un apport de sol provenant d'une source convenable. Dans cette étude, il s'agissait de sols provenant de jeunes plantations vigoureuses.

[Traduit par la revue]

Introduction

Most forest tree species of the Pacific Northwest are ectomycorrhizal (Molina and Trappe 1982*a*). Benefits to the host plant include increased water and nutrient uptake, resistance to root pathogens, and increased tolerance to environmental extremes (Marx and Krupa 1978). Formation of ectomycorrhizae depends on a source of inocula but is also influenced by environmental variables and soil properties such as soil moisture, temperature, pH, fertility, and organic matter (Slankis 1974). Harvest and site preparation alter these factors and therefore potentially impact microbial numbers and diversity. Reduced mycorrhiza formation on seedlings grown in clear-cut soils (particularly where slash has been burned) has been reported by numerous researchers (Wright and Tarrant 1958; Harvey *et al.* 1980; Perry *et al.* 1982; Parke *et al.* 1984). Moreover, harvest-related changes in forest floor and soil (Amaranthus and McNabb 1984) may affect not only ectomycorrhizae but other soil microorganisms with which they interact (Perry and Rose 1983).

Little is known of the persistance and distribution of ectomycorrhizae in the absence of living hosts. It has been suggested (Hacskaylo 1973) that ectomycorrhizal fungi do not persist long in the absence of host-supplied substrates. Total elimination of active ectomycorrhizae was reported 1 year after clear-cutting a high-elevation site in western Montana (Harvey *et al.* 1980). Ectomycorrhizae from an adjacent, undisturbed stand did not occur beyond 4.5 m into the clear-cut, and numbers of ectomycorrhizae were reduced 7.5 m into the adjacent stand. Recolonization of this clear-cut would depend on external inoculum (Maser *et al.* 1978).

Mycorrhiza formation may be of primary importance in water uptake and drought resistance (Reid 1979; Parke *et al.* 1983*a*), and early mycorrhiza formation is particularly important to seedling growth and survival in dry areas (Mikola 1970). However, drier climates may limit the activity of mycorrhizal fungi as well as decrease the time in which conditions for spore germination and mycelial growth are optimal, thus decreasing the chances for planted seedlings to be colonized. In contrast,

TABLE 1. Site characteristics of the three clear-cut and broadcast-burned study sites (Klamath Mountain region, southern Oregon, and northern California)

Characteristic	Cedar Camp (site 1)	Crazy Peak (site 2)	Wood Creek (site 3)
Age after clear-cut (years)	16	27	8
Elevation, aspect, slope	1720 m, SW, 50%	1005 m, E, 15%	500 m, W, 40%
Precipitation and air temperature	165 cm (>50% is snow), 5°C	230 cm (>50% is snow), 7°C	260 cm (<10% is snow), 9°C
Soil			
Classification	Sandy skeletal, excessively drained, mixed Entic Cryumbrept	Clayey skeletal, mesic Ultic Haploxeralf	Clayey skeletal, mixed mesic Ultic Haploxeralf
Parent material	Quartz diorite	Serpentinized gabbro	Metasedimentary
Temperature (°C), 35-cm depth			
April 28, 1985	2.2	5.6	7.2
May 28, 1985	4.4	7.8	10.6
Plant association[a] (adjacent, undisturbed forest)	ABCO/ABMAS/SYMO	LIDE3/RHCA	LIDE3/GASH/BENE
Dominant vegetation[b]			
Clear-cut	Annual grasses, herbs, bracken fern, red elderberry, greenleaf manzanita	Greenleaf manzanita, pinemat manzanita, coffeeberry, huckleberry oak, tanoak, golden chinkapin, ponderosa pine, knobcone pine, Douglas-fir	Pacific madrone, tanoak, canyon live oak, white manzanita, golden chinkapin
Adjacent, undisturbed forest	White fir, Douglas-fir, Shasta red fir	Douglas-fir, sugar pine, white fir, incense cedar	Douglas-fir, sugar pine

[a]ABCO/ABMAS/SYMO, *Abies concolor*/*Abies magnifica* var. *shastensis*/*Symphoricarpos mollis*; LIDE3/RHCA, *Lithocarpus densiflorus*/*Rhamnus californica*; LIDE3/GASH/BENE, *Lithocarpus densiflorus*/*Gaultheria shallon*/*Berberis nervosa* (From Atzet and Wheeler 1984).

