Functional Ecology 1996
10, 662–667

Growth responses to vesicular–arbuscular mycorrhizae and elevated CO_2 in seedlings of a tropical tree, *Beilschmiedia pendula*

C. E. LOVELOCK, D. KYLLO* and K. WINTER

*Smithsonian Tropical Research Institute, PO Box 2072, Balboa, Republic of Panama and *Department of Biology, University of Missouri-St Louis, St Louis, MO 63121-4499, USA*

Summary

1. Vesicular–arbuscular (VA) mycorrhizae increased relative growth rates (RGR) of the shade-tolerant tropical tree species *Beilschmiedia pendula* at both ambient and doubled CO_2 concentrations.

2. RGR was correlated with the net assimilation rate (NAR) of plants. Within this general correlation, in plants with similar RGR, NAR was decreased in VA-mycorrhizal plants compared with non-mycorrhizal plants. As RGR is the product of NAR and the leaf area ratio (LAR, the ratio of leaf area to plant mass), increases in RGR in VA-mycorrhizal plants were the results of increased LAR. Thus, VA-mycorrhizae increased growth rates of *B. pendula* by altering the morphology of the seedlings.

3. Under elevated CO_2 the amount of fungus within roots increased in VA-mycorrhizal plants compared with those grown under ambient CO_2 and this was associated with a greater post-inoculation depression in leaf growth. Post-inoculation depressions in leaf growth and the lower NAR (in plants with similar RGR) of VA-mycorrhizal plants indicate there is increased carbon transfer to soils under elevated CO_2.

Key-words: Elevated CO_2, plant-growth analysis, tropical forests, VA-mycorrhizae

Functional Ecology (1996) **10**, 662–667

Introduction

The formation of mycorrhizal symbioses between plant roots and vesicular–arbuscular (VA) fungi has been shown to improve the growth and survivorship of tropical tree species and may influence forest succession (Janos 1980). VA-mycorrhizae increase plant growth by improving phosphate nutrition (Koide 1991). More recent studies have shown VA-mycorrhizae also influence the accumulation of toxic ions, concentrations of compounds that influence defences against leaf herbivores, susceptibility to root pathogens and probably plant water relations (Newsham, Fitter & Watkinson 1995). In addition, there is evidence that VA-mycorrhizae increase growth of plants by altering their biomass allocation patterns (Baas, van der Werf & Lambers 1989; Tinker, Durall & Jones 1994). The study of Baas *et al.* (1989) found that increased growth of VA-mycorrhizal *Plantago major* plants was associated with an increased proportion of the plant biomass as leaves (leaf area ratio, LAR), thereby increasing the potential for carbon gain and growth. They found that increased carbon allocation to leaves had more influence over plant growth than did increases in net carbon assimilation rate calculated on a leaf area basis (NAR). In tree species of tropical forests it is not known whether VA-mycorrhizae influence plant growth by improving phosphorus nutrition and net assimilation rates or by increasing the carbon allocation to plant leaves. In this study we aimed to determine whether VA-mycorrhizae improve growth of tropical tree seedlings through (1) altering biomass allocation patterns and/or (2) increasing the net assimilation rate through increasing leaf phosphate concentrations and net photosynthetic rates.

Growth under elevated atmospheric CO_2 concentrations influences plant morphology and nutrient status (Norby & O'Neill 1991) and also the interactions of plants with their root micro-organisms (D'ıas *et al.* 1993). Because of the importance of tropical forests to the global carbon budget (Dixon *et al.* 1994), and because most tropical forest tree species have VA-mycorrhizae (Redhead 1980), we also wished to determine how growth under elevated CO_2 concentrations alters the factors contributing to increased growth of VA-mycorrhizal tree seedlings.

