Effects of CO₂ enrichment on growth and root $^{15}$NH₄⁺ uptake rate of loblolly pine and ponderosa pine seedlings

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Summary We examined changes in root growth and $^{15}$NH₄⁺ uptake capacity of loblolly pine (Pinus taeda L.) and ponderosa pine (Pinus ponderosa Douglas Ex Laws.) seedlings that were grown in pots in a phytotron at CO₂ partial pressures of 35 or 70 Pa with NH₄⁺ as the sole N source. Kinetics of $^{15}$N-labeled NH₄⁺ uptake were determined in excised roots, whereas total NH₄⁺ uptake and uptake rates were determined in intact root systems following a 48-h labeling of intact seedlings with $^{15}$N. In both species, the elevated CO₂ treatment caused a significant downregulation of $^{15}$NH₄⁺ uptake capacity in excised roots as a result of a severe inhibition of the maximum rate of root $^{15}$NH₄⁺ uptake ($V_{\text{max}}$). Rates of $^{15}$NH₄⁺ uptake in intact roots were, however, unaffected by CO₂ treatment and were on average 4- to 10-fold less than the $V_{\text{max}}$ in excised roots, suggesting that $^{15}$NH₄⁺ absorption from the soil was not limited by the kinetics of root $^{15}$NH₄⁺ uptake. Despite the lack of a CO₂ effect on intact root absorption rates, $^{15}$NH₄⁺ uptake on a per plant basis was enhanced at high CO₂ concentrations in both species, with the relative increase being markedly higher in ponderosa pine than in loblolly pine. High CO₂ concentration increased total $^{15}$NH₄⁺ uptake and the fraction of total biomass allocated to fine roots (< 2 mm in diameter) to a similar relative extent. We suggest that the increased uptake on a per plant basis in response to CO₂ enrichment is largely the result of a compensatory increase in root absorbing surfaces.

Keywords: ammonium uptake, elevated CO₂, Pinus ponderosa, Pinus taeda, root biomass.

Introduction

Uptake and assimilation of carbon (C) and nitrogen (N) by plants are interrelated, and changes in availability or acquisition of one often lead to changes in availability and acquisition of the other (Rufty et al. 1988, Raab and Terry 1995). The projected doubling of the atmospheric CO₂ concentration by mid- to late 21st century (Watson et al. 1990) will increase C availability, but the consequences on plant N acquisition are still unclear. Short-term responses of C₃ species to elevated CO₂ generally include an enhancement of growth (Eamus and Jarvis 1989, Bazzaz 1990, Bowes 1993) and a decline in tissue N concentrations (Conroy 1992), conditions that typify increased N demand. In many natural systems, however, the increased demand for N in response to increasing atmospheric CO₂ concentrations may be compounded by inherently low soil N availability (Allen et al. 1990, Vitousek and Howarth 1991).

Although N limitation does not preclude a short-term positive growth response to CO₂ enrichment, it may negate any long-term positive effects (Kramer 1981, Eamus and Jarvis 1989, Bazzaz 1990) if N gain does not increase in concert with gain in biomass. It is, therefore, crucial to obtain a mechanistic understanding of whether elevated CO₂ can elicit compensatory adjustments (Norby 1994, Rogers et al. 1994) to allow plants to meet the increased N demand. These mechanisms may involve increased association with mycorrhizae and N fixation. Other characteristics that may play an important role in plant nitrogen acquisition in response to elevated CO₂ include changes in root absorption capacity and root growth (Barber 1984, Chapin 1988). According to the models of whole-plant carbon–nutrient balance (Bloom et al. 1985, Johnson 1985, Robinson 1986), resources of abundant availability should be allocated to optimize the acquisition of the most limiting resources. One may, therefore, expect N uptake rate per unit root mass and root growth to be positively affected by CO₂ enrichment.