[b]Bracken fern, *Pteridium aquilinium* (L.) Kuhn.; red elderberry, *Sambucus racemosa* L.; greenleaf manzanita, *Arctostaphylos patula* Greene; pinemat manzanita, *Arctostaphylos nevadensis* Gray; white manzanita, *Arctostaphylos viscida* Parry; coffeeberry, *Rhamnus californica* Esch. var. *occidentalis* (How.) Jeps.; Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco; white fir, *Abies concolor* (Gord. & Glend.) Hildebr.; shasta red fir, *Abies magnifica* var. *shastensis* Lemm.; sugar pine, *Pinus lambertiana* Dougl.; huckleberry oak, *Quercus vaccinifolia* Kellogg; canyon live oak, *Quercus chrysolepis* Liebm.; Tanoak, *Lithocarpus densiflorus* (Hook. & Arn.) Rehd.; golden chinkapin, *Chrysolepis chrsophylla* (Dougl.) DC.; Pacific madrone (*Arbutus menziesii* Pursh); Ponderosa pine, *Pinus ponderosa* Laws.; knobcone pine, *Pinus attenuata* Lemm.; incense cedar (*Libocedrus decurrens* Torr.).

seedlings in wetter climates are exposed to available moisture for a longer period and can thus survive longer without mycorrhizae and increase their probability of eventually becoming colonized.

Because relatively small amounts of inocula are adequate for effectively colonizing seedlings (Pilz and Perry 1984), reduced ectomycorrhiza formation owing to disturbance might be offset by transferring soil from the feeder-root zone of actively growing, compatible host species to impacted sites. In our study, we transferred soil from the feeder-root zones of burned and unburned plantations, as well as pasteurized and unpasteurized soil from adjacent undisturbed mature forest, into planting holes on three old clear-cut and burned sites that had not been successfully reforested. The study was designed to (*i*) investigate mycorrhiza formation and conifer seedling performance after soil transfer, (*ii*) examine a range of sources of transferred soil to determine the most effective, and (*iii*) assess the environmental conditions under which soil transfer contributes to seedling growth and survival.

Methods

Site characteristics

Three sites representing a range of elevations, soils, and vegetation (Table 1) were selected in the Klamath Mountain region of northern California and southern Oregon. The Klamath Mountains are characterized by rugged, steeply dissected terrain with shallow, skeletal soils. The forests are typically mixed evergreen. Summers are hot and dry, and winters are wet.

Sites had been clear-cut and broadcast burned between 8 and 27 years before study installation. Cedar Camp (site 1) and Crazy Peak (site 2) have a history of reforestation failure and are poorly stocked despite repeated planting with conifers. Conifer regeneration at Wood Creek (site 3) has been more successful than that on the other two sites; however, large unstocked areas are common within the clear-cut. Previous work at Cedar Camp and Wood Creek had shown reduced ectomychorrhiza formation relative to that in the adjacent, undisturbed forest (Perry and Rose 1983).

Soil transfer

At each site, five replicate blocks (3 × 3 m) were cleared of preexisting vegetation with chainsaws and hoes 1 week before soil treatment and seedling planting in spring 1985. Seedlings to be planted were nonmycorrhizal 1–0 Douglas-fir and 1–0 sugar pine stock grown in Ray Leach fir cells at Dean Creek Nursery, Oregon.

Each seedling was placed in a planting hole to which 150 mL of soil was simultaneously added from one of four soil-transfer treatments: soil from a Douglas-fir plantation established on a previously burned clear-cut (BC), soil from a plantation established on an unburned clear-cut (UC), unpasteurized soil from undisturbed mature forest (MF), or pasteurized soil from undisturbed mature forest (PMF). The fifth treatment, no soil transfer (NT), was the control. Plantations, ranging from 10 to 15 years of age, were on the same soil type and at similar elevations as the study sites.

