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Effects of phosphorus availability and vesicular–arbuscular mycorrhizas on the carbon budget of common bean (*Phaseolus vulgaris*)

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SUMMARY

Low phosphorus availability is often a primary constraint to plant productivity in native soils. Here we test the hypothesis that root carbon costs are a primary limitation to plant growth in low P soils by assessing the effect of P availability and mycorrhizal infection on whole plant C budgets in common bean (*Phaseolus vulgaris* L.). Plants were grown in solid-phase-buffered silica sand providing a constant supply of low (1 μM) or moderate (10 μM) P. Carbon budgets were determined weekly during the vegetative growth phase. Mycorrhizal infection in low-P plants increased the root specific P absorption rate, but a concurrent increase in root respiration consumed the increased net C gain resulting from greater P uptake. The energy content of mycorrhizal and non-mycorrhizal roots was similar. We propose that the increase in root respiration in mycorrhizal roots was mainly due to increased maintenance and growth respiration of the fungal tissue. Plants grown with low P availability expended a significantly larger fraction of their total daily C budget on below-ground respiration at days 21, 28 and 35 after planting (29–40 %) compared with plants grown with moderate P supply (18–25 %). Relatively greater below-ground respiration in low P plants was mainly a result of their increased root:shoot ratio, although specific assimilation rate was reduced significantly at days 21 and 28 after planting. Specific root respiration was reduced over time by low P availability, by up to 40 %. This reduction in specific root respiration was due to a reduction in ion uptake respiration and growth respiration, whereas maintenance respiration was increased in low-P plants. Our results support the hypothesis that root C costs are a primary limitation to plant growth in low-P soils.

Key words: Carbon budget, *Phaseolus vulgaris* L. (common bean), phosphorus efficiency, root respiration, vesicular–arbuscular mycorrhiza.

INTRODUCTION

Suboptimal phosphorus availability is a primary limitation to plant growth over much of the earth's land surface. Phosphorus deficiency is often difficult to correct agronomically because P binds to several soil constituents in forms of limited availability to plants (Fixen & Grove, 1990). For example, it has been estimated that > 50 % of the beans grown in Latin America are grown in low-P soils (CIAT, 1987). Phosphorus-deficient plants exhibit retarded growth and an increase in the ratio of roots to shoots (Anghinoni & Barber, 1980; Bougher, Grove & Malajczuk, 1990). It has been hypothesized that the reduction of bean growth under low-P availability is primarily due to increased below-ground biomass partitioning and reduced rate of leaf appearance, rather than to altered leaf photosynthesis (Lynch, Läuchli & Epstein, 1991; Lynch & Beebe, 1995).

A general observation in P-deficient plants is that photosynthesis is diminished (Fredeen *et al.*, 1990; Qiu & Israel, 1992; Halsted & Lynch, 1996). Qiu & Israel (1992) observed accumulated starch concen-

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trations in leaves and stems, restricted starch utilization in the dark, and growth processes that were more restricted than photosynthetic capacity. They suggested that more efficient carbohydrate utilization in roots might be associated with greater root growth relative to shoot growth in P-deficient plants.

Roots of P-deficient plants are often thinner and have a higher specific root length (Christie & Moorby, 1975; Anghinoni & Barber, 1980) and greater mycorrhizal colonization (Stribley, Tinker & Snellgrove, 1980; Graham, Leonard & Menge, 1981) than P-sufficient plants. Mycorrhizas have been found to enhance P uptake resulting in increased plant growth. This might result from a better distribution of the absorbing surface as suggested by Cooper (1984), i.e. greater length of absorbing tissue (root and fungal hyphae), higher P inflow rates (Gianinazzi-Pearson & Gianinazzi, 1983; Jakobsen, 1986) and higher P-use efficiency (Koide, 1991). Conversely, mycorrhizal infection alters belowground C allocation (Jakobsen & Rosendahl, 1990; Eissenstat *et al*., 1993). Peng *et al*. (1993) observed increased specific root/soil respiration in mycorrhizal *Citrus*. They attributed this to increased accumulation of lipid-rich roots, greater root biomass and increased maintenance and growth respiration of the fungal tissue.

The main objective of this study was to evaluate if the observed reduction in relative growth rate (RGR) in P-deficient plants is caused primarily by an increased C loss to root respiration and if this proposed relative increase is due to the increased root:shoot ratio. Our secondary objective was to compare C budgets for mycorrhizal and non-mycorrhizal plants grown under contrasting P regimes, specifically to assess the root and shoot respiratory costs.

MATERIALS AND METHODS

Plant material

Bean (*Phaseolus vulgaris* L.) seeds of the CIAT breeding line DOR-364 were obtained from CIAT (Cali, Colombia). This Mesoamerican genotype has an indeterminate bush habit, erect stems and small dark brown seeds. In field studies the genotype has been characterized as P-inefficient yet responsive to P fertilization (D. Beck, pers. comm.). Seeds were surface-sterilized in 7 mM NaOCl and 0·1 % Triton® X-100 (Sigma Chemical Co., St. Louis, MO, USA) for 10 min, then germinated in 0·5 mM $CaSO_4$ for 36 h at 25 °C. The seedlings were then planted at a depth of 3 cm. Planting as well as gas-exchange measurements and destructive harvests of duplicate plants were staggered two days, giving a total of six replicates per treatment.

