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EFFECT OF ATMOSPHERIC CO_2 ENRICHMENT ON ROOT GROWTH AND CARBOHYDRATE ALLOCATION OF *PHASEOLUS* SPP.

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A glasshouse experiment was conducted with plants of *Phaseolus* grown in liquid culture. Root growth parameters (biomass, diameter, length, growth rate, zone of cell division), root rheological components (wall extensibility, water potential yield threshold, water potential), shoot growth, carbon allocation, and abscisic acid (ABA) concentration were measured in *Phaseolus acutifolius* A. Gray at ambient (550 μmol mol^{-1}) and elevated (700 μmol mol^{-1}) atmospheric CO_2 concentrations. For contrast, measurements of above- and belowground growth were conducted on *Phaseolus vulgaris* L. in the same treatments. Under nonlimiting conditions of water and nutrients, elevated CO_2 increased root and shoot growth of *P. acutifolius* but not *P. vulgaris*. While root mass was increased by nearly 60% in *P. acutifolius*, there was no effect of atmospheric CO_2 on any of the rheological components measured. In contrast, starch and ABA accumulated in roots of *P. acutifolius*. The concentration of starch in roots of *P. acutifolius* increased by 10-fold, while root concentrations of ABA doubled. From the data it is concluded that CO_2 enrichment is favorable for root growth in some species in that more carbon is allocated to belowground growth. In addition, ABA may play a role in growth responses and/or allocation of photosynthates at elevated CO_2 in *P. acutifolius*.

Keywords: elevated CO_2, roots, carbohydrate allocation, abscisic acid, species-specific response, ecophysiology.

Introduction

Most scientists agree that global warming has come to pass and that, as a result, there will be higher concentrations of atmospheric carbon dioxide in the future. Therefore, research efforts to determine the effects of elevated atmospheric carbon dioxide levels on plant responses are timely. In particular, following reports that elevated atmospheric CO_2 can enhance root growth in some species (Kimball 1983; Rogers et al. 1992), there has been increased interest in root responses when plants are exposed to elevated atmospheric CO_2.

Mechanistic studies of the factors controlling root growth are becoming more common. In recent years, several researchers have focused upon rheological properties to understand how roots grow (Ferris and Taylor 1994; Crookshanks et al. 1998). For example, when root elongation is decreased by exposing tissues to increasing osmotic pressure, growth is related to several factors, including a rapid decrease of the yield threshold (Y, decrease of cell wall mechanical resistance), turgor (P) adjustment, and increased wall extensibility (Frensch and Hsiao 1995). In addition, adjustments of wall properties (yield threshold and extensibility) can reestablish growth-effective turgor ($P > Y$).

Besides wall properties, solute flow rate (largely carbohydrates) within the growing zone may also be an important determinant of the rate of root elongation (Minchin et al. 1994). Huber (1983) and Huber and Huber (1992) suggest that carbon allocation to the root has a strong effect on root : shoot ratios. How (and if) root growth is regulated by carbon allocation is still unclear. Other data suggest that hormones may play an important role in root growth. Several laboratories have reported that roots have the capacity to produce significant amounts of abscisic acid (ABA; Walton et al. 1976; Cornish and Zeevaart 1985; Zhang and Davies 1987). Applications of ABA have been shown to both increase (Mulkey et al. 1983; Pilet and Saugy 1987) and decrease root growth (Watts et al. 1981; Jones et al. 1987).

To assess the responses of root growth under elevated atmospheric CO_2, plants were grown in a hydroponic system to prevent possible mitigating effects of limited nutrient or water availability. In addition, liquid culture is useful for studies of root biology because plants are grown under conditions where root restriction is avoided and tissues can be sampled without large disturbances of the root environment. The purpose of this study is to characterize root responses of a herbaceous legume to elevated atmospheric CO_2. Growth, rheological properties, carbohydrate concentrations, and ABA concentrations were determined under elevated atmospheric CO_2 in an attempt to elucidate possible mechanisms (biochemical and physical) whereby atmospheric CO_2 enhancement influences root growth. In some studies, comparisons were made between *Phaseolus acutifolius* and *Phaseolus vulgaris*.