Soil and air temperature, humidity, and wind speed were measured at planting; no seedlings were planted when air temperature exceeded 15.5°C. Soil moisture was at field capacity at planting. Transfer soil, collected within 7 h of planting, was taken from the feeder-root zone (top 20 cm of mineral soil) of 12 randomly selected Douglas-fir trees per plantation for the BC and UC treatments and one crown width from the base of 12 randomly selected mature conifers (white fir at Cedar Camp, Douglas-fir at Crazy Peak, Douglas-fir and sugar pine at Wood Creek) for the MF and PMF treatments. Undisturbed-forest soil used for the PMF treatment was steam heated for 3 h at 70°C, sealed, and returned to the field for transfer within 48 h. Twenty-five seedlings per treatment per block were planted 40 cm apart in a 5 × 5 array, at least 1 m separating treatments from one another, in a randomized block design. One worker planted all five treatment units in a block.

Basal diameter 1 cm above the soil surface was measured with calipers within 1 week of planting. Seedling survival was monitored at 4-week intervals throughout the study period (one growing season). At the end of the growing season, diameters and leaders were measured on all surviving seedlings. Fifty live seedlings per site were carefully excavated in November 1985 following fall rains and soil-moisture recharge, placed on ice in the field, and transported to the laboratory, where they were stored at 2°C. Seedling roots were examined for numbers and types of mycorrhizal tips within 14 days of excavation.

Soil was gently washed from roots and roots were subsampled in three 1.5-cm sections cut across the entire root system in upper, middle, and lower positions. All short roots and the number of active root tips per short root were tallied in these sections and tips identified as nonmycorrhizal or mycorrhizal. Throughout, the terms "branching ratio" and "mycorrhizal branching" are used to denote the average number of tips per short root. Numerous root cross sections were examined for the presence of a Hartig net to aid in determining mycorrhizal root colonization. Tips that appeared inactive or dead were not counted.

Soil nutrients and moisture

In May 1986, soil was collected from Cedar Camp, Crazy Peak, and Wood Creek and from the plantation and mature-forest sites used as soil-transfer sources. At each site, soil was randomly sampled from four points along each of three transects; samples were composited by transect. Soil samples were analyzed at the Oregon State University Soils Laboratory for pH; phosphorus (P, molybdate blue method); extractable calcium (Ca), magnesium (Mg), and potassium (K); and total nitrogen (N).

Soil moisture was determined gravimetrically from samples taken at 2- to 3-week intervals throughout the growing season at 10-, 35-, and 60-cm depths at Cedar Camp and Crazy Peak. Samples were packed in airtight containers and transported to the laboratory, where they were weighed, oven-dried for 24 h at 105°C, and reweighed. For each sampling interval and depth, available soil moisture was determined by calculating the difference between the observed and the minimum (peak of summer drought) moisture content. Precipitation amounts were recorded at 2- to 3-week intervals from rain gauges on the two sites. Soil moisture and precipitation were not measured at Wood Creek.

Statistical analysis

Data were subjected to analysis of variance. Root-tip counts were log transformed to compensate for lognormally distributed values (Steel and Torrie 1980). Percentage survival data were transformed to an inverse sine and diameter measurements were converted to basal area. Tukey's multiple range test was used to compare differences ($p \leq 0.05$) among treatment means for seedling basal area growth, survival, mycorrhizal and nonmycorrhizal root tips and branching, and also for soil nutrient and pH levels.

Results

Soil transfer

At Cedar Camp, Douglas-fir seedlings receiving BC, UC, and PMF treatments had significantly greater 1st-year basal area growth, survival, numbers of mycorrhizal root tips, and mycorrhizal branching than seedlings receiving no soil transfer (Fig. 1). Soil from the BC treatment had a particularly striking effect: it doubled the number of mycorrhizal tips, almost tripled basal area growth, and increased survival by 50% (from 42 to 62%) relative to the controls. The MF treatment also increased basal area growth relative to the controls but did not influence the other variables.

Patterns were similar but less definitive at Crazy Peak (Fig. 2). BC, UC, and PMF treatments increased basal area growth by 40–50% relative to the controls. Numbers of mycorrhizal tips and degree of mycorrhizal branching averaged higher in all treatments in which soil was transferred than in the controls; however, differences were statistically significant only for BC (mycorrhizal numbers and branching) and PMF (branching). Survival exceeded 95% in all treatments.

