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Role for the photosynthate demand of ectomycorrhizas in the response of Douglas fir seedlings to drying soil

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SUMMARY

Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] seedlings were inoculated with different species of ectomycorrhizal fungi, *Rhizopogon vinicolor* FSL788-5, *Laccaria laccata* S238-A, or *Hebeloma crustuliniforme* HeCr2, to determine how different fungi affect the response of photosynthesis and water relations of seedlings to drying soil. Potted seedlings were grown in a greenhouse for 6 months under well-watered conditions, then transferred to a growth chamber where measurements were made as the soil dried.

Rhizopogon enhanced both net photosynthesis rate and stomatal conductance compared to non-mycorrhizal controls ($P < 0{\cdot}01$) over the soil water potential range of $-0{\cdot}05$ to $-0{\cdot}50$ MPa, despite 0·2 to 0·3 MPa lower leaf water potential. *Hebeloma* tended to enhance, while *Laccaria* decreased net photosynthesis rate and stomatal conductance of host seedlings over this range of soil water potential, but neither fungus affected leaf potential. Our observations for *Rhizopogon* and *Laccaria* could not be explained by existing hypotheses based on mycorrhizal effects on plant size, nutrition, osmotic adjustment, or water uptake characteristics. Nutrition may have been a factor for *Hebeloma*.

We propose that in the absence of nutritional and water uptake effects, net photosynthesis rate and stomatal conductance are correlated with rate of export of photosynthate to the mycorrhizal fungus. Strong mycorrhizal demand for photosynthate stimulates photosynthesis, to which stomata respond by opening, notwithstanding water stress. Our results for *Rhizopogon* are consistent with this hypothesis.

Key words: Ectomycorrhizas, Douglas fir, water stress, photosynthesis, carbon allocation.

INTRODUCTION

Numerous observations suggest that mycorrhizas improve the drought tolerance of plants. Ectomycorrhizal tree seedlings and vesicular–arbuscular mycorrhizal (VAM) plants may show greater growth than non-mycorrhizal plants under cyclical drought conditions (Hardie & Leyton, 1981; Nelsen & Safir, 1982; Levy, Syvertsen & Nemec, 1983; Parke, Linderman & Black, 1983; Sweatt & Davies, 1984). Other studies clearly show greater survival of, or quicker recovery from drought periods by ectomycorrhizal seedlings and VAM plants than by non-mycorrhizal plants (Cromer, 1935; Goss, 1960; Theodorou & Bowen, 1970; Safir, Boyer & Gerdemann, 1971, 1972; Dixon *et al.*, 1980; Hardie & Leyton, 1981; Nelsen & Safir, 1982; Parke *et al.*, 1983).

Improved drought tolerance is often attributed to mycorrhiza-enhanced water uptake (Reid, 1979; Ruehle & Marx, 1979; Safir & Nelsen, 1985), making possible maintenance of higher water potential in the plant. There is often abundant hyphal growth from mycorrhizas into soil surrounding roots (Harley & Smith, 1983), and water can be taken up and transported through hyphae to plants (Duddridge, Malibari & Read, 1980; Brownlee *et al.*, 1983). Mycorrhizas might also increase root permeability to water by improving plant nutrition (Safir & Nelsen, 1985) or by altering plant hormone balance (Slankis, 1973; Allen, 1985).

Other studies, however, have not confirmed this water uptake benefit. Under drought conditions, lower leaf water potentials were measured in ectomycorrhizal oak seedlings than in non-mycorrhizal oak seedlings (Dixon *et al.*, 1980), higher stomatal conductance and net photosynthesis rate per unit leaf area were found in VAM plants with similar or lower leaf water potential than in non-mycorrhizal plants (Allen *et al.*, 1981; Stahl & Smith, 1984;

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Augé, Schekel & Wample, 1986), and ectomycorrhizal *Pinus radiata* had stomatal conductance similar to non-mycorrhizal controls, but at lower leaf water potential (Sands & Theodorou, 1978). These observations suggest that mycorrhizas may influence plant response to water stress in a way which cannot be entirely explained by enhanced water uptake, and that this influence minimizes the detrimental effect of low plant water potential on photosynthesis and stomatal aperture.