Material and Methods

Plant Material and Treatments

During the spring of 1998, seeds of *Phaseolus vulgaris* and *Phaseolus acutifolius* were germinated and grown in sand in a greenhouse on the campus of the University of Nevada,

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Las Vegas, under a natural day/night regime and prevailing Las Vegas temperatures (day, 33° ± 8°C; night 24° ± 6°C). Greenhouse temperatures were programmed to follow ambient Las Vegas temperatures and ranged from 18° to 41°C during the experiments. On the sixth day after germination (before the first trifoliate leaf was fully expanded), plants were transferred to aqueous solution culture (hydroponics) in a controlled-environment greenhouse under natural lighting. The mean recorded photosynthetically active radiation (PAR) was 930 μmol m^{-2} s^{-1} (measured by a quantum sensor at plant surfaces, model LI-190SA, Li-COR, Lincoln, Nebr.). Sixty seedlings of each species were distributed randomly into hydroponic bins in one of three atmospheric CO_2 treatment rooms within the campus greenhouse: ambient (385 ± 41 μmol mol^{-1} CO_2), 550 ± 33 μmol mol^{-1}, and 700 ± 22 μmol mol^{-1}. Entrance to the treatments rooms are carefully restricted; atmospheric CO_2 concentrations of each treatment room were monitored with an Infrared Gas Analyzer (LI-6262, Li-Cor, Lincoln, Nebr.). CO_2 was automatically injected into the treatment rooms when necessary to maintain concentrations within ±30 μmol mol^{-1} of the target concentration. Measurements began after seedlings had been under treatment conditions for 20 d (30 d after germination). In some experiments, only ambient and 700 μmol mol^{-1} CO_2 concentrations were used.

Plant roots were bathed in aerated circulating 0.1 Hoagland's solution pumped continually between the 19-L hydroponic bin and a 76-L reservoir. Because preliminary experiments indicated that root growth of *Phaseolus* is temperature responsive, hydroponic bins were kept within 1°C of each other to maintain consistent root temperatures. Nutrient solutions were refreshed every 6–7 d. Continuous gentle flushing of the root system with a large volume of nutrient solution maintained adequate growth and prevented problems of apparent nutrient deficiency (e.g., yellowing).

Root Growth Measurements

When plants were 30 d old (with three to four trifoliate leaves), estimates of day and night root growth were made. Roots were marked 2 cm from the tip with a lumocolor (Parker Pen, New Haven, England) overhead marking pen and then remeasured at 12- and 24-h intervals. In this study, maximum root growth occurred during 12 h. The five longest roots on each plant were used to obtain measurements of whole root extension growth. Length was measured from the basal point of attachment to the tip of the root. Estimates of root diameter were made using a reticule on cross sections located 15 mm from the root tip. The size of the apparent meristematic zone (zone of cell division) was measured with a calibrated eyepiece under ×40 magnification on roots cleared with chromium trioxide (Pelosi et al. 1995). At the end of the experiment, above- and belowground tissue was dried at 80°C for 48 h for dry mass determinations.

Root Rheological Properties

At the same time that root growth measurements were made, root rheological properties were studied using an osmotic immersion technique (Cleland 1976). In this method, tissues (roots) are incubated in a series of nonpenetrating osmotic solutions. The percentage change in length relative to solution osmotic pressure should give a linear response where the slope is cell wall extensibility (MPa h^{-1}) and the offset ($Y = 0$) is the yield threshold in MPa (Cosgrove 1993*a*). Because our estimates of yield are indirect and based on an osmotically generated water potential, yield will be referred to herein as "water potential yield." While there are some reports of osmotic immersion studies where measurements were taken after 15 min, the results of a preliminary time-course study indicated that measurements taken at hourly intervals for 6 h were within 5% of measurements taken after 5 min of solution immersion. In this study, excised root sections (0.75 cm; $n = 10–12$) were incubated in a graded series of mannitol solutions at water potentials from −0.25 MPa to −1.0 MPa. Water potentials of the solutions were confirmed using a thermocouple psychrometer (Decagon Devices, Pullman, Wash.). The root length at each osmotic pressure was measured using a computer-controlled digitizer connected to a microscope.