Other than increasing mycorrhizal branching in the UC treatment, soil transfer did not affect seedling performance at Wood Creek (Fig. 3). Survival was high (> 85%) in all treatments. Lower numbers of mycorrhizae and generally greater mycorrhizal branching on this site relative to the other two probably reflect differences in seedling species (sugar pine at Wood Creek vs. Douglas-fir at Cedar Camp and Crazy Peak).

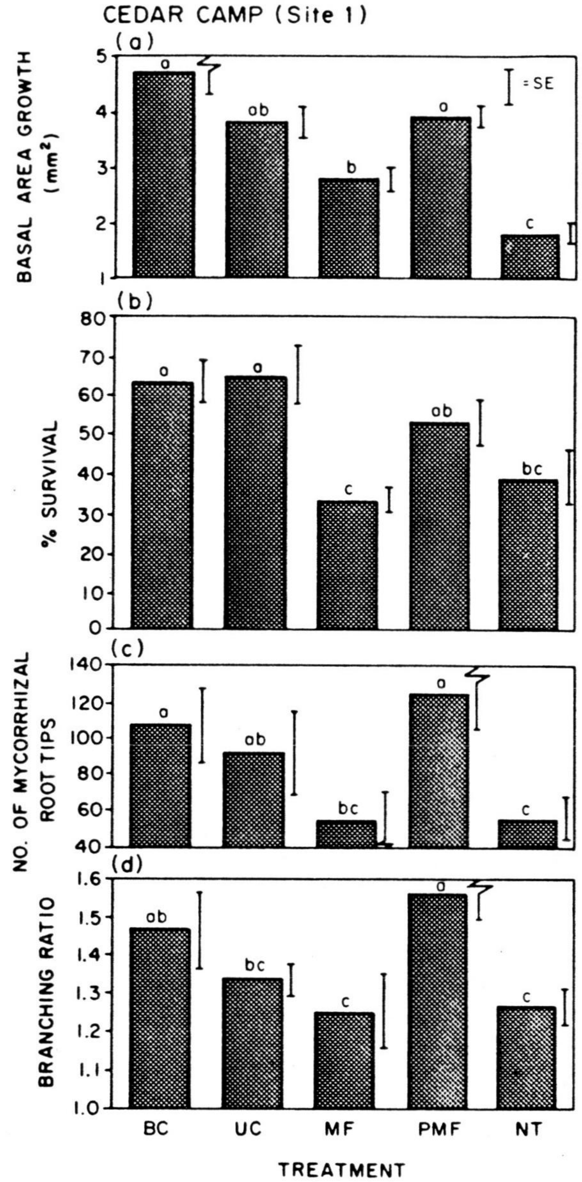

FIG. 1. Mean 1st-year basal area growth (*a*), survival (*b*), number of mycorrhizal root tips (*c*), and degree of mycorrhizal branching (*d*) of Douglas-fir seedlings following soil transfer at Cedar Camp (site 1). BC, soil from plantation on a previously broadcast-burned clear-cut; UC, soil from plantation on a previously unburned clear-cut; MF, soil from adjacent mature forest; PMF, pasteurized soil from adjacent mature forest; NT, no soil transfer. Bars with the same lowercase letters are not significantly different ($p \leq 0.05$), Tukey's multiple range test; SE, standard error.