Changes induced by mycorrhizas in the relationship between stomatal conductance and leaf water potential have been recognized (Levy & Krikun, 1980; Hardie & Leyton, 1981), although no mechanism has been clearly identified to explain it. Enhanced osmotic adjustment in VAM plants during drought stress has been suggested as a possible mechanism to account for higher water flux and lower leaf water potential (Levy & Krikun, 1980; Hardie & Leyton, 1981; Allen & Boosalis, 1983; Augé *et al.*, 1986). Altered phytohormone levels, due to the activity of the mycorrhizal fungi, might trigger an osmotic adjustment response or act directly upon stomata (Levy & Krikun, 1980; Sweatt & Davies, 1984), but there are insufficient data to test these hypotheses. Alternatively, mycorrhiza-enhanced plant nutrition might explain such observations because VAM effects in general seem to disappear in comparisons with non-mycorrhizal plants provided with high levels of phosphorus fertilizer (Safir & Nelsen, 1985).

We propose another possibility, namely that greater stomatal conductance in mycorrhizal plants arises from high mycorrhizal demand for photosynthate from the plant. Mycorrhizal fungi obtain most, if not all, of their carbon as current photosynthate from the host plant (Harley & Smith, 1983; Read, 1987) and mycorrhizal root systems provide a stronger demand for photosynthate than non-mycorrhizal root systems (Reid, Kidd & Ekwebelam, 1983; Koch & Johnson, 1984; Paul, Harris & Fredeen, 1985). It is well-established that photosynthate sink activity can exert control on the rate of photosynthesis (Sweet & Wareing, 1966; Wareing & Patrick, 1975; Herold, 1980; Bagnall, King & Farquhar, 1988; Robbins & Pharr, 1988) and mycorrhizal colonization is associated with higher net photosynthesis rate (Allen *et al.*, 1981; Paul & Kucey, 1981; Ekwebelam & Reid, 1983; Brown & Bethlenfalvay, 1987; Nylund & Unestam, 1987). Furthermore, the rate of photosynthesis can control stomatal aperture (Meidner & Mansfield, 1968; Wong, Cowan & Farquhar, 1979; Farquhar & Sharkey, 1982; Morison, 1987). In this way, increased demand for photosynthate by mycorrhizal fungi could translate into greater stomatal conductance in spite of low leaf water potential.

The objective of this study was to determine the manner in which ectomycorrhizal colonization modifies the response of photosynthesis and water relations of Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] seedlings to drying soil and whether such modification is consistent with the photosynthate source–sink concept.

MATERIALS AND METHODS

Seedling inoculation and culture

Douglas fir seedlings were grown from seed, initially in a mixture of vermiculite and peat moss. At ages 6 and 8 wk, seedlings were transplanted into 21×4 cm diameter tubes containing a mixture of 3 parts pasteurized soil [sandy loam; organic matter 0·8 %, CEC 19 $cmol_c\ kg^{-1}$; available P (Bray) 10 $mg\ kg^{-1}$; pH 6·5] and 1 part mycorrhizal inoculum substrate (v/v; bulk density 1060 $kg\ m^{-3}$).

Inoculum substrate of *Laccaria laccata* S238-A and *Hebeloma crustuliniforme* HeCr2 consisted of mycelium cultures grown for three months on a mixture of vermiculite, peat moss and modified Melin–Norkrans solution (Marx & Kenney, 1982). Fungus-free control substrate was identically prepared but contained no fungal culture. Prior to mixing with soil, the substrate was rinsed in cool tap water to remove residual nutrient solution.

Inoculum of *Rhizopogon vinicolor* FSL788-5 was prepared by macerating sporocarps in distilled water with a blender, making a spore suspension of approximately 6×10^5 spores ml^{-1}.