We used a 48-h $^{15}$NH₄⁺ labeling method to examine the effects of a doubling of the atmospheric CO₂ concentration on total N uptake of loblolly pine (Pinus taeda L.), and ponderosa pine (Pinus ponderosa Douglas Ex Laws.). Seedlings of both species were germinated and grown at CO₂ partial pressures of 35 or 70 Pa for six months. These species dominate more than 20 million ha of southern and western USA forests (Baker and Langdon 1990, Oliver and Ryker 1990) and are both ecologically and commercially important. The major objective was to make a qualitative assessment of the relative importance of root growth and physiological uptake capacity in determining plant N uptake responses to elevated CO₂.
Root/shoot ratio is commonly used to assess compensatory changes in root growth characteristics in response to CO\textsubscript{2} enrichment (Norby 1994, Rogers et al. 1994). Although root/shoot is an important index of compensatory changes in C allocation, it is a poor index of plant potential for nutrient acquisition. This is particularly true for woody species where a large proportion of changes in root biomass may result from changes in the tap root or other highly suberized roots that are not involved in nutrient uptake. We used fine root ratio, defined as the fraction of total plant biomass allocated to fine roots, as a more meaningful measure of root growth, which can potentially alter plant N procurement at elevated CO\textsubscript{2}. We also directly measured net \(^{15}\text{NH}_4^+\) uptake rates both in intact potted root systems and excised root segments and assessed the effects of elevated CO\textsubscript{2} on excised root \(^{15}\text{NH}_4^+\) uptake kinetic parameters, \(V_{\text{max}}\) and \(K_m\).

Materials and methods

**Plant material and growth conditions**

Seeds from a single, wild-type of loblolly pine from the North Carolina Piedmont, USA (North Carolina Forestry Commission, Lot No. LB-NC-P-84-27), and seeds of a half-sib family of ponderosa pine collected from an elevation of 915 m in El Dorado County, CA (California Department of Forestry, Lot No. CDF 526) were germinated and grown in two glasshouses in the Duke University Phytotron (Helmers and Giles 1979). Three seeds of each species were planted in each 3-liter PVC pot filled with sterilized, acid-washed river sand and covered with 1 cm of similarly prepared gravel to reduce evaporative water loss. Approximately two weeks after emergence, seedlings were thinned to one plant per pot.

Diurnal temperature for the duration of the study was maintained at 27/22 °C (day/night), with the thermoperiod adjusted to follow the photoperiod. Relative humidity was 70/90% and solar transmission in the glasshouses was greater than 90%, with a natural photoperiod throughout the experiment (May to November). The CO\textsubscript{2} treatments were initiated on Day 0 by automatically maintaining the ambient CO\textsubscript{2} partial pressures at 35 or 70 Pa. Pots were watered to saturation twice a day for the two-day labeling period was also determined. Thereafter, each pot was irrigated with a nutrient solution in the morning and deionized water every evening. The nutrient solution contained 1 mM of NH\textsubscript{4}Cl as the sole source of N. Ammonium was used as the sole source of N to facilitate calculation of tissue construction cost (Griffin et al. 1996). The nutrient solution was adjusted to pH 4.5 and contained 3.0 μM B, 0.6 mM Ca, 1.2 mM Cl, 2.0 μM Cu, 50.0 μM Fe, 0.8 mM K, 0.5 mM Mg, 6.0 μM Mn, 1.0 μM Mo, 1.0 μM Na, 0.8 mM P, 0.5 mM S and 0.5 μM Zn.

**Biomass and rates of root ammonium uptake**

Seedlings, at about six months old, were harvested, divided into individual plant parts (fine roots, coarse roots, primary needles, fascicles and stems), oven dried to a constant mass and used for biomass determination. Before harvest, two groups of randomly selected seedlings from each CO\textsubscript{2} treatment were used to determine rates of NH\textsubscript{4}\textsuperscript{+} absorption by either an excised or intact root technique. Fine roots were assumed to be exclusively involved in \(^{15}\text{NH}_4^+\) uptake and were defined as white or light-colored roots with a diameter of less than 2 mm.

The excised root method was conducted immediately before harvest. After washing off the adsorbed soil, excised segments (1–2 cm in length) of fine roots from individual plants (five plants per CO\textsubscript{2} treatment) were separated into six random subsamples and placed in a 0.5 mM CaSO\textsubscript{4} solution. The uptake assays were always conducted within half an hour after excision to minimize a possible depression in root carbohydrate reserves. Excised root segments were then placed in tea bags and immersed in a well-aerated assay solution of 99.9 atom% enriched \(^{15}\text{NH}_4\text{Cl}\) at concentrations ranging from 5 to 500 μM. After a 30-min incubation assay period, the roots were rinsed in cold solution containing unlabeled N to replace adsorbed \(^{15}\text{N}\). The roots were subsequently oven-dried and analyzed for \(^{15}\text{N}\) with an element combustion analyzer linked to a mass spectrometer. Kinetic parameters of excised root \(^{15}\text{NH}_4^+\) uptake, \(V_{\text{max}}\) and \(K_m\), were calculated from uptake versus concentration data using Haynes’ plot transformation (Price and Stevens 1989).