Table 1

Root and Shoot Dry Mass, Root Length, Leaf Number, and Root : Shoot Ratio

Species and growth parameter	CO_2 concentration (μmol mol^{-1})		Change (%)
	Ambient (385)	Elevated (700)	
Phaseolus vulgaris:			
Root mass (g)	0.71 ± 0.06[a]	0.73 ± 0.05[a]	3
Shoot mass (g)	1.49 ± 0.09[a]	1.85 ± 0.15[a]	24
Leaf number	8.18 ± 0.51[a]	8.57 ± 0.70[a]	5
Root : shoot ratio	0.47 ± 0.01[a]	0.39 ± 0.01[b]	−17
Phaseolus acutifolius:			
Root mass (g)	0.27 ± 0.01[a]	0.43 ± 0.04[b]	59
Root length (cm)	32.00 ± 1.33[a]	49.70 ± 0.71[b]	55
Shoot mass (g)	0.32 ± 0.02[a]	0.60 ± 0.05[b]	88
Leaf number	8.20 ± 0.33[a]	14.14 ± 0.40[b]	73
Root : shoot ratio	0.89 ± 0.02[a]	0.71 ± 0.02[b]	−20

Note. Data are means (±SE) for *Phaseolus vulgaris* ($n = 12$) and *Phaseolus acutifolius* ($n = 19$). Plants were sampled at ca. 50 d in culture. Means with a different letter within a given row indicate statistical differences at $P < 0.05$.

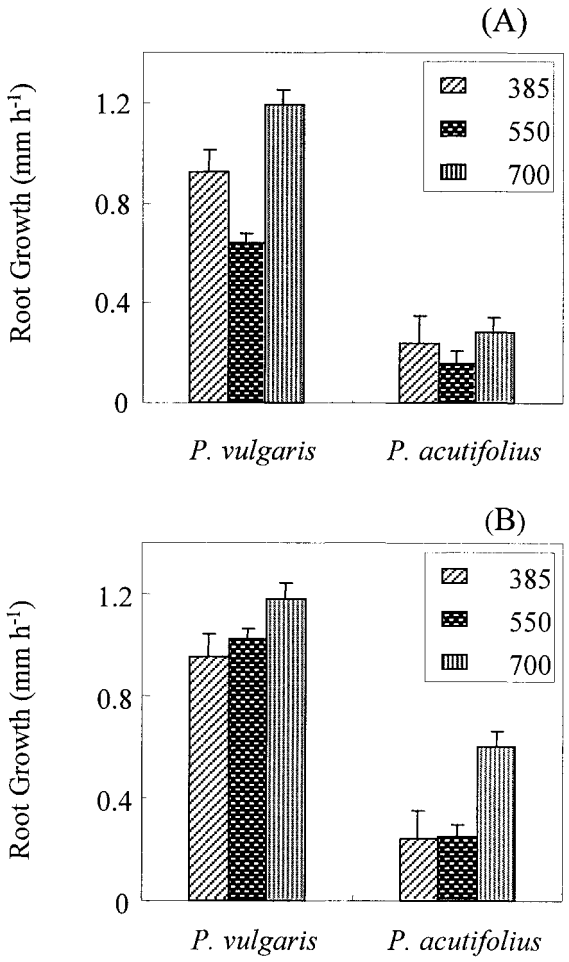

Fig. 1 Root growth rate (mm h^{-1}) under ambient (385 μmol mol^{-1}) and elevated (550 μmol mol^{-1} and 700 μmol mol^{-1}) CO_2 at (*A*) night and (*B*) day in *Phaseolus vulgaris* and *Phaseolus acutifolius*. Plants were sampled after ca. 40 d in culture. Data are means for six to 11 roots. Means with a different letter within a species are statistically different at $P < 0.05$.