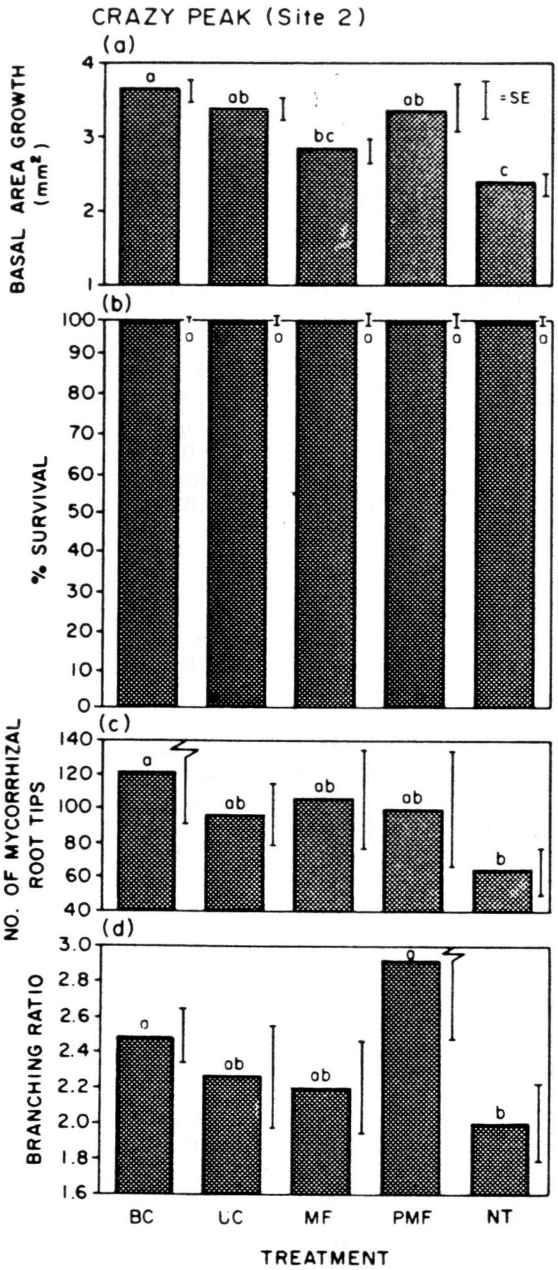

FIG. 2. Mean 1st-year basal area growth (*a*), survival (*b*), number of mycorrhizal root tips (*c*), and degree of mycorrhizal branching (*d*) of Douglas-fir seedlings following soil transfer at Crazy Peak (site 2). See Fig. 1 caption for soil-treatment descriptions. Bars with the same lowercase letters are not significantly different ($p \leq 0.05$), Tukey's multiple range test; SE, standard error.