Rates of uptake were also determined on a separate group of intact roots (five replications per treatment). The soil was labeled with a 99.9 atom% enriched \(^{15}\text{NH}_4^+\) for about 48 h and rates of \(^{15}\text{NH}_4^+\) uptake and transport to the shoot from total \(^{15}\text{N}\) accumulated in the plant were estimated. Labeling was accomplished by injecting 180 ml of a 1 mM \(^{15}\text{NH}_4\text{Cl}\) applied with a long-needle syringe at various rooting depths to insure a uniform root exposure to \(^{15}\text{N}\) throughout the pot. To reduce dilution of the added \(^{15}\text{N}\) by the residual soil \(^{15}\text{N}\), each pot was rinsed several times to free drainage with deionized water before labeling. The volume of the labeling solution added to each pot was determined to be sufficient to wet the entire pot without causing free drainage. The labeling solution contained other essential elements as described earlier. The procedure was repeated twice during the 48 h of labeling and labeling was terminated by harvesting the plants. The harvested seedlings were then divided into parts (fine roots, coarse roots, primary needles, fascicles and stems), oven-dried and analyzed for \(^{15}\text{N}\). Rates of net root \(^{15}\text{NH}_4^+\) uptake and transport to the shoot were expressed on a fine root dry mass basis only. In addition to estimating rates of \(^{15}\text{NH}_4^+\) absorption and transport to the shoot in intact seedlings, percent allocation of \(^{15}\text{N}\) to various plant parts during the two-day labeling period was also determined.

All data were tested for normal distribution and were log or square root transformed when necessary. Differences between CO\textsubscript{2} treatments were tested by one-way ANOVA, and the Scheffé-box test (Sokal and Rohlf 1981) was used for mean separation of the dependent variables for each species.

**Results**

**Biomass and compensatory root growth**

After 168 days, seedlings grown at elevated CO\textsubscript{2} were substantially larger than those grown at ambient CO\textsubscript{2}. Total biomass increased in response to CO\textsubscript{2} enrichment by 48% (\(P \leq 0.05\)) and 41% (\(P = 0.085\)) in seedlings of ponderosa pine and
loblolly pine, respectively (Table 1). The elevated CO₂ treatment significantly increased fine and coarse root production of seedlings of both species. More importantly, the fraction of total biomass allocated to fine roots (fine root ratio) increased significantly in response to a doubling of the ambient CO₂, i.e., elevated CO₂ led to a 25 and 41% increase in fine root ratio in loblolly pine and ponderosa pine, respectively (Table 1).

**Rate of ¹⁵NH₄⁺ uptake and ¹⁵N allocation**

Rates of ¹⁵NH₄⁺ uptake in excised root segments from both CO₂ treatments were significantly higher in loblolly pine than in ponderosa pine at almost all external ¹⁵NH₄⁺ solution concentrations (Figure 1). However, in both species, CO₂ enrichment negatively affected excised root ¹⁵NH₄⁺ uptake capacity. In both species, the elevated CO₂ treatment reduced maximum root ¹⁵NH₄⁺ uptake rate (Vₘₐₓ) but Kₘ, apparent affinity, was not significantly affected by the CO₂ treatments, although CO₂ enrichment consistently lowered excised root affinity for ¹⁵NH₄⁺ absorption (Figure 1).