At age 6 wk, one group of 400 seedlings was transplanted into tubes with soil mix containing fungus-free inoculum substrate. Half of these seedlings were inoculated by injecting 5 ml of *Rhizopogon* spore suspension into each tube. At age 8 wk, a group of 600 seedlings was transplanted into tubes with soil mix containing either *Laccaria*, *Hebeloma*, or fungus-free substrate.

Seedlings were maintained in a greenhouse for four more months under 15 h daylength. Natural light was supplemented with high-pressure sodium-vapour lamps (150 $\mu mol\ m^{-2}\ s^{-1}$ in the 400–700 nm waveband) during 4 h periods in the morning and evening. Seedlings were watered as needed to maintain soil water potential higher than about −0·05 MPa. With every fifth watering, each seedling received 15 ml of nutrient solution containing (in $mg\ kg^{-1}$ solution) 120 N (7:1, NO_3^-:NH_4^+), 20 P, 100 K, 100 Ca, 36 Mg, 64 S, and Long-Ashton micronutrient solution (Hewitt, 1966). By the end of this 4 month period, leaf expansion had ceased and terminal buds had formed. No differences between treatments were observed in timing of growth and budset.

Seedling response to drying soil

Seedling response to drying soil was evaluated by withholding irrigation and measuring stomatal con-

ductance, net photosynthesis rate, leaf water potential, and leaf osmotic potential for several days as the soil dried. To accomplish this, randomly selected seedlings were transferred to a walk-in growth chamber three days prior to the beginning of the drydown period. Growth chamber conditions were: 15 h daylength from a bank of fluorescent and incandescent lamps; photon flux density 350 μmol m^{-2} s^{-1} in the 400–700 nm waveband for 13 h per day with 1 h gradual on and off periods in morning and evenings, respectively; 26 °C day/22 °C night; 50 % RH day/80 % RH night; estimated windspeed 0·15 m s^{-1}; CO_2 concentration from 13 to 15 mmol m^{-3}, depending upon outdoor levels.

All seedlings were thoroughly watered the evening before the drydown period was begun. Aluminum foil was loosely secured over the soil surface to minimize evaporation. Preliminary data indicated transpiration could become limited after about 5 d, when bulk soil water potential decreased below about −0·15 MPa. Subsequently, the soil was allowed to dry through normal transpiration for 3 d, and measurements were taken daily thereafter for 8 d. During the measurement period, bulk soil water potential decreased at about 0·04 MPa d^{-1} for 3 d then 0·10 MPa d^{-1} for 4 d, corresponding to a range of about −0·05 MPa to −0·60 MPa.

Measurements were made on 70 seedlings from each treatment over the 8 d period. Each day, measurements were made on 6–12 plants from each treatment between 1 and 4 h before the end of the light period. Measurements were made once on each seedling.

First, stomatal conductance and net photosynthesis rate were measured using the LI-6000 Portable Photosynthesis Meter (Li-Cor, Lincoln, NE) connected to a 2 l cuvette, designed to enclose the whole plant shoot without touching the leaves. Leaf area was estimated from a conversion function based on leaf dry mass (Dosskey, Linderman & Boersma, 1990).

Leaf water potential was then measured on the excised shoot using a pressure chamber. Osmotic potential was determined by osmometer (Wescor, Logan, UT) on expressed sap from a sample of 30 frozen and rethawed needles. The osmometer values were adjusted to estimate leaf symplast osmotic potential, assuming an apoplast water content of 20 % (Joly 1984).

Bulk soil water potential was approximated by predawn soil water potential (McCoy *et al.*, 1984). To obtain soil water potential at predawn, soil water content was determined gravimetrically following removal of the shoot. This value was adjusted for pot weight loss during the day and then converted to water potential using the water release function obtained for this soil.