Root water potentials were estimated by thermocouple psychrometry. Roots ($n = 5$–6) were placed in sample cups of a dew-point psychrometer (model SC-10 with the NT-3 nanovoltmeter, Decagon Devices, Pullman, Wash.) and allowed to equilibrate for 5 h before measurements were recorded. Solutions of known osmotic potential were used to calibrate each set of measurements. All incubations and measurements were conducted at room temperature.

Measurements of Plant Components

When plants were 40 d old, roots, stems, and leaves were assayed for starch and six-carbon sugars (hexoses) to study carbohydrate allocation. All tissues were collected at the same time of day (11:00 AM) to minimize the confounding effects of diurnal starch cycling. Main stems were carefully partitioned into upper xylem, upper phloem, lower xylem, and lower phloem components by separating tissues at the cambium. For this particular species, the phloem and outer layers readily separate at the cambium. Leaves were categorized as source or sink leaves. To identify the developmental stage of individual leaves, the fourth trifoliate leaf was marked as "0." From leaf 0, new leaves were considered sink leaves, whereas older leaves were considered source leaves. Using this method, the source leaves were −2 and −3 and the sink leaves were 3 and 4.

Starch was assayed after the method of Kerr et al. (1984). Briefly, 25 mg of tissue were extracted in 80% ethanol. Samples were shaken for 30 min, centrifuged, and the supernatant removed and saved for quantification of six-carbon sugars. The pellet was washed in 80% ethanol at 85°C until the supernatant was clear. Tissue samples were dried, resuspended, and

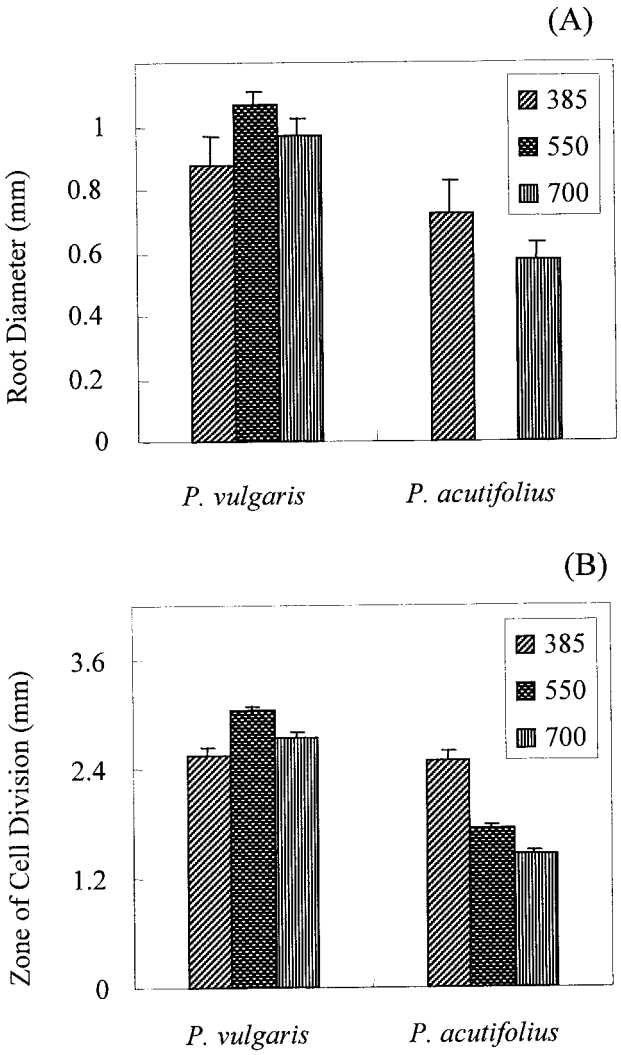

Fig. 2 Estimates of the (*A*) root diameter (mm) and (*B*) length of the zone of cell division (mm) for *Phaseolus vulgaris* and *Phaseolus acutifolius* under ambient (385 μmol mol^{-1}) and elevated (550 μmol mol^{-1} and 700 μmol mol^{-1}) CO_2. Plants were sampled after ca. 40 d in culture. Data are not presented for root diameter of *P. acutifolius* under 550 μmol mol^{-1}. Data are means for 12–15 ± SE. Means with a different letter within a species indicate statistical differences at $P < 0.05$.