Materials and methods

Seedlings of *Beilschmiedia pendula* (Sw.) Hemsl. (Lauraceae), a common shade-tolerant species of humid forests of Panama, were grown without VA-mycor-

rhizae (controls) or inoculated with VA-mycorrhizae for 20 weeks in large pots (15 litres) of sterilized forest soil in four open-top chambers in a forest clearing on Barro Colorado Island, Panama (9° 10'N 79° 51'W). The soil used was a mix of red clay soil, obtained from 30–100 cm below the soil surface close to the laboratories, and washed river sand (two parts soil to one part sand). Soil from a similar depth from another location on the Island was found to have very low nutrient concentrations, approximately 0·2 g kg^{-1} phosphorus, 1·1 g kg^{-1} nitrogen, 0·3 g kg^{-1} sulphur and 3·0 g kg^{-1} carbon (Yavitt *et al.* 1993).

VA-mycorrhizal inoculum was obtained from a mix of forest soil and feeder roots of the palm *Oenocarpus panamanus*. This inoculum was chosen because it has provided high levels of infection (Janos 1980; D. Kyllo, unpublished data). All soil and half the inoculum were sterilized using methyl-bromide gas. To ensure similar carbon addition to each pot, plants were either inoculated with sterilized or unsterilized inoculum. In order to reintroduce soil bacteria to the controls a solution of the unsterilized inoculum filtered through a fine mesh (40 μm) to remove fungal spores was added. Plants were watered daily. Three times a week 50 ml of dilute nutrient solution (1/5 strength Hoaglands solution), that either included phosphate or was phosphate free was added to each pot after watering. Plants were randomly assigned to open-top growth chambers arranged in two blocks across the clearing and exposed to ambient air (two chambers where CO_2 concentrations varied between 350 and 400 μl l^{-1}), or air in which the CO_2 concentration had been doubled (two chambers where CO_2 concentrations were 790 ± 70 μl l^{-1}). Photon flux densities within the chambers ranged between 4 and 10 mol m^{-2} day^{-1} depending on cloud conditions. Leaf temperature varied between 24 and 36 °C and air temperature between 25 and 33 °C. Relative humidity within the chambers was ambient (approximately 80%).

During the experiment growth of leaf area was measured approximately every 2 weeks by tracing leaf areas for each plant. At the end of the experiment plants were harvested and sub-samples of the roots were checked for the extent of VA-mycorrhizae infection. Infection was scored using the following classes: 0 (0%), 1 (0–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), 5 (76–100%). Differences in the extent of infection were assessed using a Kruskal–Wallis statistical test.

Average relative growth rate (RGR) was calculated as $(\ln W_2 - \ln W_1)/(t_2 - t_1)$ where W_2 and W_1 are the dry masses at the end and the beginning of the experiment respectively, and $t_2 - t_1$ is the duration of the experiment in days. Plant dry mass at the beginning of the experiment was 0·465 ± 0·074 ($n = 10$ plants) and $t_2 - t_1$ was 144 days. Net assimilation rate (NAR) was calculated as $[(W_2 - W_1)/(t_2 - t_1)]/[LA_2 - LA_1)/(\ln LA_2 - \ln LA_1)]$ where LA_2 and LA_1 are the leaf area at the end and the beginning of the experiment respectively.

Samples for phosphorus (P) analysis were taken from plants in one pair of chambers. Leaves were dried at 60 °C for at least 48 h, ground and analysed at the University of Würzburg (Germany) using an ICP spectrometer (JY 70 Plus, ISA, München, Germany). Measurements of net photosynthesis were made under growth conditions with a portable photosynthesis measuring system (CI-301PS, CID Inc., Vancouver, WA) in the closed mode on a single leaf per plant with a 0·5-l leaf chamber. Net photosynthesis was measured three times during the experiment and averaged over the 3 days.