Seedling nutrition, growth, and colonization

Leaf nutrient concentrations were measured prior to the soil drydown experiment on twelve randomly selected seedlings from each treatment. Total N and P concentrations were determined colorimetrically (RFA Method, Alpkem, Clackamas, OR) from Kjeldahl-digested leaves. Potassium and Ca concentrations were determined by atomic absorption spectrophotometry on perchloric acid-digested leaves.

Root and shoot dry masses (65 °C, 48 h) were measured prior to the soil drydown experiment on 60 randomly selected plants from each treatment. Root systems were thoroughly washed of soil, with no attempt made to separate fungal tissue from root tissue.

Root systems of each plant used in the soil drydown experiment were thoroughly and carefully washed of soil and microscopically examined to estimate the percentage of root tips which had formed well-developed mycorrhizae. Root systems were measured manually for total length by the line-intersect method (Newman, 1966).

Statistical analysis

Data for nutrition and dry mass parameters were examined by analysis of variance. Where significant differences were found in comparisons of three treatment means, the Least Significant Difference (LSD) was used to identify dissimilar treatment means.

Data for physiological responses to drying soil were fitted to a logistic model,

$$Y = a/(1+\exp^{b+cX})+d,$$

by nonlinear regression or to a linear model. Treatment differences were examined by analysis of variance (SAS Institute Inc., Cary, NC). Physiological responses of the control treatments of the two groups behaved nearly identically in all cases, so these data were pooled. To simplify analysis and presentation, data from the three fungal treatments were compared with data for the pooled control treatment.

RESULTS

Effect of ectomycorrhizal fungi on seedling response to drying soil

Figure 1 shows that colonization by *Rhizopogon* enhanced stomatal conductance of Douglas fir seedlings by about 43 % compared to nonmycorrhizal controls at −0·05 MPa soil water potential. This effect decreased gradually as the soil dried, until it disappeared near −0·50 MPa. *Hebeloma* slightly enhanced stomatal conductance over the middle part of this soil water potential range and *Laccaria* slightly reduced stomatal conductance over the entire range.

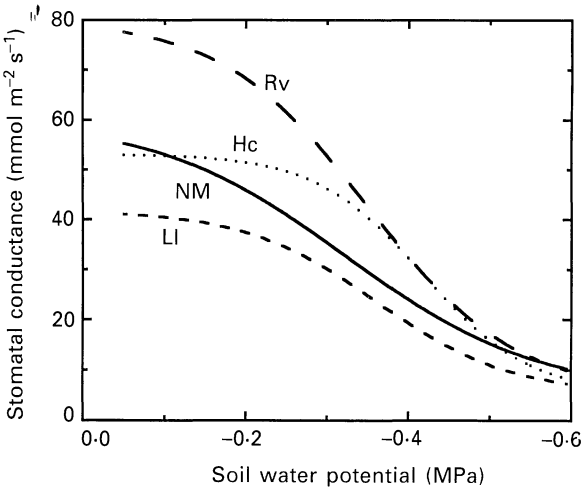

Figure 1. Stomatal conductance of mycorrhizal and non-mycorrhizal Douglas fir seedlings as a function of soil water potential. NM, non-mycorrhizal; Rv, *Rhizopogon vinicolor*; Ll, *Laccaria laccata*; Hc, *Hebeloma crustuliniforme*. Comparison of regression lines; $P < 0{\cdot}01$ for Rv × NM, LI × NM and Hc × NM.