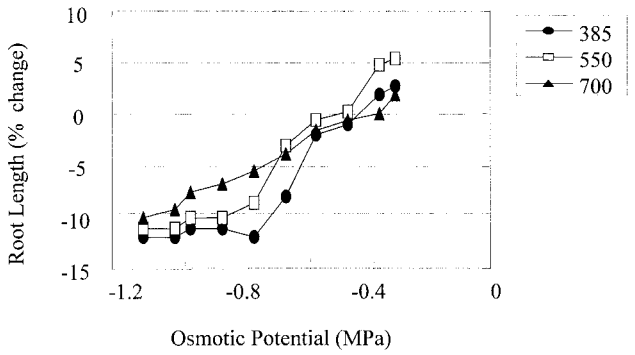

Fig. 3 Relationship between osmotic potential and length change of *Phaseolus acutifolius* roots. The root length at each osmotic pressure was estimated using a computer-controlled digitizer connected to a microscope. Plants were sampled after ca. 40 d in culture. Each point represents the mean (±SE) of 10–12 measurements.

boiled in 1 mL of 0.2 M KOH. Polysaccharides were broken down with amyloglucosidase (Sigma Chemical, St. Louis) at 30°C overnight. Glucose was detected enzymatically (Sigma Chemical, Glucose Kit 510-A) and spectrophotometrically quantified at 340 nm. The supernatant from the above tissue extraction procedure was assayed for hexoses, using the anthrone reaction (Hansen and Moller 1975).

For ABA, root tissue was weighed, lyophilized, ground, and extracted with 5 mL of cold 80% methanol/BHT (butylated hydroxytoluene) extraction buffer, shaken for 2 h and centrifuged for 10 min. ABA concentrations were estimated by immunoassay after partial purification as previously described (Smit et al. 1990). To check losses by isotope recovery, [3H]-(±)-ABA (Amersham, Uppsala) was added to all samples. Cross reactivities of the antisera for ABA were previously reported (Smit et al. 1990).

Statistics

All data were analyzed using one-way ANOVA in JMP IN (SAS Institute 1996). All the experiments reported here were repeated one or more times with similar results. Results are pooled from several experiments and considered statistically significant at $P < 0.05$.

Results

Under our experimental conditions, *Phaseolus vulgaris* was generally nonresponsive to elevated atmospheric CO_2, whereas *Phaseolus acutifolius* responded to elevated CO_2 with increased shoot and root dry mass and leaf number (table 1). The only CO_2-responsive growth component for *P. vulgaris* was the rate of root growth during the day (fig. 1), which resulted in a reduced root : shoot ratio (table 1). When *P. vulgaris* was grown under elevated atmospheric CO_2, the rate of root growth increased during the night, whereas in *P. acutifolius*, elevated CO_2 enhanced root growth during the day (fig. 1). While visual observation of *P. vulgaris* roots suggested an increase in length, quantitative measurement was impossible as a result of the degree of entanglement between the root systems of the plants. Root length for *P. acutifolius* was significantly greater under elevated CO_2 (table 1). In addition, root diameter was decreased by ca. 25% under elevated CO_2 for this species; root diameter of *P. vulgaris* was nonresponsive to CO_2 (fig. 2). A similar response was found for estimates of the zone of cell division. The zone of cell division was 87% shorter in *P. acutifolius* grown under elevated CO_2, but there was no response in *P. vulgaris* (fig. 2).

Rheological and metabolic experiments were performed on *P. acutifolius*. Kinetics shown in figure 3 indicate nonlinear responses to increasing osmotic pressure. The results indicated no effect of elevated atmospheric CO_2 on any root rheological properties or water relations components tested including extensibility, water potential yield, and root water potential (table 2).