Growth conditions

The plants were grown in a glasshouse in University Park, PA, USA, in March and April 1996. Temperature ranged from a maximum of 28 °C (day) to a minimum of 20 °C (night). Natural light was supplemented from 0900–1100 hours and 1500–1700 hours with an average photosynthetic photon flux density of 100 μmol photons m^{-2} s^{-1}, and from 1100–1500 hours with an average of 200 μmol photons m^{-2} s^{-1} with metal halide lamps. Maximum midday photosynthetic photon flux densities reached 1400 μmol photons m^{-2} s^{-1} on clear days and 500 μmol photons m^{-2} s^{-1} on days with heavy cloud cover.

Plants were grown in PVC tubes (300-mm long, 76-mm inner diameter, 1·4-l volume) filled with solid-phase-buffered silica sand (Lynch *et al*., 1990) providing a constant availability of low (1 μM) or moderate (10 μM) P. Twice daily (0700 and 1400 hours), the pots were irrigated with nutrient solution containing (in mM) 3·1 NO_3^-, 1·8 K^+, 1·2 Ca^{2+}, 1·4 SO_4^{2-}, 1·0 NH_4^+, 0·825 Mg^{2+}, 0·05 Cl^-, 0·005 Fe-EDTA, 0·002 B, 0·0015 Mn^{2+}, 0·0015 Zn^{2+}, 0·000143 Mo, and 0·0005 Cu^{2+} as well as the concentration of KH_2PO_4 as described above.

Sand substrate in the top 15 cm of inoculated pots was evenly mixed with a surplus of root debris of sudan grass (*Sorghum bicolor* L.) with spores of *Glomus intraradices* Schenck & Smith (INVAM isolate UT143–2). A spore-less bacterial wash from the inoculum described above was applied to non-inoculated pots to provide comparable soil microorganism inoculum (Koide & Li, 1989).

Gas exchange measurements

Shoot CO_2 exchange rates were measured with a portable infra-red gas analyser (LI-COR 6200, LI-COR, Lincoln, NE, USA). To estimate the daily shoot C flux, measurements were taken four times throughout the day. Net photosynthesis was measured mid-morning (0930–1030 hours), noon (1130–1230 hours), and mid-afternoon (1530–1630 hours). Shoot respiration was measured *c*. 2 h after sunset (2030–2130 hours). Numerical analysis was used to integrate shoot photosynthesis measurements into daily shoot CO_2 assimilation and shoot respiration (Lynch & Rodriguez, 1994). Daily shoot CO_2 assimilation rate was calculated as net C assimilation minus shoot respiration, assuming constant shoot respiration during the light period without considering photorespiration and increased shoot respiration due to increased leaf temperature during the light period.

Root respiration rates were estimated with an infra-red gas analyser (LI-COR 6252, Lincoln, NE, USA) in differential mode, in an automated system sampled between 12 root cuvettes, with a 4-min time

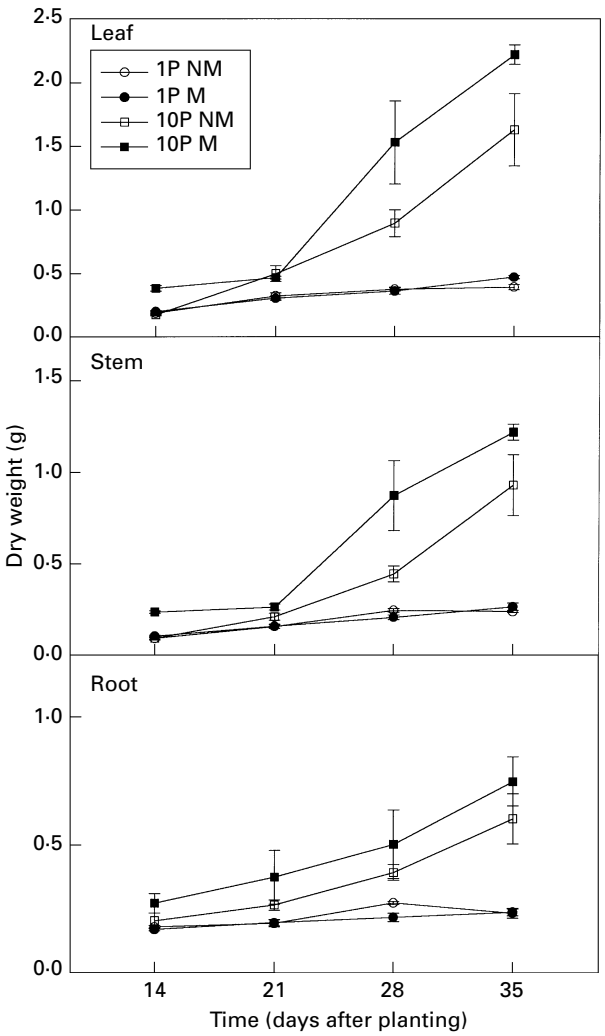

Figure 1. Dry weight of leaves, stem, and roots of low P non-mycorrhizal (1P NM), low P mycorrhizal (1P M), moderate P non-mycorrhizal (10P NM), and moderate P mycorrhizal (10P M) common bean. Data are shown as mean ± SE of the mean ($n = 6$).

interval (Bouma *et al.*, 1997). Below-ground CO_2 generation due to decomposition of the vesicular–arbuscular mycorrhizal (VAM) inoculum was measured on pots with inoculum but without plants. Root-derived respiration of plants inoculated with mycorrhizal fungi was calculated as gross below-ground respiration minus respiration due to decomposition of inoculum.