Data were analysed by ANOVA. VA-mycorrhizae, phosphate fertilization and CO_2 concentrations were considered as fixed effects and blocks as a random effect. Replication for VA-mycorrhizae and phosphate fertilization was five plants. Because there were only two blocks, replication for the CO_2 effect was two. Thus tests of significance for the effects of VA-mycorrhizae and phosphate fertilization and their interactions were stronger than those used to test for an effect of CO_2. Simple linear regressions were fitted to describe the relationship between RGR and NAR for VA-mycorrhizal plants under elevated and ambient levels of CO_2. An F test for overall differences between regression lines for VA-mycorrhizal and non-mycorrhizal plants was performed (Snedecor & Cochran 1980, p. 385).

Results

Phosphate fertilizer had no influence on the growth of seedlings or photosynthetic rates (Tables 1 and 2). Because of this, plots of leaf area and plant biomass are combined over phosphate treatments. Growth of leaf area after inoculation with VA-mycorrhizae was initially depressed compared with controls, particularly under elevated CO_2 (Fig. 1). However, by the second half of the experiment, leaf growth of VA-mycorrhizal plants was proceeding at a faster rate than in non-mycorrhizal plants. Leaf growth rates were increased under elevated CO_2 in both VA-mycorrhizal and non-mycorrhizal plants.

By the end of the experiment biomass of VA-mycorrhizal plants was greater than that of non-mycorrhizal plants (Fig. 2). Elevated CO_2 increased biomass in both VA-mycorrhizal and non-mycorrhizal plants (Fig. 2). Measures of carbon allocation between roots and shoots showed that VA-mycorrhizal plants had a lower proportion of their total biomass as root tissue under both elevated and ambient CO_2 (Fig. 2). Inspection of sub-samples of roots at the completion of the experiment showed that plants grown without VA-mycorrhizae did not have fungi within the roots. In VA-mycorrhizal plants, those growing under elevated CO_2 had levels of fungi within the roots that were greater than in plants grown under ambient CO_2. The average infection class for VA-mycorrhizal plants grown under ambient levels of CO_2 was 2·28, while for plants grown under elevated CO_2 was 3·19 (Kruskal–Wallis statistic = 5·04, differences significant at $P < 0·05$).

Average relative growth rates (RGR) of plants over

Table 1. Results of ANOVA of relative growth rate (RGR, mg g^{-1} d^{-1}), net assimilation rate (NAR, g m^{-2} day^{-1}), leaf area ratio (LAR, m^2 kg^{-1}), specific leaf weight (SLA, m^2 kg^{-1}) and leaf weight ratio (LWR, g g^{-1}). Seedlings of *Beilschmiedia pendula* were either grown under ambient or elevated levels of CO_2 (CO_2), with or without VA-mycorrhizae (VAM) and with or without phosphate fertilizer (P). For LWR a square-root transformation of the data was used to satisfy the constant variance criteria of ANOVA models. The denominator for the *F* ratio was the Block × ANOVA term

	ANOVA term	MS error	df	*F*	*P*
RGR	CO_2	124·3	1	4·54	0·28
	VAM	25·8	1	1356	0·017
	P	9·76	1	1·13	0·48
	CO_2 × VAM	4·21	1	6·50	0·24
	CO_2 × P	0·653	1	0·0469	0·86
	VAM × P	39·1	1	2·60	0·35
	CO_2 × VAM × P	4·98	1	1·98	0·40
NAR	CO_2	3·23	1	4·33	0·29
	VAM	0·474	1	39·88	0·10
	P	0·410	1	0·744	0·55
	CO_2 × VAM	0·0279	1	0·249	0·71
	CO_2 × P	0·00741	1	0·0278	0·90
	VAM × P	1·24	1	2·82	0·34
	CO_2 × VAM × P	0·418	1	1·32	0·46
LAR	CO_2	2·03	1	11·5	0·18
	VAM	49·9	1	398·6	0·032
	P	1·72	1	15·8	0·16
	CO_2 × VAM	1·18	1	0·469	0·62
	CO_2 × P	0·00441	1	0·0227	0·91
	VAM × P	1·14	1	1·24	0·47
	CO_2 × VAM × P	0·942	1	1·63	0·42
SLA	CO_2	88·6	1	5·87	0·25
	VAM	8·42	1	3006	0·012
	P	0·298	1	13·52	0·17
	CO_2 × VAM	2·89	1	1·09	0·46
	CO_2 × P	0·788	1	0·893	0·52
	VAM × P	8·96	1	17·96	0·15
	CO_2 × VAM × P	8·37	1	7·14	0·23
LWR	CO_2	0·0147	1	5·17	0·26
	VAM	0·0592	1	419·0	0·031
	P	0·00416	1	195·4	0·046
	CO_2 × VAM	0·00602	1	3·04	0·33
	CO_2 × P	0·000481	1	0·364	0·65
	VAM × P	0·000326	1	0·552	0·59
	CO_2 × VAM × P	0·000256	1	2·36	0·37