Elevated CO_2 affected metabolic responses of *P. acutifolius*. Allocation of carbon to roots was greater under increased atmospheric CO_2 concentration (table 3). At 700 μmol mol^{-1} CO_2, starch concentrations in roots increased approximately 10-fold over that of tissues grown under ambient CO_2. Elevated CO_2 also resulted in a significant increase in starch concentrations in aboveground tissues of *P. acutifolius*. At 700 μmol mol^{-1} CO_2, the concentration of starch approximately doubled in leaves and in lower xylem tissues, and concentrations tripled in stem phloem (table 3). While there was no effect of increased atmospheric CO_2 on the concentrations of six-carbon sugars in roots or stems, six-carbon sugars significantly increased in leaves of *P. acutifolius*. Under exposure of 700 μmol mol^{-1} CO_2, six-carbon sugars in sink leaves increased twofold, and source leaves increased 1.5-fold (table 3). Root ABA was higher under increasing concentrations of

Table 2

Summary of the Effects of Elevated CO_2 on Root Rheological Properties and Water Relations Components of *Phaseolus acutifolius*

Measurement	CO_2 concentration (μmol mol^{-1})		
	Ambient (385)	Moderate (550)	Elevated (700)
Extensibility (MPa^{-1} h^{-1})	0.07 ± 0.01	0.11 ± 0.01	0.11 ± 0.02
Water potential yield (MPa)	−0.41 ± 0.15	−0.49 ± 0.05	−0.39 ± 0.09
Root water potential (MPa)	−0.61 ± 0.07	−0.57 ± 0.05	−0.64 ± 0.09

Note. Plants were sampled after ca. 40 d in culture. Data are means for five to six plants (±SE). No statistically significant differences were indicated at $P < 0.05$.

Table 3

Summary of the Effects of Elevated CO_2 on Starch and Sugar Concentrations of *Phaseolus acutifolius*

	CO_2 concentration (μmol mol^{-1})		
	Ambient (385)	Moderate (550)	Elevated (700)
Starch:			
Leaf:			
Sink (mg cm^{-2})	0.5 ± 0.1^{A}	0.5 ± 0.6^{A}	1.2 ± 0.1^{B}
Source (mg cm^{-2})	3.5 ± 1.4^{A}	3.6 ± 0.9^{A}	10.7 ± 3.2^{B}
Stem:			
Xylem:			
Upper[a]	3.3 ± 0.6^{A}	2.8 ± 3.8^{A}	3.1 ± 1.4^{A}
Lower[a]	15.0 ± 1.5^{A}	13.9 ± 6.2^{A}	30.0 ± 0.7^{B}
Phloem:			
Upper[a]	1.4 ± 0.1^{A}	3.6 ± 0.9^{B}	4.2 ± 0.6^{B}
Lower[a]	4.2 ± 1.1^{A}	12.3 ± 1.9^{B}	11.3 ± 1.3^{B}
Root[a]	1.2 ± 0.1^{A}	5.9 ± 0.9^{B}	12.0 ± 0.2^{C}
Six-carbon sugars:			
Leaf:			
Sink ($\times 10^{-3}$ mg cm^{-2})	5.2 ± 0.1^{A}	12.0 ± 2.9^{B}	10.0 ± 1.8^{B}
Source ($\times 10^{-3}$ mg cm^{-2})	6.1 ± 0.2^{A}	7.9 ± 0.9^{A}	9.4 ± 0.1^{B}
Stem:			
Xylem:			
Upper[a]	4.9 ± 1.6^{A}	4.2 ± 0.9^{A}	3.7 ± 1.3^{A}
Lower[a]	1.6 ± 0.1^{A}	1.4 ± 0.3^{A}	1.5 ± 0.1^{A}
Phloem:			
Upper[a]	6.0 ± 0.9^{A}	5.8 ± 0.6^{A}	5.1 ± 0.2^{A}
Lower[a]	4.0 ± 0.2^{A}	3.9 ± 0.9^{A}	4.0 ± 0.2^{A}
Root[a]	1.1 ± 0.1^{A}	1.2 ± 0.8^{A}	0.9 ± 0.1^{A}

Note. To identify individual leaves, the fourth trifoliate leaf was marked as "0" at the beginning of the experiment. From the "0" leaf, new leaves were considered sink leaves, whereas older leaves were considered source leaves. Using this method, the source leaves were −2 and −3 and the sink leaves were 3 and 4. Data are means for five to six plants (±SE). Means with a different capital letter within a given row indicate statistical significance at $P < 0.05$.