Growth measurements

Plants were harvested for biomass and leaf area determination after gas exchange measurements at days 14, 21, 28, and 35 after planting. Shoots were excised and separated into leaves and stem. Petioles were included in the stem fraction. Roots were separated from the sand and rinsed in deionized water. The leaves were scanned using a flat-bed scanner (HP ScanJet II, Hewlett Packard, USA). Leaf areas were calculated using image-analysis software (Delta-T SCAN, Delta-T Devices Ltd., Cambridge, England). Leaves, stems, and roots were freeze dried at −60 °C for 72 h before d. wt determination. We calculated relative growth rate (RGR_{DW}) by numerical differentiation of the d. wt data using least-square fittings of quadratic polynomial by three-point fomulae (Erickson, 1976).

Relative growth rate (RGR_C) was also calculated based on net C assimilation rate, from gas exchange measurements. The following equations were used:

$$LAR = SLA \times LWR \quad (1)$$

$$RGR_C = NAR \times LAR, \quad (2)$$

where RGR_C is the relative growth rate (mg plant d. wt (g plant d. wt)$^{-1}$ d^{-1}), NAR is the net assimilation rate (g plant d. wt (m^2 leaf)$^{-1}$ d^{-1}), derived from gas exchange measurements (shoot assimilation minus root and shoot respiration) and tissue C concentration measurements, LAR is the leaf area ratio (m^2 leaf (kg plant d. wt)$^{-1}$), SLA is the specific leaf area (m^2 leaf (kg leaf d. wt)$^{-1}$), and LWR is the leaf weight ratio (g leaf d. wt (g plant d. wt)$^{-1}$).

Tissue analysis

After d. wt determination of root, stem, and leaves, tissues were ground and analysed for C, hydrogen, nitrogen, and oxygen concentration (Fison Elemental Analyser EA1108, Fison Instruments, Italy). Tissue P concentration was determined colorimetrically (Murphy & Riley, 1962). Specific P absorption rate (SAR) was calculated as the rate of P uptake (calculated after Hunt (1990)) expressed per unit of root d. wt (mg P (g root d. wt)$^{-1}$ d^{-1}).

Construction cost of the roots were calculated from elemental composition of C, H, N, and O (McDermitt & Loomis, 1981). Growth respiration was derived by multiplying root construction cost with the relative growth rate (RGR_{DW}). The nitrate uptake rate was estimated by multiplying the relative growth rate by the total plant N-concentration. Respiration associated with ion uptake was estimated by multiplying the net uptake rate of N by the specific cost of N uptake (1·2 mol CO_2 (mol N)$^{-1}$; reviewed by Bouma, Broekhuysen & Veen (1996). Maintenance respiration was calculated by subtracting growth and ion uptake respiration from overall respiration (Peng *et al.*,1993).

Mycorrhizal colonization

Mycorrhizal colonization was evaluated on a random sub-sample of approx. 25 root segments collected before drying the root system. Root pieces were cleared for 10 min. in 10 % KOH at 121 °C, rinsed with water, 5 % HCl, and stained with 0·05 % trypan blue in equal amounts of glycerol, lactic acid, and water overnight. The following day, the sub-sample was destained in equal amounts of glycerol, lactic

acid and water (Phillips & Hayman, 1970). Percent colonization was estimated using a grid intersect method (Tennant, 1975).

Statistical analysis

Dry weights and elemental content of root, stem, and leaves, as well as mycorrhizal colonization, and NAR, SLA, LWR, LAR, relative growth rate (RGR_C) were analysed by ANOVA (randomized block design) for main effects, planting date, and first order interactions (SYSTAT, 1992). Relative growth rates (RGR_{DW}) were derived from average tissue d. wt values of three replicates in a harvest and analysed for main effects by ANOVA.

RESULTS

Mycorrhizal colonization

Mycorrhizal infection was between 30 and 55 % in inoculated plants and always < 10 % in non-inoculated plants. At the last harvest low-P mycorrhizal plants had a significantly larger percentage of their root length infected with mycorrhizal fungi (52 %) compared with moderate P mycorrhizal plants (31 %) as expected (e.g. Stribley *et al*., 1980; Lynch *et al*., 1991).

Growth measurements

The solid-phase-buffered silica sand used in this experiment provided a constant availability of low (1 μM) or moderate (10 μM) P. The 10 μM P observed in the moderate treatment was in excess of the 3 *m*M required for maximal growth in this medium (Lynch *et al*., 1991). Despite this we observed a growth response to mycorrhizal infection after 4 wk of growth (Fig. 1), indicating that the moderate P non-mycorrhizal plants were slightly deficient and that the plant requirements to P concentration in the soil solution could not be satisfied in the amount of sand substrate available at moderate P.