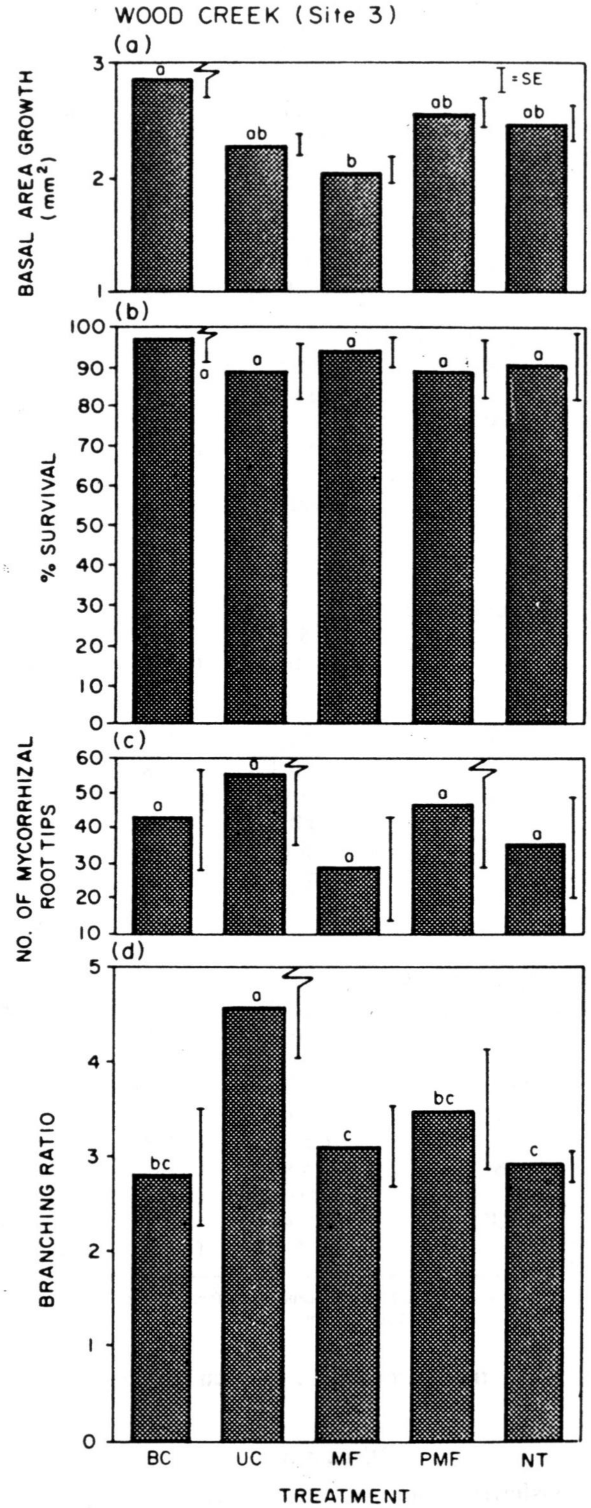

FIG. 3. Mean 1st-year basal area growth (*a*), survival (*b*), number of mycorrhizal root tips (*c*), and degree of mycorrhizal branching (*d*) of sugar pine seedlings following soil transfer at Wood Creek (site 3). See Fig. 1 caption for soil-treatment descriptions. Bars with the same lowercase letters are not significantly different ($p \leq 0.05$), Tukey's multiple range test; SE, standard error.

Soil nutrients and moisture

Levels of soil macronutrients did not vary significantly among unreforested clear-cut (Cedar Camp, Crazy Peak, Wood Creek), plantation (BC, UC), and mature forest (MF, PMF) soils at each study site, nor did pH (Table 2). Levels of N, probably the most limiting nutrient in these soils, were moderate at Cedar Camp but low at the other two sites. P. levels were quite low at Crazy Peak.

Available soil moisture was greater at Crazy Peak than Cedar Camp, and soils at the former remained moist longer into the growing season (Fig. 4). Both sites experienced 80 days (mid-June to early September) when virtually no rain fell; however, Crazy Peak still had available soil moisture an additional 2 weeks into this droughty period. In 1985, seedlings at Cedar Camp had approximately 28 days, whereas those at Crazy Peak had approximately 95 days, when soil temperatures

TABLE 2. Mean pH and nutrient levels (±SE) from various soil sources. Values did not vary significantly ($p \leq 0.05$) among unreforested clear-cut, plantation, and mature-forest soils

Soil source	pH	P (ppm)	Ca (mequiv./100g)	Mg (mequiv./100g)	K (mequiv./100g)	Total N (%)
			Cedar Camp			
Unreforested clear-cut	6.05 (±0.39)	54 (±14.2)	16.4 (±3.2)	1.7 (±0.43)	164 (±23.0)	0.16 (±0.028)
Transferred soils						
MF	5.8 (±0.22)	38 (±8.2)	12.0 (±4.3)	2.1 (±0.27)	203 (±27.4)	0.19 (±0.042)
BC	6.1 (±0.29)	28 (±9.6)	12.7 (±2.6)	1.6 (±0.28)	245 (±38.2)	0.13 (±0.032)
UC	5.9 (±0.19)	32 (±8.9)	12.6 (±3.2)	1.7 (±0.32)	230 (±16.4)	0.15 (±0.036)
			Crazy Peak			
Unreforested clear-cut	5.6 (±0.38)	9 (±3.6)	2.6 (±0.46)	2.1 (±0.40)	104 (±14.9)	0.07 (±0.008)
Transferred soils						
MF	5.4 (±0.30)	7 (±1.8)	3.4 (±0.53)	2.2 (±0.28)	145 (±42.1)	0.08 (±0.021)
BC	5.9 (±0.16)	5 (±1.2)	2.9 (±0.81)	2.4 (±0.42)	105 (±16.0)	0.07 (±0.014)
UC	5.8 (±0.14)	6 (±0.6)	3.0 (±0.18)	3.4 (±0.83)	126 (±38.2)	0.07 (±0.006)
			Wood Creek			
Unreforested clear-cut	5.89 (±0.26)	36 (±12.0)	2.8 (±0.42)	0.75 (±0.14)	117 (±22.0)	0.09 (±0.038)
Transferred soils						
MF	6.09 (±0.40)	34 (±6.8)	3.9 (±0.99)	0.93 (±0.23)	174 (±51.3)	0.11 (±0.012)
BC	5.93 (±0.18)	21 (±6.5)	2.7 (±0.43)	0.84 (±0.29)	117 (±20.8)	0.09 (±0.009)
UC	5.48 (±0.42)	26 (±3.6)	1.8 (±0.89)	0.59 (±0.30)	138 (±18.0)	0.12 (±0.008)