Despite the apparent downregulation of excised root NH₄⁺ uptake kinetics by elevated CO₂, the treatment also led to a significant increase in total ¹⁵N gain on a per plant basis in both species when potted seedlings were labeled with ¹⁵NH₄⁺ for 48 h (Table 2). Carbon dioxide enrichment increased total ¹⁵N acquisition by 40 and 20% in ponderosa pine and loblolly pine seedlings, respectively. In both species, rates of ¹⁵NH₄⁺ uptake in intact roots were not significantly affected by CO₂, whereas rates of ¹⁵N transport to the shoot were significantly inhibited by CO₂ enrichment (Table 2). Ammonium uptake rates in intact roots were on average 4- to 10-fold less than the corre-

**Table 1.** Total fine root and coarse root biomass production in loblolly pine and ponderosa pine seedlings grown for six months in either 35 or 70 Pa CO₂. Fine roots are defined as white or light-brown colored roots with a diameter of < 2 mm. Fraction of total biomass allocated to fine roots (last column) is defined as fine root ratio. Values are means ± 1 SE. Means followed by different letters are significantly different at P ≤ 0.05.

<table>
<thead>
<tr>
<th>Species</th>
<th>CO₂ (Pa)</th>
<th>Fine roots (g dry wt)</th>
<th>Coarse roots (g dry wt)</th>
<th>Total biomass (g dry wt)</th>
<th>Fine root ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loblolly pine</td>
<td>35</td>
<td>1.4 ± 0.3 a</td>
<td>0.9 ± 0.1 a</td>
<td>5.6 ± 0.5</td>
<td>0.24 ± 0.01 a</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>2.5 ± 0.3 b</td>
<td>1.7 ± 0.4 b</td>
<td>7.9 ± 1.2</td>
<td>0.30 ± 0.01 b</td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>35</td>
<td>1.10 ± 0.1 a</td>
<td>2.3 ± 0.2 a</td>
<td>6.6 ± 0.5 a</td>
<td>0.17 ± 0.01 a</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>2.30 ± 0.3 b</td>
<td>2.9 ± 0.3 b</td>
<td>9.8 ± 0.9 b</td>
<td>0.24 ± 0.01 b</td>
</tr>
</tbody>
</table>

**Figure 1.** Rates of net ¹⁵NH₄⁺ uptake by excised fine roots of loblolly pine and ponderosa pine seedlings as a function of the external ¹⁵NH₄⁺ concentration. Seedlings were grown for almost six months in either 35 or 70 Pa CO₂. Values are means ± 1 SE. The kinetic parameters are calculated from the Michaelis-Menten relationship between uptake rate and external solution concentration. Means followed by different letters are significantly different at P ≤ 0.05.
sponding $V_{\text{max}}$ values estimated for excised roots (Figure 1 and Table 2).

Elevated CO$_2$ significantly altered the allocation pattern of absorbed $^{15}$N by the intact seedlings of loblolly pine and ponderosa pine. In both species, doubling the ambient CO$_2$ concentration significantly decreased the shoot $^{15}$N pool (Table 2) and significantly increased the $^{15}$N pool of fine roots (Figure 2). With the exception of stems in loblolly pine and stems and primary needles in ponderosa pine, tissue N concentrations of both species were unaffected by the CO$_2$ treatments (Table 3).

**Discussion**

Maximum root NH$_4^+$ uptake rate, $V_{\text{max}}$, was severely depressed in response to CO$_2$ enrichment in both species. The inhibitory effects of CO$_2$ on excised root NH$_4^+$ uptake capacity are consistent with our previous findings for ponderosa pine (BassiriRad et al. 1996a), but not for loblolly pine seedlings (BassiriRad et al. 1996a, BassiriRad et al. 1996b). Nitrogen sources and concentrations can dramatically affect subsequent N uptake, assimilation and partitioning in plants (Haynes and Goh 1978, Bloom 1988, Raab and Terry 1995) and may, therefore, explain the discrepancy observed between the present study and those reported previously. In this study, NH$_4^+$ was the sole source of N and was applied to the seedlings at a concentration of 1 mM every day, whereas in our previous studies, seedlings were grown in the presence of both NH$_4^+$ and NO$_3^-$, with a total N concentration either lower (BassiriRad et al. 1996b) or higher (BassiriRad et al. 1996a) than the present study, and so the results presented here may not be directly comparable with those reported in our previous work.