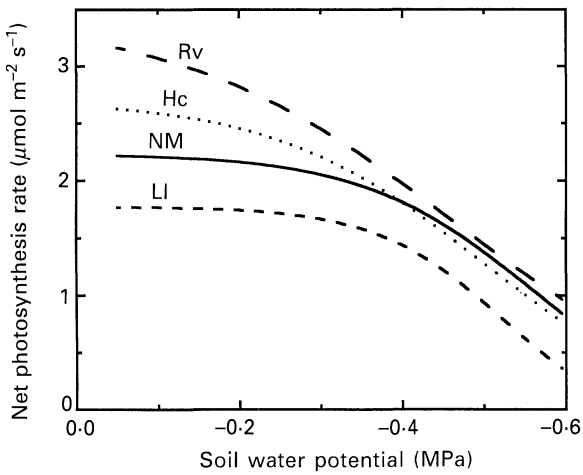

Figure 2. Net photosynthesis rate of mycorrhizal and non-mycorrhizal Douglas fir seedlings as a function of soil water potential. Legend same as Figure 1. Comparison of regression lines; $P < 0{\cdot}01$ for Rv × NM, $P < 0{\cdot}05$ for Ll × NM, non-significant for Hc × NM.

These fungi affected net photosynthesis rate in a similar manner to their effect on stomatal conductance (Fig. 2). *Rhizopogon* enhanced net photosynthesis rate by about 45% at −0·05 MPa soil water potential, an effect which decreased gradually as the soil dried and disappeared between −0·40 and −0·50 MPa. *Hebeloma* did not affect net photosynthesis rate and *Laccaria* decreased it.

Corresponding leaf water potential and osmotic potential are shown in Figure 3. Leaf water potential of *Rhizopogon*-colonized seedlings was significantly lower than non-mycorrhizal controls by 0·2 to 0·3 MPa over the soil water potential range of −0·05 to −0·40 MPa. *Hebeloma* and *Laccaria* had no effect on leaf water potential.

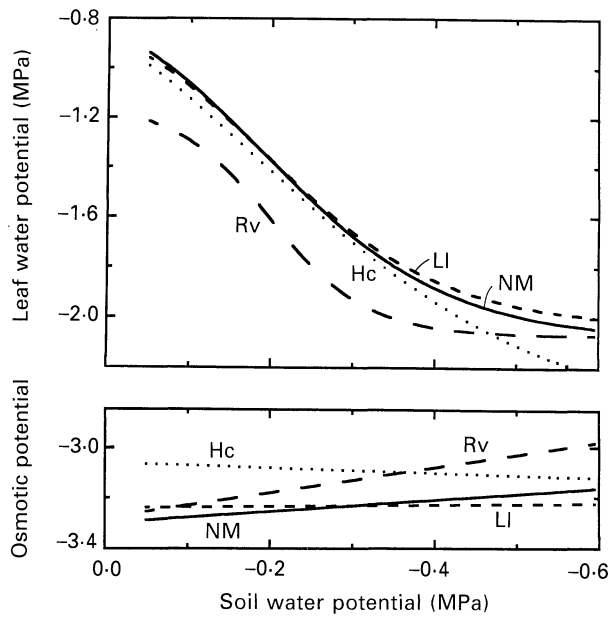

Figure 3. Leaf water potential and leaf osmotic potential of mycorrhizal and non-mycorrhizal Douglas fir seedlings as functions of soil water potential. Legends same as Figure 1. Comparison of regression lines: Leaf water potential, $P < 0{\cdot}01$ for Rv × NM, non-significant for Ll × NM and Hc × NM; Leaf osmotic potential, $P < 0{\cdot}01$ for Rv × NM and Hc × NM, non-significant for Ll × NM.

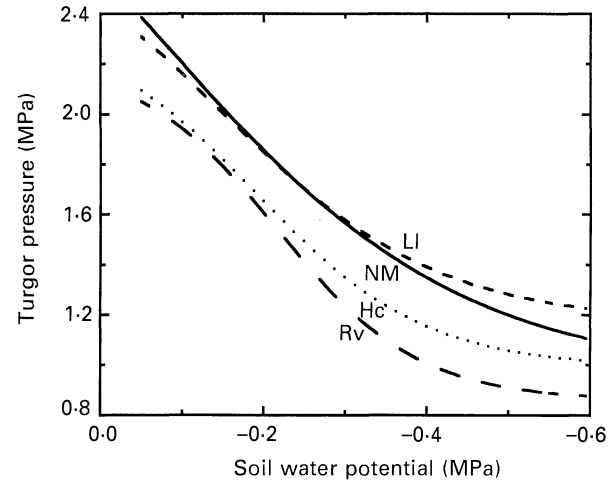

Figure 4. Leaf turgor pressure of mycorrhizal and non-mycorrhizal Douglas fir seedlings as a function of soil water potential. Legend same as Figure 1. Comparisons of regression lines; $P < 0{\cdot}01$ for Rv × NM and Hc × NM, non−significant for Ll × NM.