Root d. wt increased over time for all treatments, but significantly more in moderate P plants than in low-P plants (Fig. 1). No significant mycorrhizal effect on root d. wt was observed when comparing low-P mycorrhizal with low-P non-mycorrhizal plants. Stem and leaf d. wt also increased over time and were significantly higher in moderate-P compared with low-P plants. Significantly higher d. wt were also found in moderate-P mycorrhizal plants compared with moderate-P non-mycorrhizal plants. No significant difference was observed in stem and leaf d. wt between low-P mycorrhizal and low-P non-mycorrhizal plants (Fig. 1). The biomass-based relative growth rate (RGR_{DW}) was severely reduced by P deficiency (Table 1).

Root : shoot ratio decreased over time (Table 1) and was significantly higher in low-P than in moderate P plants and higher in non-mycorrhizal than mycorrhizal plants. The change in root : shoot ratio was slower in low-P plants. The higher RSR in low-P than moderate P plants (Table 1) was a result of a greater reduction in stem and leaf growth than root growth (Fig. 1).

Table 1. *Biomass-based relative growth rate* (*RGR_{DW}*, *calculated according to Erickson, 1976*) *and root : shoot ratio* (*RSR*) *for common bean measured at days 14, 21*, 28, *and 35 after planting, as influenced by P availability in the growth media and mycorrhizal symbiosis*

Days after planting	P-level	Myco	RGR_{DW} (mg g^{-1} d^{-1})	RSR (g g^{-1})
14	1	NM	62 a	0·65 a
	1	M	56 a	0·56 b
	10	NM	113 a	0·65 a
	10	M	122 a	0·67 a
21	1	NM	48 b	0·40 a
	1	M	36 b	0·42 a
	10	NM	93 a	0·38 a
	10	M	103 a	0·33 b
28	1	NM	17 b	0·44 a
	1	M	26 b	0·38 ab
	10	NM	73 a	0·30 b
	10	M	93 a	0·30 b
35	1	NM	−30 c	0·37 a
	1	M	28 bc	0·32 ab
	10	NM	52 ab	0·26 b
	10	M	89 a	0·26 b

For RGR_{DW} each value is the mean of two subgroups. Each sub-group consists of three replicates. For RSR each value is the mean of six replicates. Within group of four values in columns, means followed by the same letter are not significantly different according to ANOVA *post hoc* test ($P \leqslant 0{\cdot}05$) (SYSTAT, 1992).

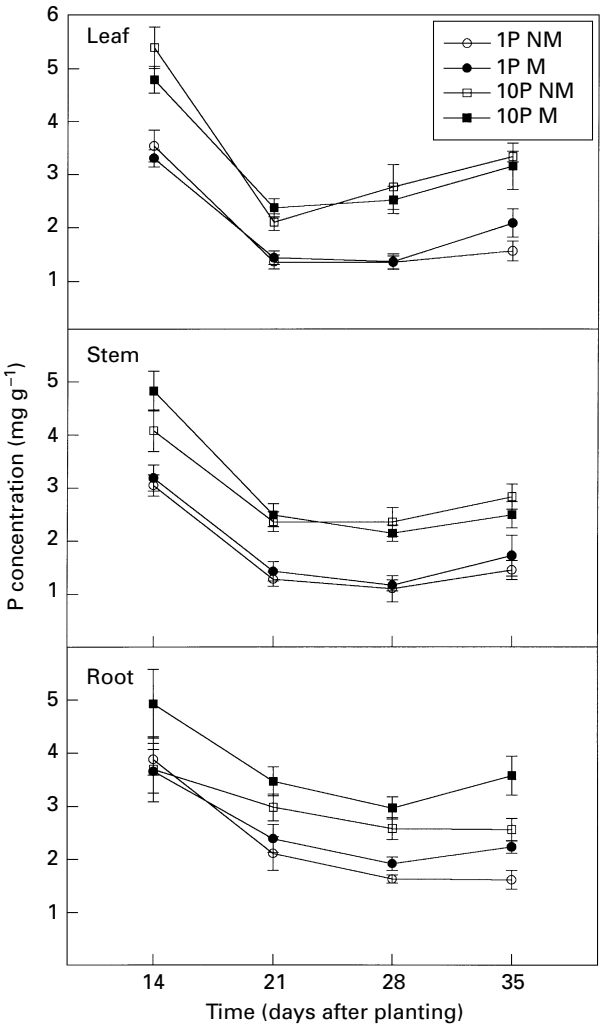

Figure 2. Phosphorus concentration in leaves, stem, and roots of low P non-mycorrhizal (1P NM), low P mycorrhizal (1P M), moderate P non-mycorrhizal (10P NM), and moderate P mycorrhizal (10P M) common bean. Data shown as mean ± SE of the mean ($n = 6$).