There is no obvious explanation for the apparent downregulation of NH$_4^+$ uptake capacity in response to elevated CO$_2$ concentration. Uptake of NH$_4^+$ is an energy-requiring process (Haynes and Goh 1978, Bloom et al. 1992) and because high CO$_2$ enhances the supply of root respiratory substrates (Tschaplinski et al. 1993, BassiriRad et al. 1996b), we expected an upregulation of root NH$_4^+$ uptake capacity in response to CO$_2$ enrichment. Ammonium uptake is also known to be regulated under a feedback control by shoot demand and by root pool of reduced N, e.g., amino acids (Glass and Siddiqi 1995). A significantly larger proportion of the reduced N pool (assuming that after 48 h of labeling tissue, $^{15}$N exists almost exclusively in the reduced N form) remained in the fine root fraction of seedlings in the elevated CO$_2$ treatment than in the ambient CO$_2$ treatment (Figure 2). Accumulation of reduced N in fine roots may therefore be responsible for the inhibitory effects of CO$_2$ on NH$_4^+$ uptake. Although we have shown that CO$_2$ enrichment significantly inhibited $^{15}$N transport capacity to the shoot (Table 2), we were unable to determine if this response was caused by a change in root transport properties per se or by changes in shoot N demand.

Despite the repression of NH$_4^+$ absorption capacity, actual uptake rates estimated on intact root systems were not significantly affected by CO$_2$ and were as much as 10-fold lower than the estimated $V_{\text{max}}$ in excised roots (Table 2, Figure 1). These observations strongly suggest that soil solution concentration of NH$_4^+$ near the intact root surfaces must have been considerably less than that associated with excised roots (Figure 1), and that changes in root kinetic parameters had no significant effect on actual NH$_4^+$ uptake regardless of the CO$_2$ treatment. Although NH$_4^+$ is a relatively mobile ion, i.e., it is more mobile than PO$_4^{3-}$ but less mobile than NO$_3^-$ and K$^+$, its movement to

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**Table 2. Effects of CO$_2$ concentration on $^{15}$N uptake from a two-day labeling of 6-month-old seedlings of loblolly pine and ponderosa pine grown at either 35 or 70 Pa CO$_2$: Net $^{15}$N gain is expressed on a per plant basis for the entire two days of labeling. Rates of uptake and transport to the shoot are expressed on a fine root dry mass basis. The % $^{15}$N translocated to the shoot was calculated from the data in Figure 2. Means followed by a different letter are significantly different at $P \leq 0.05$.**

<table>
<thead>
<tr>
<th>Species</th>
<th>CO$_2$ (Pa)</th>
<th>Net $^{15}$N gain rate (µmol g$^{-1}$ h$^{-1}$)</th>
<th>Net $^{15}$N transport rate to shoot (µmol g$^{-1}$ h$^{-1}$)</th>
<th>$^{15}$N Allocation to shoot (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loblolly pine</td>
<td>35</td>
<td>2.3 ± 0.1</td>
<td>1.4 ± 0.2</td>
<td>61 ± 2 b</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>1.9 ± 0.2</td>
<td>0.9 ± 0.1</td>
<td>43 ± 4 a</td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>35</td>
<td>2.9 ± 0.4</td>
<td>1.7 ± 0.2</td>
<td>59 ± 1 b</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>2.3 ± 0.1</td>
<td>1.1 ± 0.1</td>
<td>50 ± 2 a</td>
</tr>
</tbody>
</table>

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Figure 2. Allocation pattern of $^{15}$N between various tissue types of loblolly pine and ponderosa pine seedlings grown for almost six months in either 35 or 70 Pa CO$_2$. Potted seedlings were labeled with a 1 mM $^{15}$NH$_4^+$Cl for 48 h and the $^{15}$N pool in each tissue type was determined from the product of dry biomass and $^{15}$N concentration.
Table 3. Nitrogen concentration (mg g$^{-1}$) in various tissues of loblolly and ponderosa pine seedlings grown for 6 months at either 35 or 70 Pa CO$_2$. Values are means followed by ± 1 SE.