the 20 weeks of the experiment were not influenced by fertilization with P (Tables 1 and 2), but were influenced by VA-mycorrhizae (a mean increase of 8·2% in normal CO_2 and 16·9% in elevated CO_2) and the CO_2 concentration at which they were grown (Tables 1 and 2). Enhancement in RGR as a result of elevated CO_2 was not statistically significant (Table 1) owing to the low level of replication for CO_2. Mean RGR was increased by growth under elevated CO_2 by 37·5% in control plants and 48·5% in VA-mycorrhizal plants (Table 2).

By examining trends in NAR and LAR it is possible to determine the relative importance of each in determining plant RGR. Mean NAR was decreased in VA-mycorrhizal plants compared with control plants and was greater in plants grown at elevated CO_2 compared with those grown at ambient CO_2, although the CO_2 effect was not significant (Table 1). Net assimilation rate (NAR; also called unit leaf rate), which is a measure of the efficiency of the assimilatory organs in producing new growth, was not influenced by P fertilization (Tables 1 and 2).

In contrast to NAR the leaf area ratio (LAR; the proportion of leaf area per dry weight of plant) was greater in VA-mycorrhizal plants compared with controls (Table 2). Growth under elevated CO_2 and P fertilization tended to reduce LAR (Table1). The LAR is the product of the leaf weight ratio (LWR; the proportion of the plant weight as leaves) and the specific leaf area (SLA; the leaf area per g dry weight of leaves). LWR was increased in VA-mycorrhizal plants as was SLA (Table 2). Elevated CO_2 had little influence on the LWR but tended to reduce SLA. Fertilization with P had a positive influence on SLA and a negative influence on LWR, thus resulting in little change in the resultant LAR.

RGR was highly correlated with NAR in all plants (Fig. 3) but the regression between RGR and NAR differed between VA-mycorrhizal plants and controls (ambient CO_2, $F_{6,31}=3·44$, $P<0·025$; elevated CO_2,

Table 2. Mean and standard errors of relative growth rate (RGR, mg g^{-1} day^{-1}), net assimilation rate (NAR, g m^{-2} day^{-1}), leaf area ratio (LAR, m^2 kg^{-1}), specific leaf weight (SLA, m^2 kg^{-1}), leaf weight ratio (LWR, mg g^{-1}), net photosynthesis (μmol m^{-2} s^{-1}) and leaf phosphorus concentrations for seedlings of *Beilschmiedia pendula* grown under ambient or elevated levels of CO_2. Seedlings were grown with or without VA-mycorrhizae (VAM) and with or without phosphate fertilizer (P)

