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# Root system adjustments: regulation of plant nutrient uptake and growth responses to elevated $CO_2$

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**Abstract** Nutrients such as nitrogen (N) and phosphorus (P) often limit plant growth rate and production in natural and agricultural ecosystems. Limited availability of these nutrients is also a major factor influencing long-term plant and ecosystem responses to rising atmospheric $CO_2$ levels, i.e., the commonly observed short-term increase in plant biomass may not be sustained over the long-term. Therefore, it is critical to obtain a mechanistic understanding of whether elevated $CO_2$ can elicit compensatory adjustments such that acquisition capacity for minerals increases in concert with carbon (C) uptake. Compensatory adjustments such as increases in (a) root mycorrhizal infection, (b) root-to-shoot ratio and changes in root morphology and architecture, (c) root nutrient absorption capacity, and (d) nutrient-use efficiency can enable plants to meet an increased nutrient demand under high $CO_2$. Here we examine the literature to assess the extent to which these mechanisms have been shown to respond to high $CO_2$. The literature survey reveals no consistent pattern either in direction or magnitude of responses of these mechanisms to high $CO_2$. This apparent lack of a pattern may represent variations in experimental protocol and/or interspecific differences. We found that in addressing nutrient uptake responses to high $CO_2$ most investigators have examined these mechanisms in isolation. Because such mechanisms can potentially counterbalance one another, a more reliable prediction of elevated $CO_2$ responses requires experimental designs that integrate all mechanisms simultaneously. Finally, we present a functional balance (FB) model as an example of how root system adjustments and nitrogen-use efficiency can be integrated to assess growth responses to high $CO_2$. The FB model suggests that the mechanisms of increased N uptake highlighted here have different weights in determining overall plant responses to high $CO_2$. For example, while changes in root-to-shoot biomass allocation, $r$, have a small effect on growth, adjustments in uptake rate per unit root mass, $\bar{v}$, and photosynthetic N use efficiency, $p^*$, have a significantly greater leverage on growth responses to elevated $CO_2$ except when relative growth rate (RGR) reaches its developmental limit, maximum RGR ($RGR_{max}$).

**Keywords** Elevated $CO_2$ · Nutrients · Root system adjustments · Mycorrhizae

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## Introduction

As the debate about the potential impact of high $CO_2$ levels on plant communities intensifies, it is becoming increasingly evident that both the magnitude and direction of such responses will be determined by the availability of other environmental resources (e.g., water, nutrients, and light) and regulators (e.g., temperature and salinity). Even though short-term exposure to $CO_2$ enrichment often stimulates growth and photosynthetic C fixation, in most managed and natural ecosystems long-term growth and photosynthetic responses may be confined by the limited availability of mineral nutrients, particularly nitrogen (N) and phosphorus (P) (Kramer 1981; Eamus and Jarvis 1989; Bazzaz 1990; Conroy 1992; Sinclair 1992; McKee and Woodward 1994; Wolfenden and Diggle 1995; Lloyd and Farquhar 1996). Therefore, factors that may affect availability and uptake of nutrients are critical in determining plant and ecosystem responses to high $CO_2$.

During the initial stages of acclimation to high $CO_2$, higher growth rate should increase plant nutrient demand (Conroy and Hocking 1993; Baxter et al. 1994). Although this greater demand can be partially offset by increased nutrient use efficiency (Conroy et al. 1992; Xu et

al. 1994; Newbery et al. 1995), there is no evidence that such a positive response to elevated $CO_2$ can be sustained over the long term without a concomitant increase in availability and/or acquisition of growth limiting nutrients. There are several ecosystem- and plant-level mechanisms that could compensate for the greater nutrient demand under high $CO_2$. Here we make a clear distinction between responses in ecosystem availability of nutrients as opposed to plant ability to take up nutrients. For example, a greater belowground C allocation in response to elevated $CO_2$ may result in increased microbial activity (Dhillion et al. 1996) accompanied by higher mineralization and plant uptake (Zak et al. 1993; Rice et al. 1994) though this effect is not universally observed (Diaz et al. 1993). In a grassland system, Hungate et al. (1997) also showed enhanced microbial activity and N mineralization in response to elevated $CO_2$, but this enhancement was caused by reduced transpiration and improved soil moisture rather than improved C supply to the soil. Because elevated $CO_2$ generally reduces transpiration rate, it is also possible that availability of other nutrients at the root surface becomes affected by changes in soil moisture, mass flow, and diffusion. Van Vuuren et al. (1997) showed that high $CO_2$ suppressed water use in wheat and improved soil water availability. They suggested that the reduced water use observed in plants grown under high $CO_2$ decreased mass flow of $K^+$ to the root but this effect was offset by faster diffusion which resulted from the wetter soil.