<table>
<thead>
<tr>
<th>Species</th>
<th>CO$_2$ (Pa)</th>
<th>Fine roots (mg N g$_{dw}$$^{-1}$)</th>
<th>Coarse roots (mg N g$_{dw}$$^{-1}$)</th>
<th>Primary needles (mg N g$_{dw}$$^{-1}$)</th>
<th>Fascicles (mg N g$_{dw}$$^{-1}$)</th>
<th>Stem (mg N g$_{dw}$$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loblolly pine</td>
<td>35</td>
<td>11.5 ± 0.7</td>
<td>5.6 ± 0.2</td>
<td>19.3 ± 0.8</td>
<td>21.3 ± 0.8</td>
<td>9.6 ± 1.0 a</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>12.2 ± 1.2</td>
<td>7.3 ± 0.7</td>
<td>20.8 ± 1.8</td>
<td>21.2 ± 1.2</td>
<td>13.7 ± 1.5 b</td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>35</td>
<td>11.8 ± 0.3</td>
<td>8.5 ± 0.4</td>
<td>24.3 ± 1.7 b</td>
<td>19.5 ± 0.6</td>
<td>16.6 ± 1.4 b</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>11.5 ± 0.5</td>
<td>6.7 ± 0.7</td>
<td>17.1 ± 1.1 a</td>
<td>18.4 ± 1.3</td>
<td>11.0 ± 1.0 a</td>
</tr>
</tbody>
</table>

the root is diffusion limited (Nye and Tinker 1977). We conclude, therefore, that even if CO$_2$ had induced a compensatory increase in root NH$_4^+$ uptake capacity, the adjustment had no effect on NH$_4^+$ uptake responses to high CO$_2$. This conclusion may not be valid when soil NH$_4^+$ concentration adjacent to root surfaces is high and is continuously replenished.

Sensitivity analyses of NH$_4^+$ uptake models often indicate that root growth and morphological characteristics such as root diameter, root length density and total root length are more important than kinetics of root NH$_4^+$ uptake in determining actual uptake of NH$_4^+$ (Barber and Silberbush 1984). We also conclude that compensatory root growth adjustment was more important in determining the NH$_4^+$ uptake response of these two conifers to a doubling of the CO$_2$ concentration than the kinetics of root NH$_4^+$ uptake. We found that CO$_2$ enrichment increased fine root ratio and total plant $^{15}$N uptake to a similar extent, i.e., elevated CO$_2$ increased total $^{15}$NH$_4^+$ gain per plant by 20 and 40% and increased fine root ratio by 25 and 40% in loblolly pine and ponderosa pine seedlings, respectively. In an earlier study, we found that when N (both NH$_4^+$ and NO$_3^-$) was applied daily at a concentration of almost 4 mM, the fractions of total biomass allocated to fine roots of the two species were about half of those reported here and that they did not change with increased CO$_2$ concentrations (BassiriRad et al. 1996a). When two dominant shrubs of the southwestern US deserts, Larrea tridentata (DC.) Cov. and Prosopis were grown on a relatively high NO$_3^-$ supply (2 mM daily), elevated CO$_2$ decreased the fine root ratio (BassiriRad, unpublished observations). Furthermore, enhancement of biomass allocation to roots in response to CO$_2$ enrichment, which is commonly observed under nutrient-limiting conditions (McDonald et al. 1991, Ericsson et al. 1992), can be suppressed if nutrient limitation is avoided (Pettersson and McDonald 1992).

Conclusions

We conclude that the relative contribution of changes in root growth versus physiological uptake capacity in determining N acquisition responses to elevated CO$_2$ may largely depend on N concentration or N form or both. Hence, in developing a mechanistic understanding of how roots may alter plant N acquisition in response to high CO$_2$, caution must be exercised in interpreting the data. We suggest that if soil available N is relatively low and is dominated by NH$_4^+$, compensatory changes in root growth may be the most important root characteristic determining plant N uptake responses to high CO$_2$.

Because elevated CO$_2$ often leads to an ontogenic shift in plant growth and development (Coleman 1993, 1994), it is also important to determine if phenotypic or physiological adjustments represent direct effects of CO$_2$ or simply a change in stages of development. Furthermore, a more accurate prediction of plant and ecosystem responses to elevated CO$_2$ must include other factors that may affect nutrient acquisition. For example, acquisition of relatively immobile ions such as phosphorus can be substantially facilitated by increased association with symbiotic ectomycorrhizal fungi. Mycorrhizae also play a crucial role in regulating plant N uptake in many temperate forest species and must be considered when examining compensatory changes in plant nutrient acquisition in response to CO$_2$ enrichment.

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References