	Ambient CO_2				Elevated CO_2			
	–VAM		+VAM		–VAM		+VAM	
	–P	+P	–P	+P	–P	+P	–P	+P
RGR (mg g^{-1} day^{-1})	9·43 ± 0·99	9·31 ± 1·20	9·1 ± 1·5	11·0 ± 1·2	12·2 ± 1·2	11·0 ± 1·3	12·1 ± 1·2	14·4 ± 0·8
NAR (g m^{-2} day^{-1})	1·38 ± 0·18	1·41 ± 0·24	1·06 ± 0·19	1·34 ± 0·14	1·92 ± 0·19	1·70 ± 0·20	1·43 ± 0·13	1·91 ± 0·20
LAR (m^2 kg^{-1})	7·21 ± 0·61	6·97 ± 0·36	8·49 ± 0·54	8·20 ± 0·43	6·39 ± 0·21	6·54 ± 0·35	8·57 ± 0·33	7·92 ± 0·42
SLA (m^2 kg^{-1})	17·57 ± 0·70	17·5 ± 0·4	18·7 ± 0·6	18·7 ± 0·9	14·9 ± 0·5	16·7 ± 0·6	16·5 ± 0·6	15·5 ± 0·5
LWR (mg g^{-1})	451 ± 38	400 ± 21	457 ± 32	446 ± 24	433 ± 24	393 ± 16	520 ± 10	509 ± 20
Net photosynthesis (μmol m^{-2} s^{-1})	4·82 ± 0·37	6·21 ± 0·75	6·78 ± 0·82	5·98 ± 0·58	5·86 ± 0·72	6·83 ± 0·81	8·18 ± 0·59	9·90 ± 0·89
Leaf P concentration (mg m^{-2})	52 ± 11	52 ± 15	53 ± 8	64 ± 14	59 ± 16	40 ± 7	63 ± 7	74 ± 8

$F_{2,35}=8{\cdot}06$, $P<0{\cdot}005$). VA-mycorrhizal plants had a steeper regression of the RGR–NAR curve than non-mycorrhizal plants (Fig. 3). Because RGR is a product of NAR and LAR, the increase in the slope of the RGR–NAR curve is mainly the result of increased LAR in VA-mycorrhizal plants that counteracts slight reductions in NAR by VA-mycorrhizae (Table 2).

Average net photosynthetic rates were unaffected by fertilization with phosphate but were increased in VA-mycorrhizal plants and under elevated CO_2 concentrations (Table 2). Concentrations of P within plant leaves were also largely unaffected by fertilization with P (Table 2). Leaf P concentrations were increased in VA-mycorrhizal plants compared with non-mycorrhizal plants. In non-mycorrhizal plants P concentrations were slightly reduced in plants growing under elevated CO_2 (Table 2). RGR and NAR showed no correlation with P concentrations within leaves, net photosynthetic rates, LAR or SLA.

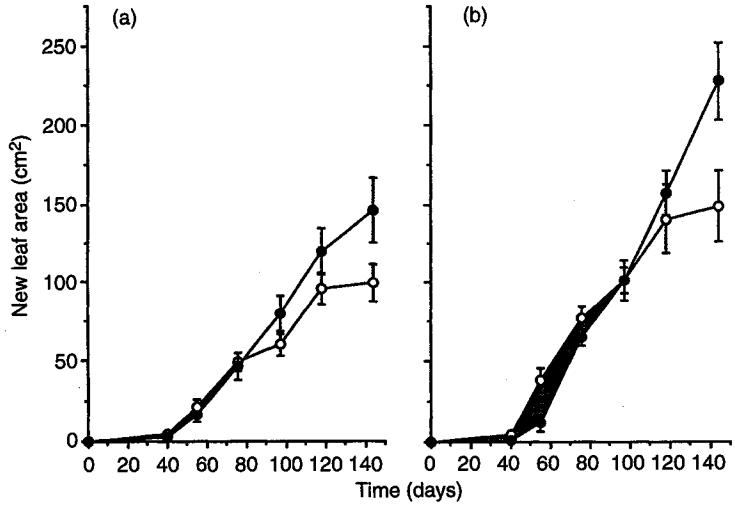

Fig. 1. Mean and standard error of new leaf area grown over time for VA-mycorrhizal (closed symbols) or non-VA-mycorrhizal plants (open symbols) growing in (a) ambient or (b) elevated CO_2. Shaded areas indicate the difference in leaf growth between VA-mycorrhizal and non-mycorrhizal plants following inoculation. Initial leaf areas (cm^2) were: ambient CO_2, –VAM, 42·9±6·3; ambient CO_2, +VAM, 52·3±5·2; elevated CO_2, –VAM, 51·3±5·0; elevated CO_2, +VAM, 64·1±9·8. Final (day 144) leaf areas of the initial leaves were: ambient CO_2, –VAM, 40·4±5·5; ambient CO_2, +VAM, 46·0±5·7; elevated CO_2, –VAM, 42·7±4·2; elevated CO_2, +VAM, 51·3±6·2.