NOTE: MF, soil from adjacent mature forest; BC, soil from plantation on a previously broadcast-burned clear-cut; UC, soil from plantation on a previously unburned clear-cut.

exceeded 4°C at the 35-cm depth and when soils had available water.

Discussion

Soil transferred from well-stocked plantations increased seedling basal area growth and mycorrhiza formation on two clear-cut sites and increased mycorrhizal branching on a third. In general, soil from plantations on sites that had been broadcast burned produced greater effects than that from plantations on unburned sites. Soil from mature forest adjacent to each of the study clear-cuts had relatively little effect, increasing basal area growth on only one site. However, in some cases, pasteurizing adjacent forest soil increased the magnitude of its effect.

At Cedar Camp, soil transferred from both burned and unburned plantations increased 1st-year seedling survival from <40 to >60%. Although growth of the previous stand on this clear-cut, and of the adjacent mature stand, is quite good, seedling establishment is difficult; four previous reforestation attempts have failed. Soils are coarse textured (<3% clay) loamy sands with low water-holding capacity; they remain frozen late into spring because of the high elevation and lose moisture early to summer drought, giving seedlings a very short time in which to become established. Rapid, extensive mycorrhizal formation is perhaps most critical on this site, where seedlings must rapidly attain the necessary nutrients and water not only to survive severe summer drought but to come through in sufficiently good condition to also survive a long winter. Early observations of a new set of soil-transfer experiments on this site show that seedlings growing with transferred plantation soil form root tips at a significantly higher rate in early spring than those growing without transferred soil.

Although soils on the other two sites have higher water-

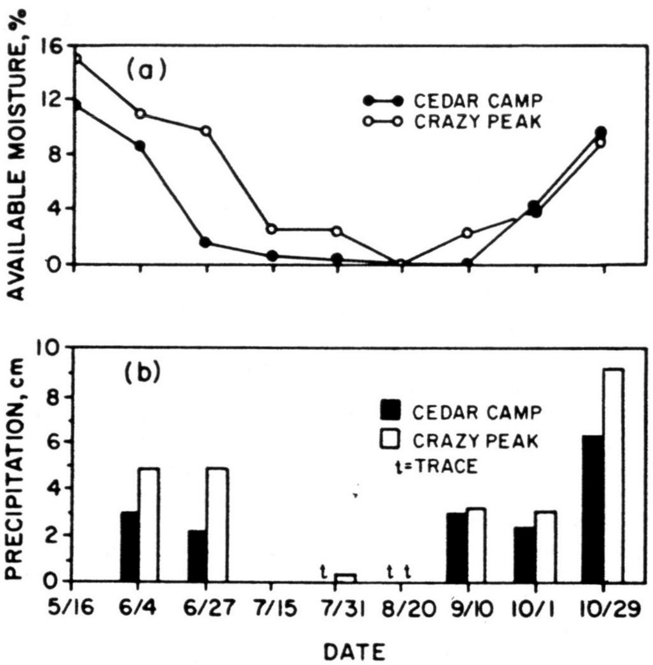

FIG. 4. Soil moisture at the 35-cm depth (*a*) and precipitation (*b*) at Cedar Camp and Crazy Peak throughout the 1985 growing season.