[a] Units are mg g^{-1} dwt.

atmospheric CO_2 (fig. 4). At 700 μmol mol^{-1} CO_2, ABA concentrations in roots were increased by ca. 40% over that of roots grown under ambient CO_2.

Discussion

The occurrence of a root response to elevated atmospheric CO_2 was investigated in a hydroponic system. In this study, CO_2 enrichment of the atmospheric environment significantly altered the growth of roots and shoots of *Phaseolus acutifolius* but not *Phaseolus vulgaris*. The fact that species of the same genus respond differently to CO_2 has been reported before (Bazzaz 1990). In this study, the hydroponic system allowed an investigation of increased atmospheric CO_2 without the mitigating influences of limited belowground space (McConnaughay et al. 1993), nutrient deficiency (Wong and Osmond 1991), and water deficit (Conroy et al. 1986; Bazzaz 1990) that often occur in pot studies. In contrast to several reports of increased allocation of biomass into roots of plants grown under elevated CO_2 (Rogers et al. 1994), including legumes (Mjwara et al. 1996), our results revealed decreased allocation of dry matter to roots of *Phaseolus* (table 1). Radoglou and Jarvis (1992), also using *P. vulgaris*, found similar results. While the great variation in plant response to elevated CO_2 is still not well understood, it has been suggested that biomass allocation is responsive to nutrient status (Petterson and McDonald 1992). Because our experiments were conducted under conditions of nonlimiting nutrient availability, this may explain the reduced root : shoot ratios reported here, as well as other reports where elevated atmospheric CO_2 had little effect on dry matter allocation between roots and shoots (Bowler and Press 1993; Baxter et al. 1994). Taken together, this suggests that allocation may be a poor standard for measuring plant response to elevated atmospheric CO_2 because of the sensitivity of resource allocation to factors other than CO_2 concentration.

While we observed no increase of root : shoot ratio, there was a significant effect of elevated atmospheric CO_2 on overall root length, with length increasing by ca. 55% in *P. acutifolius* (table 1). Ferris and Taylor (1993) and Petterson and McDonald (1992) have reported similar effects on root length in several downland herbs and in *Betula*. While wall properties may play a role in the control of elongation, we did not find any significant effect of elevated CO_2 on root rheological properties (water potential yield and extensibility) or root water potential. In contrast, Ferris and Taylor (1994) reported that elevated atmospheric CO_2 changed wall properties of plants, in particular, cell wall extensibility. This discrepancy may be a result of differences in experimental approach. Here, an osmotic immersion technique was used to generate the rheolog-

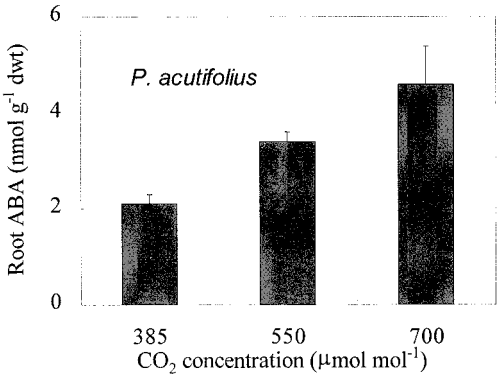

Fig. 4 Root abscisic acid concentrations (nmol g dwt^{-1}) in *Phaseolus acutifolius* under ambient (385 μmol mol^{-1}) and elevated (550 μmol mol^{-1} and 700 μmol mol^{-1}) CO_2. Plants were sampled after ca. 50 d in culture. Data are means for five to six plants ± SE.