Leaf osmotic potential for all treatments did not change much as the soil dried from −0·05 to −0·60 MPa (Fig. 3). However, *Rhizopogon*- and Hebeloma-colonized seedings had higher osmotic potentials, by about 0·05 to 0·20 MPa, compared to non-mycorrhizal controls over this soil water potential range. *Laccaria* had no effect on osmotic potential.

Leaf turgor pressure was calculated for each seedling by the difference between leaf water po-

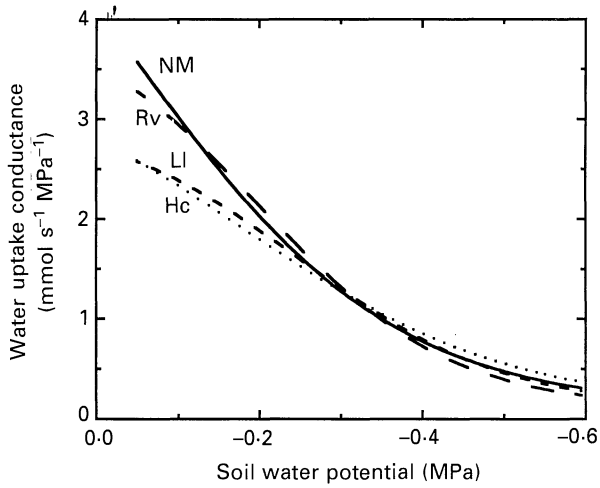

Figure 5. Water uptake conductance of mycorrhizal and non-mycorrhizal Douglas fir seedlings as a function of soil water potential. Legend same as Figure 1. Comparison of regression lines; $P < 0{\cdot}01$ for Ll × NM and Hc × NM, non-significant for Rv × NM.

tential and osmotic potential (Nobel, 1983). These results are illustrated in Figure 4. Both *Hebeloma*- and *Rhizopogon*-colonized seedlings had significantly lower leaf turgor pressure than non-mycorrhizal controls over the entire soil water potential range of −0·05 MPa to −0·60 MPa. *Laccaria* had no effect of leaf turgor.

Ability of a seedling to extract water from soil was evaluated using an index, defined here as water uptake conductance, calculated by dividing transpiration rate of the seedling (in mol s^{-1}) by the water potential difference between the bulk soil (estimated by predawn soil water potential) and the leaves. Figure 5 shows that *Laccaria* and *Hebeloma* reduced water uptake conductance of seedlings in soil wetter than about −0·20 MPa and had no effect in drier soil. *Rhizopogon* had no effect on water uptake conductance in wet or dry soil.

Table 2. *Mycorrhizal colonization and total length of roots of mycorrhizal and non-mycorrhizal Douglas fir seedlings*

Fungal treatment	Colonization (%)	Root length (cm)
Group 1		
Non-mycorrhizal	0	2079 ± 62 a
Rhizopogon vinicolor	43 ± 2	1347 ± 39 b
Group 2		
Non-mycorrhizal	0	2519 ± 83 a
Laccaria laccata	46 ± 3	2277 ± 58 b
Hebeloma crustuliniforme	85 ± 2	1720 ± 57 c

Values are means ± 1 SE. For each comparison group, values not followed by the same letter are significantly different at the $P < 0{\cdot}05$ level.