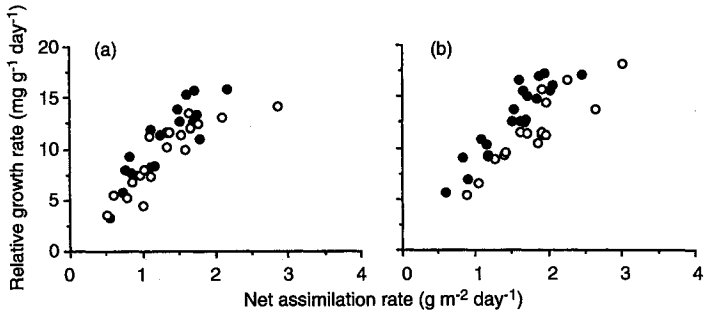

Fig. 3. Relative growth rates (RGR) of *Beilschmiedia pendula* as a function of net assimilation rate (NAR) under (a) ambient and (b) elevated CO_2 concentrations. Open circles are plants grown without VA-mycorrhizae (–VAM) and closed circles are plants grown with VA-mycorrhizae (+VAM). Regression equations are: ambient CO_2, –VAM, RGR=3·758+4·033×NAR ($r^2=0{\cdot}593$); ambient CO_2, +VAM, RGR=1·204+7·351×NAR ($r^2=0{\cdot}847$); elevated CO_2, –VAM, RGR=1·3479+5·682×NAR ($r^2=0{\cdot}783$); elevated CO_2, +VAM, RGR=2·183+6·954×NAR ($r^2=0{\cdot}828$).

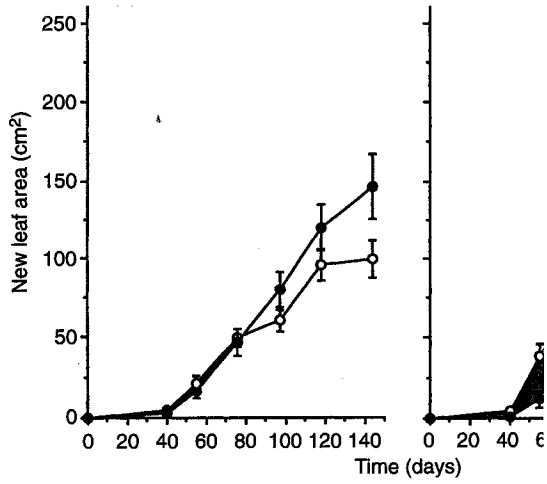

Fig. 2. Biomass accumulation and the proportion of biomass as roots or shoots (leaves and stems). Plants were either VA-mycorrhizal (solid bars), or non-mycorrhizal and grown under either ambient (left) or elevated CO_2 (right). Means and standard errors were obtained from 10 plants for the initial biomass, and 20 plants per treatment for the final estimate of biomass. A different letter after the mean indicates a difference from other means of root biomass or shoot biomass using a Scheffe post hoc test at $P<0{\cdot}05$.