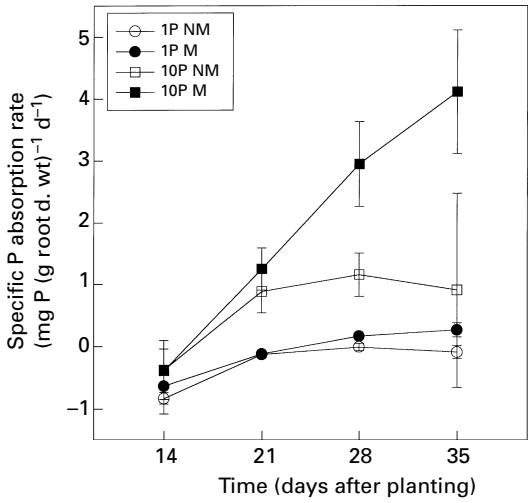

Figure 3. Specific P absorption rate of low P non-mycorrhizal (1P NM), low P mycorrhizal (1P M), moderate P non-mycorrhizal (10P NM), and moderate P mycorrhizal (10P M) common bean roots at days 14, 21, 28, and 35 after planting. Data are shown as mean ± SE of the mean ($n = 6$).

Tissue analysis

Tissue P concentrations were higher at day 14 after planting than at the following harvests for all treatments in both root, stem, and leaves (Fig. 2). Before germination the cotyledon P content averaged 1·5 mg, which was equivalent to the P content of low-P plants at day 14 after planting. A slight drop in P content was observed at day 21. The cotyledons were depleted after 7–10 d (data not shown). No significant mycorrhizal effect was observed for P concentration in stem and leaves. Root P concentration was significantly higher in moderate-P than in low-P plants and in mycorrhizal than in non-mycorrhizal plants.

We observed an increase in specific P absorption rate (SAR) over time regardless of treatment (Fig. 3). Uptake of P was very limited before day 14 after planting owing to relatively large seed P reserves. Mycorrhiza substantially increased SAR at high P. For low-P plants SAR was very low or negative. At days 28 and 35 after planting SAR was slightly higher in low-P mycorrhizal compared with low-P non-mycorrhizal and substantially higher in moderate P mycorrhizal plants compared with moderate P non-mycorrhizal plants.

Root C, H, N, and O concentrations were not significantly affected by P treatment or mycorrhizal infection (data not shown). From day 14 to day 28 we observed an increase in root C (from 35·4 to 40·8 %) and H (from 5·1 to 5·7 %). Leaf C, H, and N concentrations did not change significantly from day 14 to day 28. We did not observe any significant mycorrhizal effect on elemental concentration. Phosphorus supply, however, did affect leaf N concentration, presumably because of biomass dilution. At day 28 after planting the leaf N concentration was greater in low (5·7 %) than in moderate P plants (4·8 %). Conversely, leaf C and H concentrations were greater in moderate (42·9 % C and 6·1 % H) than in low-P plants (41·0 % C and 5·8 % H). Root construction cost was not significantly affected by P availability or mycorrhizal symbiosis and did not change over time (Table 2). Nitrogen uptake rate, calculated from N concentration and relative growth rate, was higher in moderate-P plants, owing to their much higher rate of growth and ion uptake compared with that of low-P plants. Higher ion uptake rate in moderate P plants led to significantly higher respiratory costs for ion uptake (Table 2). The estimated fraction of overall root respiration used for root maintenance respiration was therefore higher in low-P plants. Mycorrhizal plants had a significantly higher root respiration rate compared with non-mycorrhizal plants at days 14 ($P < 0·05$) and 28 ($P < 0·01$) after planting (Fig. 4), but the partitioning of

Table 2. *Root construction cost* (*Const. cost*), *N-uptake rate per unit root d. wt* (*N-uptake rate*), *and the fractionation of root respiration into growth, uptake and maintenance* (*maint.*) *respiration for common bean as calculated at days* 14 *and* 28 *after planting, as influenced by P availability in the growth media and mycorrhizal symbiosis*

Days after planting	P-level	Mycol	Const. cost (mmol CO_2 (g root d. wt)$^{-1}$)	N-uptake rate (mmol N (g root d. wt.)$^{-1}$ d^{-1})	Percentage of root resp.		
					Growth	Uptake	Maint.
14	1	NM	8·8 a	0·21 b	19 b	9 b	72 a
	1	M	9·4 a	0·18 b	12 b	5 b	83 a
	10	NM	7·9 a	0·38 a	29 a	14 a	57 b
	10	M	7·7 a	0·40 a	25 a	12 a	63 b
28	1	NM	8·5 a	0·06 b	6 b	4 b	89 a
	1	M	8·3 a	0·10 b	10 b	5 b	85 a
	10	NM	8·9 a	0·27 a	25 a	11 a	64 b
	10	M	10·9 a	0·26 a	25 a	9 a	67 b

Each value is the mean of six replicates. Within a group of four values in columns, means followed by the same letter are not significantly different according to ANOVA *post hoc* test ($P \leqslant 0{\cdot}05$).