Availability of nutrients such as N in many ecosystems could also increase due to chronic deposition of atmospheric N (Ollinger et al. 1993; Lovett 1994; Galloway et al. 1995; Vitousek et al. 1997; Norby 1998). Whether ecosystem availability of nutrients in response to rising $CO_2$ concentration will keep pace with increased plant nutrient demand will not be the focus of this review. However, such information is important for models designed to reliably predict $CO_2$ responses in natural ecosystems.

The main focus of this paper is to evaluate plant-level processes that influence nutrient acquisition under high $CO_2$. We discuss here specifically the relative growth rate (RGR) and net primary productivity (PP; gross or net) as two primary measures of performance. Plants posses a suite of potential mechanisms that could enhance their capacity to capture nutrients. These compensatory adjustments are depicted in Fig. 1 and include: (a) increased symbiotic association with mycorrhizal fungi or $N_2$-fixing organisms, (b) increased root-to-shoot ratio and changes in root morphology and architecture, and (c) enhanced root physiological uptake capacity for nutrients. All these compensatory mechanisms would require additional expenditure of C and should potentially benefit from elevated $CO_2$. Alternatively, plants could (d) decrease physiological demand to circumvent nutrient limitation of growth (Fig. 1). The extent to which these mechanisms have been demonstrated to respond to $CO_2$ enrichment is reviewed in the following section. Because very few $CO_2$ studies have addressed nutrients other than N, this review is largely focused on the role of these mechanisms in N uptake and growth responses to high $CO_2$.

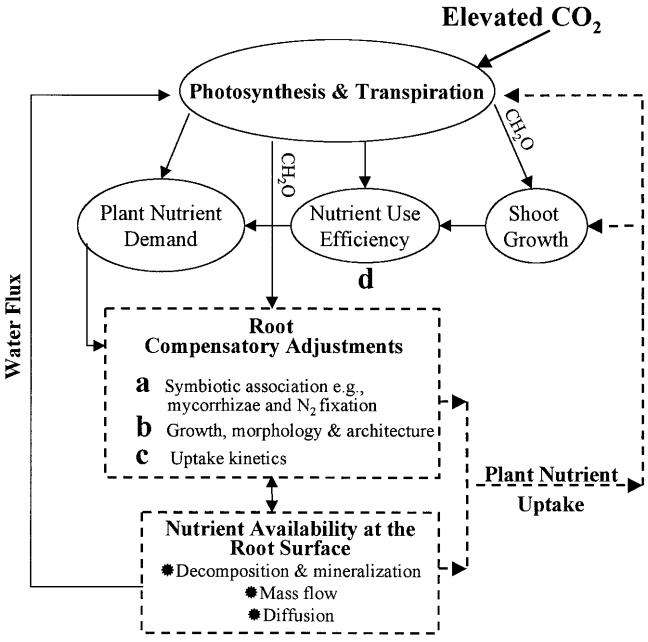


**Fig. 1** A conceptual model depicting various mechanisms by which plants can meet increased nitrogen demand under elevated $CO_2$ levels. *Dashed* and *solid lines* represent supply and demand components of plant nutrient status, respectively

The review presented here examines these as compensatory mechanisms, rather than as single variables. Finally, a physiologically based functional balance model is proposed as an example of how these mechanisms can be incorporated into a model designed to determine relative leverage of each of the mechanisms discussed here on overall nutrient uptake and growth responses to high $CO_2$.