Discussion

Despite a final increase in biomass and leaf area in VA-mycorrhizal plants compared with those that were non-mycorrhizal (Figs 1 and 2) VA-mycorrhizae initially caused a depression in leaf growth (Fig. 1). Post-inoculation depression in leaf growth has been observed in other species and has been attributed to the carbon cost of fungal growth when the symbiosis is established (Bethlenfalvay 1982). There was a greater post-inoculation depression of leaf growth in plants growing under elevated CO_2, compared with ambient CO_2 levels, which was associated with increased levels of VA-mycorrhizae infection. Higher levels of fungus within roots under elevated CO_2 may indicate more carbon is utilized for fungal growth at elevated CO_2 than at ambient CO_2 levels. Higher levels of fungal infection have also

been observed in Pine roots with ectomycorrhizal symbionts (Ineichen, Wiemken & Wiemken 1995). This is probably because of enhanced root carbohydrate concentrations in plants growing under elevated CO_2 and thus increased substrate availability for fungal growth and respiration (Baas *et al.* 1989; Ineichen *et al.* 1995; Sachar-Hill *et al.* 1995).

Fertilization with P had little effect on RGR (Table 1). *Beilschmiedia pendula* is similar to other tropical tree species within the Laurales and Magnoliales in that it has few fine roots and no root hairs (St John 1980). Thus without a VA-mycorrhizal symbiont, the root morphology of *B. pendula* and of many other tropical species limits their ability to explore for available nutrients within the soil (Koide 1991).

Despite low P concentrations within leaves of non-mycorrhizal plants, these plants grew more under elevated CO_2 than ambient CO_2 (Table 2) indicating that growth enhancements are possible under elevated CO_2 even when nutrient concentrations are low. Conroy *et al.* (1988) also found that growth was enhanced in conifers under elevated CO_2 despite P deficiencies. However, growth enhancements owing to elevated CO_2 were greater in plants with sufficient P.

In many studies nutrient concentrations of leaf tissue are reduced under elevated CO_2 (Bazzaz 1990; Ceulemans & Mousseau 1994). Similar to the study of Conroy *et al.* (1990) with ectomycorrhizal Pines, VA-mycorrhizal plants grown under elevated CO_2 in the current study did not have reduced leaf P concentrations (Table 2). This may occur because under elevated CO_2 plants are generally bigger and able to explore a greater soil volume than plants grown at ambient levels of CO_2. Alternatively, elevated CO_2 may have altered the fungal composition to favour symbionts with more efficient phosphate uptake systems (proposed by Conroy *et al.* 1990) or phosphate uptake may be increased because of increased levels of carbohydrate available as a substrate for nutrient uptake processes.

RGR over all treatments was correlated with NAR (Fig. 3). RGR and NAR were also correlated in *P. major* exposed to elevated CO_2, with increases in RGR and NAR under elevated CO_2 owing to increased photosynthetic rates (Poorter, Pot & Lambers 1988). Within this general correlation, VA-mycorrhizal plants had a steeper slope (Fig. 3). Thus at any given RGR, VA-mycorrhizal plants had a reduced NAR compared with non-mycorrhizal plants. A similar observation was made by Baas *et al.* (1989) in VA-mycorrhizal *P. major* fertilized with phosphate.

Decreases in NAR are generally associated with reduced resource availability (Chiariello, Mooney & Williams 1989) and also stress (e.g. Ball & Pidsley 1995 for salinity stress). This is probably not the case in this experiment because plants were well watered and VA-mycorrhizal plants had generally higher leaf P concentrations and higher photosynthetic rates than non-mycorrhizal plants. Lower NAR in VA-mycorrhizae at any particular RGR probably represents the carbon cost associated with VA-mycorrhizae. In the study of Baas *et al.* (1989) decreases in NAR were found to be partially correlated with increased root respiration in mycorrhizal plants. By using regression equations of RGR as a function of NAR (Fig. 3) it is possible to estimate the magnitude of the decrease in NAR at any particular RGR associated with the VA-mycorrhizae. Under ambient CO_2 where RGR was approximately $10\,mg\,g^{-1}\,day^{-1}$, the VA-mycorrhizae resulted in a 23% reduction in NAR. At elevated CO_2 where growth rates were approximately $12\,mg\,g^{-1}\,day^{-1}$ the reduction in NAR associated with the VA-mycorrhizae was 33%. In general, the proportional reduction in NAR associated with the VA-mycorrhizae increases as growth rates increase. The estimates of carbon allocated to the VA-mycorrhizae under ambient CO_2 are consistent with estimates of the carbon cost of sustaining a VA-mycorrhizal symbiosis observed in other species (Tinker *et al.* 1994).