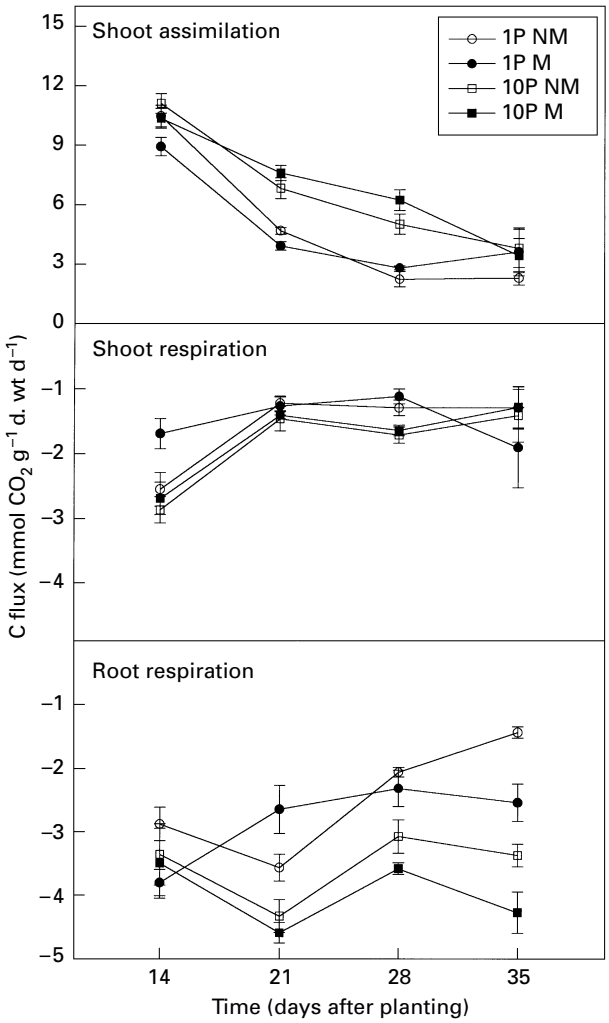

Figure 4. Specific shoot assimilation rate, shoot respiration rate, and root respiration rate of low P non-mycorrhizal (1P NM), low P mycorrhizal (1P M), moderate P non-mycorrhizal (10P NM), and moderate P mycorrhizal (10P M) common bean plants at days 14, 21, 28, and 35 after planting. Data are shown as mean ± SE of the mean ($n = 6$).

root respiration between respiratory costs of growth, ion uptake, and maintenance was not affected significantly (Table 2).

Gas exchange measurements

Specific C flux (mmol CO_2 (g d. wt)$^{-1}$ d^{-1}) for roots and shoots was calculated at days 14, 21, 28, and 35 after planting. Shoot assimilation rate (Fig. 4) declined over time, as the leaves aged, and shading by younger leaves increased. A significant effect of P was also observed. Plants with moderate P had a significantly higher shoot CO_2 assimilation rate (days 21 and 28 after planting) compared with low-P plants. Shoot respiration rate (Fig. 4) declined from day 14 to day 21 after planting and then remained fairly constant. Plants with moderate P showed a higher shoot respiration rate than low-P plants at days 14, 21, and 28 after planting. Below-ground respiration due to decomposition of inoculum did not change significantly over time and was unaffected by P availability (moderate or low). Therefore the overall average of 0·04 mmol CO2 d^{-1} per pot ($n = 16$) was subtracted from the gross soil respiration of all mycorrhizal plants. The specific root respiration rate was significantly higher in plants grown with moderate P compared with those grown with low-P supply. Mycorrhizal roots had significantly higher specific root respiration rates than non-mycorrhizal roots.

There was a significant correlation between absolute growth rate (GR_{DW}; derived from RGR_{DW}; data not shown) and estimated C gain (GR_C; derived from gas exchange measurement; data not shown).