Effect of ectomycorrhizal fungi on seedling nutrition and growth

Under greenhouse conditions, neither *Rhizopogon* nor *Laccaria* affected leaf concentration of N, P, K, and Ca (Table 1). However, *Hebeloma*-colonized seedlings had significantly higher concentrations of N, P, and Ca ($P < 0{\cdot}05$) than non-mycorrhizal controls.

Ectomycorrhizal colonization did not enhance seedling growth (Table 1). *Hebeloma* greatly reduced plant dry mass ($P < 0{\cdot}05$), and *Rhizopogon* and *Laccaria* had no effect on plant dry mass.

Shoot : root dry mass ratio was greatly reduced by *Hebeloma* but not by *Rhizopogon* or *Laccaria* (Table 1). Since fungal tissue was included in root dry mass, it is likely that actual shoot : root ratios were somewhat higher than reported here. This factor could be large for *Hebeloma* and *Rhizopogon*, both of which retained abundant extramatrical hyphae on roots after removing soil.

Table 1. *Plant dry mass and leaf nutrient concentrations of mycorrhizal and non-mycorrhizal Douglas fir seedlings.*

Fungal treatment	Plant dry mass (g)	Shoot : root (g g^{-1})	Concentration in leaves (%)			
			N	P	K	Ca
Group 1						
Non-mycorrhizal	2·08 ± 0·06 a	1·52 ± 0·06 a	0·64 ± 0·03 a	0·06 ± 0·01 a	0·66 ± 0·04 a	0·33 ± 0·02 a
Rhizopogon vinicolor	1·92 ± 0·06 a	1·46 ± 0·04 a	0·71 ± 0·03 a	0·06 ± 0·01 a	0·71 ± 0·05 a	0·33 ± 0·02 a
Group 2						
Non-mycorrhizal	2·44 ± 0·06 a	1·56 ± 0·04 a	0·63 ± 0·03 a	0·08 ± 0·01 a	0·76 ± 0·08 a	0·31 ± 0·02 a
Laccaria laccata	2·53 ± 0·05 a	1·54 ± 0·03 a	0·57 ± 0·02 a	0·09 ± 0·01 a	0·69 ± 0·04 a	0·31 ± 0·02 a
Hebeloma crustuliniforme	2·01 ± 0·06 b	1·05 ± 0·02 b	0·74 ± 0·04 b	0·11 ± 0·01 b	0·82 ± 0·04 a	0·41 ± 0·02 b

Values are means ± SE. For each comparison group, values not followed by the same letter are significantly different at the $P < 0{\cdot}05$ level.

Based on visual observation of extramatrical hyphae on roots and in soil, and of adhesion of soil to roots, *Rhizopogon* and *Hebeloma* produced relatively large amounts of hyphae throughout the soil. For *Laccaria*, there was little evidence of hyphal growth into the soil.

Total root length of seedlings, including mycorrhizal branches, was significantly reduced by all three fungi (Table 2). Root lengths were 65 % of control for *Rhizopogon*, 70 % of control for *Hebeloma*, and 90 % of control for *Laccaria*.

DISCUSSION

Each ectomycorrhizal fungus affected the response of Douglas fir seedlings to drying soil in a different manner. For all fungi, however, the effect was greater in wet soil and similar in character, but attenuated, as soil water availability decreased. *Rhizopogon* had the greatest effect on seedling behaviour. *Rhizopogon* enhanced both net photosynthesis rate and stomatal conductance, but leaf water potentials were lower compared to non-mycorrhizal seedlings. *Hebeloma* tended to enhance photosynthesis and stomatal conductance, but without effect on leaf water potentials. *Laccaria*, on the other hand, decreased photosynthesis and stomatal conductance in seedlings and had no effect on leaf water potentials. The results for *Rhizopogon* and *Hebeloma* are similar to observations reported by Sands & Theodorou (1978), Levy & Krikun (1980), Allen *et al.* (1981), Stahl & Smith (1984), and Augé *et al.* (1986).