## Plant-level responses to $CO_2$ enrichment

### Increased symbiotic association with mycorrhizal fungi

Increased association with $N_2$ fixing organisms and mycorrhizal fungi is an effective mechanism by which plants could increase their nutrient uptake per mass of root under high $CO_2$, thereby increasing RGR and PP. Several studies have shown that elevated $CO_2$ stimulates $N_2$ fixation in crop and nonagricultural species (see the review by Phillips et al. 1976; Allen et al. 1988; Arnone and Gordon 1990; Thomas et al. 1991; Soussana and Hartwig 1996) and by actinomycetes (Vogel et al. 1997), but only a small fraction of species from natural and agronomic ecosystems are $N_2$ fixers. In contrast, roots of the majority of terrestrial plants form mycorrhizal associations. Furthermore, unlike $N_2$-fixing bacteria which are beneficial only for the N economy of plants, symbiotic associations with mycorrhizal fungi can potentially

**Table 1** Plant and mycorrhizal mass increase under elevated compared with ambient $CO_2$. The mass estimate under elevated conditions was divided by the mass estimate under ambient conditions in each case. Fungal mass was estimated as length or mass of colonized root, or by multiplying percent colonization times fine root length

| Plant mass E/A ratio | Fungal mass E/A ratio | Plant species | Reference |
|---|---|---|---|
| Ectomycorrhizas | | | |
| 2.10 | 2.19 | *Quercus alba* | Norby et al. 1986 |
| 1.26 | 3.07 | *Pinus echinata* | O'Neill et al. 1987 |
| 1.35 | 1.24 | *P. sylvestris* | Perez-Soba et al. 1995 |
| 0.96 | 2.44 | *P. ponderosa*, low soil P | Walker et al. 1995 |
| 1.49 | 2.66 | *P. ponderosa*, medium soil P | Walker et al. 1995 |
| 1.46 | 1.58 | *P. ponderosa*, high soil P | Walker et al. 1995 |
| 1.14 | 1.80 | *Betula alleghaniensis* | Berntson and Bazzaz 1997 |
| 1.11 | 1.74 | *B. papyrifera* | Godbold et al. 1997 |
| 1.31 | 2.10 | *P. strobus* | Godbold et al. 1997 |
| Arbuscular mycorrhizas | | | |
| 1.35 | 1.02 | *Tsuga canadensis* | Godbold et al. 1997 |
| 1.25 | 3.50 | *Populus euroamericana* | Lussenhop et al. 1998, Pregitzer et al. 1995 |

influence uptake of a number of macronutrients, e.g., P and K, and micronutrients, e.g., Cu, Zn, and Mn (Smith and Read 1997). The quantitative expectations are twofold: (1) that mycorrhizal fungi (MRF) have greater surface-to-volume ratios than roots: thus, for similar uptake capacities per area, they have greater uptake capacity per mass or volume, and this rate is most directly related to RGR (see Modeling synthesis section); (2) there is less limitation of uptake by soil diffusive resistance, for fine structures (MRF hyphae) than for coarser structures (roots). The transport theory underlying this assertion has long been known (Nye and Tinker 1977) and is applied in the modeling section below. Of course, on a whole-ecosystem basis, MRF activity itself does not directly increase season-total nutrient availability per ground area. To a first approximation, total uptake is not altered but uptake is redistributed in time. This is less important for primary productivity than for physiological competition and for fitness (partitioning of dry matter to reproductive structures, as seeds or ramets).

The idea that mycorrhizas might benefit plants more under elevated than under ambient $CO_2$ is attractive because it is easy to assume that under elevated $CO_2$ plants will allocate more C to mycorrhizal fungi, and more nutrients will be translocated to the plant in return. But one might alternatively assume that plants allocating more C to mycorrhizal fungi will increase fungal C:nutrient ratios and make the fungus less likely to translocate nutrient to the host plant. In the absence of direct evidence of mycorrhizal benefits to plants under elevated atmospheric $CO_2$, two indices of increased benefit have been suggested. The first index is relative increase in mycorrhizal mass compared with the relative increase in plant mass. It is based on the assumption that under elevated compared with ambient $CO_2$, mycorrhizal mass should increase relatively more than plant mass. The index assumes that if plants allocate more C to mycorrhizal fungi, more nutrients will be taken up and translocated to them. The second index is the relative increase in whole-plant nutrient content compared with the relative increase in plant mass. It is based on the assumption that under elevated compared with ambient $CO_2$, whole-plant nutrient content should increase relatively more than plant mass. Simply, nutrient concentrations, $f_n$, should increase when mycorrhizal and non-mycorrhizal plants are compared. This mycorrhiza-induced shift in $f_n$ overlies a general decrease in $f_n$ caused by $CO_2$ that is well-explained by functional balance (see modeling section).