Despite decreases in the NAR in VA-mycorrhizal plants compared with non-mycorrhizal plants with similar growth rates, RGRs were on average greater than those of non-mycorrhizal plants. This suggests there is a compensatory response in VA-mycorrhizal plants for carbon cost of the symbiosis. Compensation for reduced NAR in mycorrhizal plants occurred largely through an increase in LAR (Table 2, Fig. 3). This has also been observed in *P. major* (Baas *et al.* 1989), Leek (Snellgrove *et al.* 1982) and Soybean (Harris, Pacovsky & Paul 1985). The average increase in LAR owing to VA-mycorrhizae was approximately 17% at ambient CO_2 concentrations and 27% at elevated CO_2 concentrations. These are smaller increases than observed in agricultural species (Snellgrove *et al.* 1982; Harris *et al.* 1985; Baas *et al.* 1989). As low LAR ratios are often associated with stress tolerance (Kitajima 1994 for shade tolerance; Ball & Pidsley 1995 for salinity tolerance) smaller increases in LAR owing to VA-mycorrhizal infection in *B. pendula* compared with agricultural species may reflect greater shade tolerance of *B. pendula*.

LAR is the product of LWR and SLA, both of which were increased in VA-mycorrhizal plants (Table 2). LWR was increased to a greater extent in VA-mycorrhizal plants than SLA and was thus the major cause of increased LAR. LWR was increased by approximately 13% in VA-mycorrhizal plants grown in ambient levels of CO_2 and 24% in plants growing at elevated CO_2 while SLA was increased in VA-mycorrhizal plants by 6% at ambient CO_2 and 2% at elevated CO_2. Thus, growth at elevated CO_2 tended to decrease SLA as has been observed in other species (Norby & O'Neill 1991; Farnsworth & Bazzaz 1995), therefore counteracting the positive influence of VA-mycorrhizae. Increased LWR in VA-mycorrhizal plants may be a response to improved water relations, or owing to hormonal signals from the fungus enhancing cell wall elasticity, or possibly the result of altered carbohydrate source-sink relationships.

LAR has been shown to be the most important factor

in determining growth rates among different species (Poorter & Remkes 1990; Kitajima 1994; but see Ball & Pidsley 1995 for an exception). For example, fast-growing pioneer tropical forest species have high LAR, while slower-growing shade tolerant species have low LAR (Kitajima 1994). In the study of Kitajima (1994) the relative differences in LAR among the tropical species were maintained over a wide range of light environments. For example, fast-growing species grew faster than other species under both high and low light levels owing to a greater LAR. Our analysis indicates that differences in NAR among individuals of the same species is the most important factor in determining differences in growth over a wide range of conditions. Interestingly, within this general pattern, differences in growth between VA-mycorrhizal and non-mycorrhizal plants were associated with increases in LAR. That is, in plants with similar NAR, VA-mycorrhizal plants grow faster because of increased LAR relative to non-mycorrhizal plants. VA-mycorrhizae therefore changes seedling morphology in a way that is usually associated with faster growing species.

Acknowledgements

We wish to thank Monica Meijia, Milton Garcia, Juan Posada, Isaac Quintero and Aurelio Virgo for their assistance during the experiment, and Dr Joe Wright and two reviewers for their helpful comments. The Sonderforschungsbereich 251 (University of Würzburg) provided facilities for mineral element analysis and we are grateful to F. Reisberg for performing these measurements. This study was supported by the Mellon Foundation.

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Received 7 December 1995; revised 14 March 1996; accepted 26 March 1996