This study did not confirm the hypothesis that mycorrhizas enhance water uptake by seedlings. Under wetter soil conditions, when soil provides negligible limitation to water flow to roots (McCoy *et al.*, 1984), reduced absorbing root length may have contributed to reduced water uptake conductance. Under drier soil conditions, greater efficiency of mycorrhizal hyphae for water transport through soil to absorbing roots may have counteracted reduced root length to yield no overall effect on water uptake conductance.

Ectomycorrhizal colonization altered the relationship between leaf functions and leaf water potential. This effect was particularly striking for *Rhizopogon* where greatly enhanced net photosynthesis and stomatal conductance corresponded with significantly lower leaf water potential. Several possible mechanisms which might otherwise explain this *Rhizopogon* effect did not occur in this study. Our observations cannot be explained in terms of nutritional effects, nor effects related to large differences in plant size, or enhanced turgor through osmotic adjustment. A change in plant hormone balance is a possible explanation. Lower levels of abscisic acid- and cytokinin-like substances and higher levels of gibberellin-like substances have been associated with VAM colonization (Allen, Moore & Christensen, 1980, 1982; Edriss, Davis & Burger, 1984). However, there is no evidence that such changes are of the right combination or magnitude to cause the ectomycorrhizal effects observed in this study.

Our observations for *Rhizopogon* are consistent with the photosynthate source–sink concept. According to this hypothesis, sink–strength of the root system is increased by high demand for photosynthate by the colonizing fungus. Higher sink activity feeds back to the chloroplasts to stimulate photosynthesis rate, to which stomata respond by opening further. Greater stomatal conductance in the absence of enhanced water uptake leads to lower leaf potential. *Rhizopogon* colonization did not affect plant dry mass, even though net photosynthesis rate was much higher over at least part of the growth period (Fig. 2; see also Dosskey *et al.*, 1990). This suggests that *Rhizopogon* colonization increased the photosynthate sink strength. The additional photosynthate which was produced appears to have been exported to support the abundant fungal growth observed in the soil. It remains possible that photosynthesis was stimulated directly by mycorrhiza-induced changes in plant hormone balance. However, hormone-stimulated photosynthesis in the absence of a large fungal sink should have led to greater plant dry mass, a result not observed in this study.

Under drying soil conditions, *Rhizopogon* could continue to stimulate photosynthesis, so long as mycorrhizal sink activity was maintained, since phloem transport to active sinks is relatively unaffected by water stress (Canny, 1984). Gradually decreasing fungal activity might explain the attenuation of mycorrhizal effects as the soil dried.

It is well-established that stomatal aperture is controlled to a high degree by photosynthesis rate, although the exact mechanism of control remains controversial (Wong *et al.*, 1979; Farquhar & Sharkey, 1982; Morison, 1987). Data from our study are consistent with this concept in that, for all three mycorrhizal fungi, stomatal conductance was influenced in a similar manner to net photosynthesis rate. Through this relationship, sink-stimulated photosynthesis could translate to greater stomatal conductance.

In contrast, the data for *Hebeloma* and *Laccaria* are not entirely consistent with the photosynthate source–sink concept. Plants colonized by *Hebeloma* showed evidence of a fungal photosynthate sink based on plant growth suppression and abundant hyphal growth, but there was only slight, if any, enhancement of net photosynthesis rate and stomatal conductance. There was no evidence that *Laccaria* significantly increased the fungal photosynthate sink of its hosts. Stomatal conductance and net photosynthesis rate were reduced in *Laccaria*-colonized

plants. These apparent inconsistencies with the source–sink concept might reflect short-term changes in sink activity which were not evaluated in this study. For *Hebeloma*, there might also have been an interaction with altered plant nutrition.

While our data for *Rhizopogon* are consistent with the concept that photosynthate source-sink relations play a role in mycorrhizal effects on plant water relations, confirmation is necessary through more rigorous examination of the carbon economy of mycorrhizal plants.

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