$$GR_C = 0{\cdot}9365 GR_{DW} + 0{\cdot}6335.$$

The correlation coefficient and significance level

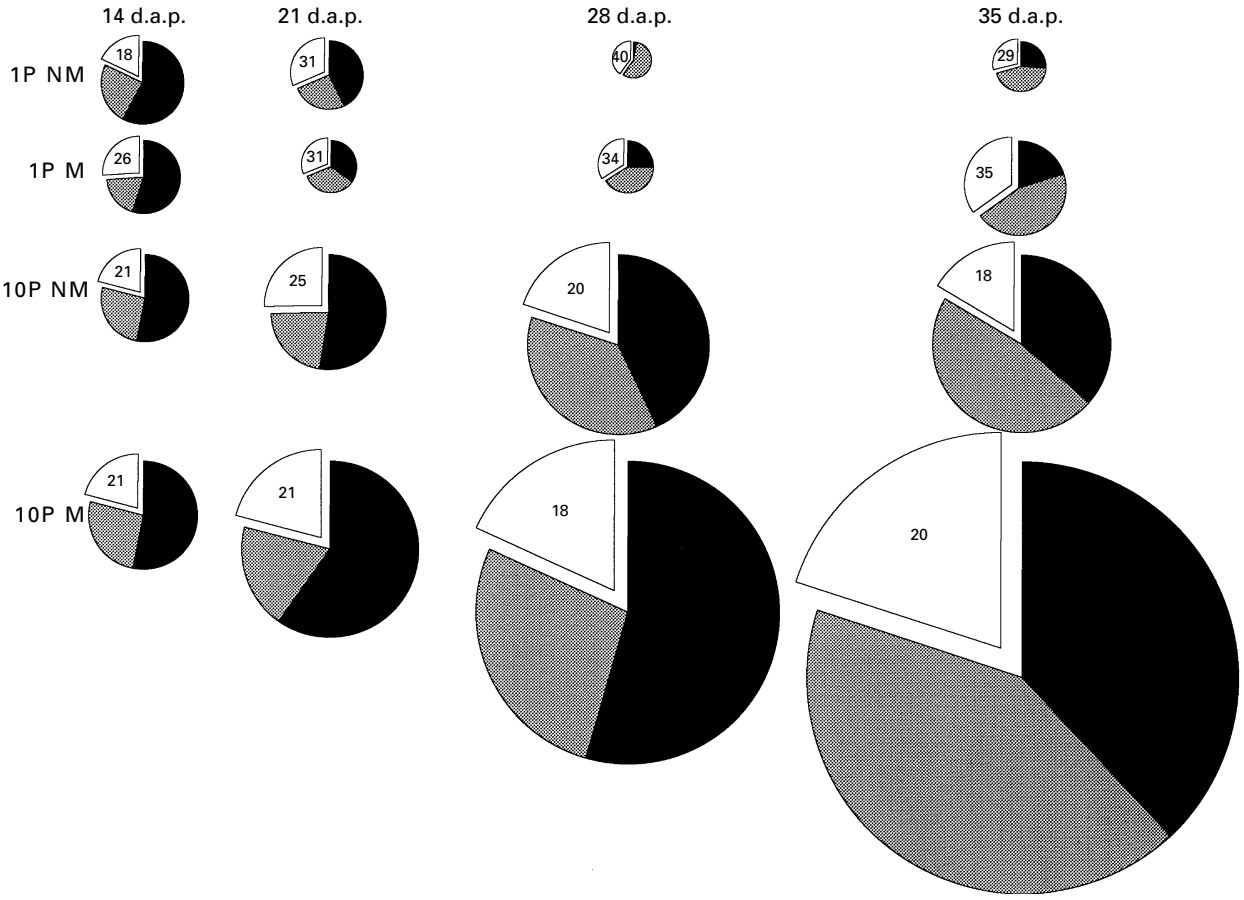

Figure 5. Allocation of a diurnal C assimilation at days 14, 21, 28, and 35 after planting (d.a.p.), as percentage used for root respiration (□), shoot respiration (⊠), and C gain (■) of low P non-mycorrhizal (1P NM), low P mycorrhizal (1P M), moderate P non-mycorrhizal (10P NM), and moderate P mycorrhizal (10P M) common bean plants. The numbers indicate the percentage of the diurnal C assimilation used for root respiration. The size of the pie charts indicate the magnitude of the diurnal C assimilation. Each value is the mean of six replicates.

($r^2 = 0{\cdot}7795$; $n = 32$; $P < 0{\cdot}01$) showed that gas exchange measurement (current CO_2 assimilation and respiration) described the current growth well. Both RGR_C and RGR_{DW} were reduced under low-P conditions. Some of the difference observed between RGR_{DW} and RGR_C can be explained by the variation in d. wt from harvest to harvest and light conditions from measurement to measurement.

The total daily C budget was fairly constant in low P plants throughout the experiment, whereas the the C budgets for moderate P plant increased over time (Fig. 5). At the first C budget measurement (day 14 after planting), the fractions used for root respiration, shoot respiration and net C gain, as well as the total C budget were similar. Allocation of gross C assimilation to existing roots and shoot was fairly constant over time in low-P plants (Fig. 5). The relative allocation of diurnal C budget at days 14, 21, 28, and 35 after planting is shown in Figure 5. Root respiration consumed approx. twice as much of the total C budget of low-P plants compared with moderate P plants at days 28 and 35 after planting.

DISCUSSION

Mycorrhizal infection and root carbon costs

In this study we found a mycorrhiza-induced increase in specific P absorption rate (Fig. 3), resulting in a higher root and leaf P concentration in low-P mycorrhizal plants at day 35 after planting compared with low-P non-mycorrhizal plants (Fig. 2). The improved P status of the low-P mycorrhizal plants led to higher rates of shoot C assimilation (Fig. 4), but not to a significant increase in plant d. wt (Fig. 1) because of the significant increase in root respiration (Fig. 4). A comparable increase in specific root/soil respiration was found in *Citrus* (Peng *et al.*, 1993). They attributed this to an increased build-up of lipid-rich roots, greater root biomass and increased maintenance and growth respiration of the fungal tissue. We did not find any differences in root elemental composition between mycorrhizal and non-mycorrhizal roots. Based on calculations of construction costs of roots (McDer-

mitt & Loomis, 1981) we therefore conclude that the energy content of the root tissue was similar in the four treatments. We did not observe any significant difference in root d. wt and N concentration under moderate or low-P conditions when comparing non-mycorrhizal with mycorrhizal plants. The increase in root respiration in mycorrhizal roots is therefore most likely a result of increased maintenance and growth respiration of the fungal tissue, represented by an increase in the residual component (maintenance respiration, Table 2) of the root respiratory calculation.