holding capacity than those at Cedar Camp, summer drought is nevertheless a factor. The importance of early mycorrhiza formation in dry areas has previously been emphasized (Parry 1953; Mikola 1970; Slankis 1974). Rhizopogon mycorrhizae, common mycosymbionts in clear-cuts of the Pacific Northwest, have been shown to reduce drought stress of Douglas-fir seedlings (Parke *et al.* 1983*a*). Drier climates may limit the activity of mycorrhizal fungi as well as decrease the time in which conditions for spore germination and mycelial growth are optimal, thus decreasing the chance that a planted seedling will quickly become colonized (Slankis 1974). Under such conditions, factors that enhance the rapidity of mycorrhiza formation, whether related to density of fungal inocula, ability of seedling roots to quickly explore a large soil volume, or other biotic or physical influences, will probably produce more vigorous seedlings. Both Crazy Peak and Wood Creek clear-cuts were occupied by ericaceous shrubs that form mycorrhizae with at least some of the same fungi as conifers (Largent *et al.* 1980; Molina and Trappe 1982*b*); hence, in contrast with Cedar Camp, viable fungus populations were present despite the absence of conifers. Even so, growth of seedlings at Crazy Peak benefited from transfers, and this early boost in growth could influence tree growth and vigor well into the future. Lack of response to soil transfer at Wood Creek may have been due to incompatibility of the sugar pine seedlings with the flora of Douglas-fir plantation soil (no sugar pine plantations were available in the area).

We cannot now say why soil from well-stocked plantations stimulated mycorrhiza formation and seedling growth. Taken from the feeder-root zone, transferred soil was undoubtedly rich in mycorrhizal inocula; however, it also contained components that could have stimulated mycorrhiza formation by fungi indigenous to the clear-cuts. Numerous abiotic and biotic soil factors influence mycorrhiza formation (see reviews by Bowen 1973; Slankis 1974). Other than direct addition of fungal inocula, the factors most likely to have stimulated mycorrhiza formation by our seedlings are as follows: (*i*) nutrients; (*ii*) organic compounds such as hormones, vitamins, humic compounds, and amino acids, and (*iii*)nonmycorrhizal biota.

Very small amounts of nutrients were added with the transferred soils, e.g., only 0.1–0.2 g of N and even less P, K, Mg, and Ca per planting hole. Moreover, levels of these nutrients in transferred soils did not differ significantly from those in the clear-cuts. We cannot be sure that some limiting micronutrient was not included; however, macronutrient fertilization is unlikely to explain differences in seedling survival and growth.

Organic matter and various root exudates have long been known to stimulate, and occassionally inhibit, mycorrhiza formation (Slankis 1974; Alvarez *et al.* 1979; Schoenberger and Perry 1982; Parke *et al.* 1983*b*; Rose *et al.* 1983). Rhizosphere organisms may either stimulate or inhibit formation of the symbiosis (Slankis 1974; Bowen and Theodorou 1979; Chakraborty *et al.* 1985). Clear-cutting followed by slash burning (all three of our sites were burned) reduces organic matter and alters the nature of the soil microbial community, in some cases increasing the proportion of pathogens or other biota that negatively impact seedlings (Widden and Parkinson 1975; Perry and Rose 1983). Soils from the root zone of healthy trees probably have numerous biotic and abiotic components not present in clear-cuts, at least some of which are likely to stimulate root-tip and mycorrhiza formation.

In our experiment, mycorrhiza formation and seedling growth were generally stimulated by soils from established plantations and, following pasteurization, mature forest. If we assume that the same factor(s) are operative in each case, the effect of pasteurized soil implies inorganic nutrient(s) or organic compound(s) that for some reason were rendered ineffective by soil biota of the mature forests. There is no reason, however, to assume that the same factor(s) were operative. Succession of mycorrhizal fungi is now firmly established (Mason *et al.* 1983), and it is possible that mycorrhizae transferred in plantation, as opposed to mature forest, soils were more compatible with seedlings in a clear-cut environment. Hence mycobiont inocula probably played an important role in seedling response to plantation soil inocula, whereas physical or biochemical properties of pasteurized mature-forest soils could have stimulated seedling mycorrhiza formation.

Although the underlying biology is uncertain, the study results nevertheless provide useful insights into reforesting clear-cuts in southwest Oregon and northwest California and, perhaps, on other difficult to reforest sites. Reduced mycorrhiza formation following disturbance can restrict the ability of seedlings to become established, particularly in physically rigorous environments where the period favorable for growth is relatively short. Under such conditions, transfer of soil from the appropriate source (in our case, well-stocked plantations) can dramatically stimulate mycorrhiza formation as well as seedling survival and growth.

Acknowledgements

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