ical data. While this technique has been shown to provide an easy way to study threshold and extensibility components of growth (Pritchard et al. 1990), we cannot discount the possibility that it is not sensitive enough to detect small changes in these components or that it is too indirect. Cosgrove (1993*b*) discussed this technique in detail and indicated that in an ideal situation, tissue size should decrease linearly as external osmotic pressure increases. However, Cosgrove (1993*b*) also pointed out that there are many instances of nonlinearity in growth curves in response to external osmotica, where some curves become flatter and others become steeper as osmotic pressure is increased, making determinations of extensibility and yield difficult with this technique. Interestingly, although our curves had nonlinear and small linear portions, we found that roots of plants grown under elevated CO_2 appeared to enter the linear portion of the curve at a higher osmotic pressure than plants grown under ambient concentrations of CO_2 (see fig. 3). This finding would suggest that elevated CO_2 altered root responsiveness to external osmotica. The significance (if any) of this observation remains unclear. Clearly, much more research is needed to confirm this observation and to understand any biological significance. Finally, as Cosgrove (1993*b*) has cautioned, turgor and water potential may not change in tandem in osmotic immersion studies. If this is true, then rheological data should not be collected without direct measurements of turgor using a micropressure probe.

In addition to a root-lengthening response, specific physiological areas of the root appeared to be differentially responsive to elevated CO_2. For example, in this study, the size of the area containing the active root meristem was found to be CO_2-dose responsive. While the significance of a change in meristem size is unclear, Cuadrado et al. (1987) reported that meristem size was inversely correlated to the size of cortical cells in some species and, therefore, may act as a determinant of final root size or length. Though little is known of the specific signals that direct meristem development, ABA has been implicated as a possible regulator of several plant developmental processes (Zeevaart and Creelman 1988). Like many other environmental parameters, elevated atmospheric CO_2 influences ABA metabolism (Brearley et al. 1997; Leymarie et al. 1998). In this study, increasing CO_2 resulted in greater ABA concentrations in roots (fig. 4). While the role of any CO_2-induced ABA is unclear, several roles for ABA in roots have been suggested in the literature that may apply to this case. On one hand, for example, in some species, ABA is known to increase root volume flow (Karmoker and Van Steveninck 1979) and permeability to water (Glinka 1973, 1980; Collins and Kerrigan 1974). On the other hand, there are also reports where applications of ABA result in decreased volume flow (Markhart et al. 1979). Alternatively, ABA may have a role in the control of growth and development of roots (Yamaguchi and Street 1977; Trewavas and Jones 1991). Watts et al. (1981) found that exogenous applications of ABA increased the extension growth of corn roots. Interestingly, Robertson et al. (1990) reported that applications of ABA decreased the size of the zone of cell division, a finding that would be consistent with a role for ABA in regulating the size of the zone of cell division under elevated CO_2.

Finally, the importance of ABA in this system may be related to assimilate mobilization between roots and shoots. Karmoker and Van Steveninck (1979), using *P. vulgaris*, found that applications of ABA induced a redistribution of assimilates from hypocotyls to roots. In this study, CO_2 enrichment of the aerial environment increased starch allocation to the roots of *P. acutifolius* compared to the same plants grown under ambient conditions. Clearly, any firm conclusion about the significance of this finding requires much more information on the distribution and compartmentalization of carbon compounds within the root. Because starch concentration in roots increased with exposure to elevated atmospheric CO_2, it is possible that CO_2 stimulates starch synthesis or decreases utilization (table 3). Our results would suggest that under elevated CO_2, roots are more competitive sinks for assimilates than are young leaves. We cannot dismiss the possibility, however, that roots cultured in hydroponic media may store photoassimilates differently than roots grown in soil. Huber (1983) found that root : shoot ratio is inversely related to starch accumulation in leaves and, therefore, carbohydrate flow may have some role in maintaining root size in *Phaseolus*.

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