In a study of the response of a set of contrasting bean genotypes to P stress (Yan, Lynch & Beebe, 1995), biomass production was higher in mycorrhizal plants (infection rates 60–80 %) compared with non-mycorrhizal plants, but the ranking of the genotypes was independent of mycorrhizal infection. It was therefore suggested that the adaptation of a genotype to low-P, relative to other genotypes, is determined by inherent root traits, rather than symbiotic efficiency. In this study we found that root construction cost was not affected significantly by either plant P status or mycorrhizal infection. Since mycorrhizal infection is high in bean plants under most field conditions, ranking of the genotypes with respect to biomass production is independent of mycorrhizal infection, and construction cost seems not to be affected significantly by mycorrhizal infection. Thus, we suggest that mycorrhizal infection is one of the specific mechanisms of P acquisition that might be less important for the development of more P-efficient cvs.

Phosphorus availability and mycorrhizal infection

Ratnayake, Leonard & Menge (1978) found a correlation between P concentration in Sudan grass and citrus roots and permeability of membranes, associated with increased leakage of amino acids and sugars from the root. Graham *et al*. (1981) demonstrated that this increase in membrane permeability and exudation of amino acids and sugars led to an increase in mycorrhizal infection. In our experiment the roots of P-deficient plants inoculated for 5 wk with *Glomus intraradices* were 52 % infected, compared with 31 % in moderate P plants, indicating that the intensity of the mycorrhizal colonization was relatively inhibited in moderate P plants. Alternatively mycorrhizal colonization could have been reduced by roots outgrowing mycorrhizal colonization in moderate P plants (as suggested by Lynch *et al*. (1991)).

Phosphorus availability and root carbon costs

At day 14 after planting there was no significant difference between the C allocation patterns of the four treatments, but as the plants aged the low P plants used increasing relative amounts of their C on root respiration. Root respiration of low-P plants represented approx. twice as much of the whole plant C budget as moderate P plants at day 35 after planting (Fig. 5). Shoot respiration in low-P plants also represented a slightly larger fraction of the total C budget than in moderate P plants. Because specific root respiration rate was generally reduced as a result of P deficiency (Fig. 4), a change in root respiration rate cannot explain the increase in relative root respiration. Specific root respiration was reduced by up to 40 % over time in low-P plants. This reduction in specific root respiration was due to a reduction in growth rate (RGR_{DW}; Table 1) and N-uptake rate (Table 2), leading to a reduction in the percentage of root respiration used for growth and ion uptake, whereas maintenance respiration was unaffected by low-P availability. Root growth was less sensitive to P deficiency than leaf and stem growth, resulting in a higher RSR (Table 1). Preferential partitioning of photosynthetic C to the roots and increased RSR is a well documented response to P stress (Ingestad & Ågren, 1991; Marschner, Kirkby & Cakmak, 1996) and partly explains the relatively large root respiratory burden for the whole plant C economy of P-deficient plants (Fig. 5). In addition to the increased RSR a significant reduction in specific shoot assimilation rate at days 21 and 28 after planting (Fig. 4) led to a smaller C economy in low-P plants (in agreement with Lambers *et al*. (1981); Bingham & Farrah (1989); Van der Werf, Welschen & Lambers (1992). Lynch *et al*. (1991) found that P deficiency caused a slower leaf area growth rate in bean by reducing the expansion of individual leaves, as well as the initiation of new leaves on both the main stem and branches.

Mechanisms for improved P efficiency

Our results support the hypothesis that increased allocation of C to the root system is a primary constraint to growth in P deficient plants. Plants that have a greater ability to acquire P from the environment, or greater ability to convert P into growth once it has been acquired would therefore perform better under low-P conditions. Using *SimRoot*, an explicit geometric model of root growth based on empirical data of root respiration, exudation and biomass deposition, we have demonstrated recently that root systems with various architectures varied in the relationship between C cost and P acquisition, providing evidence for the importance of architecture in nutrient-acquisition efficiency (Nielsen *et al*., 1994). Several possible mechanisms have been suggested for improving the P efficiency of crops, such as reduced tissue P requirements, increased seed P reserves, phenology, root exudates, mycorrhizal symbiosis, and root architecture and plasticity (e.g., Lynch & Beebe, 1995). A gravitropic response to P availability has recently been demon-

strated for bean (Bonser, Lynch & Snapp, 1996), thereby changing the proportion of the root system in the topsoil, where P in general is more available. Root systems are composed of various root types that have distinct properties (Eshel & Waisel, 1996). Variation in growth and architecture among different root types has been observed among common bean genotypes (Lynch & van Beem, 1993). Allocation of resources to root types with lower construction cost per unit root length or higher P acquisition efficiency, such as roots of small diameter or with an architecture that reduces overlap between P-depletion zones, could be beneficial under low-P conditions. Concurrent analysis of C budget and root architecture will be useful as a means of quantifying the physiological efficiency of contrasting root systems, providing the means for investigating specific mechanisms of P utilization that may be important for the development of more P-efficient cvs.

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