O'Neill (1994) summarized the literature and concluded that under elevated compared with ambient $CO_2$, arbuscular mycorrhizal mass increased in proportion to root system mass, but ectomycorrhizal mass increased more than root system mass. Her summary was based primarily on reports of percent increase in mycorrhizal colonization of roots. It is difficult to judge whether mycorrhizal mass increased relative to whole-plant mass without fine root and whole-plant biomass data in addition to percent colonization. We are aware of only eight studies that allow one to estimate the relative increase in mycorrhizal and whole-plant mass under elevated, compared with ambient $CO_2$. Almost all are for ectomycorrhizal plants. They show that in six of seven ectomycorrhizal and one of two arbuscular mycorrhizal mass increased more than plant mass under elevated compared with ambient $CO_2$. Although there have been many reports of arbuscular mycorrhizal percent infection under elevated $CO_2$, only two studies report enough information to compare plant and mycorrhizal mass responses, and they conflict (Table 1).

Mycorrhizal mass may not be a good index of mycorrhizal benefit for two reasons. First, the various structures of mycorrhizae are rarely all sampled. For example hyphae might become denser in the cortex of arbuscular mycorrhizal roots. Rillig et al. (1998) showed this by counting hyphae within arbuscular mycorrhizal roots. They found more fungal tissue in the cortex of *Bromus hordeaceus* when grown under elevated than when grown under ambient $CO_2$. A second component of mycorrhizal mass that could increase under elevated $CO_2$ is

**Table 2** Whole-plant N and P status under elevated $CO_2$ with (*M*) and without (*NM*) mycorrhizas. *Values* represent mycorrhizal divided by non-mycorrhizal plants. The data also show the relative impact of mycorrhizae on whole-plant biomass

| Whole-plant nutrient ratio M/NM | | Plant mass ratio M/NM | Plant and fungal species | References |
|---|---|---|---|---|
| P | N | | | |
| Ectomycorrhizas | | | | |
| 1.19 | n.d. | 1.19 | *Pinus taeda*+*Pisolithus tinctorius*; low P | Lewis and Strain 1996; Lewis et al. 1994 |
| 1.15 | 0.96 | 0.78 | *Pinus sylvestris*+*Paxillus involutus* | Rouhier and Read 1998a |
| 1.22 | 1.17 | 0.68 | *Pinus sylvestris*+*Suillus bovinus* | Rouhier and Read 1998a |
| Arbuscular mycorrhizas | | | | |
| 1.22 | 1.55 | 1.28 | *Trifolium repens*+*Glomus mosseae* | Jongen et al. 1996 |
| 1.98 | 1.50 | 1.32 | *Beilschmiedia pendula*+indigenous inoculum | Lovelock et al. 1996 |
| 12.16 | n.d. | 4.00 | *Plantago lanceolata*+indigenous inoculum | Rouhier and Read 1998b |
| 3.08 | 1.38 | 1.6 | *Citrus aurantium*+*Glomus intrardadices*; low soil P | Syvertsen and Graham 1999 |
| 2.33 | 1.09 | 1.49 | *Citrus sinensis*+*Glomus intraradices*; low soil P | Syvertsen and Graham 1999 |

extramatrical hyphae. Klironomos et al. (1997) reported that extramatrical hyphae of arbuscular mycorrhizas of *Populus tremuloides* increased 77% in low N soil under elevated compared with ambient $CO_2$. Also Rillig et al. (1998) reported that the length of extramatrical hyphae of arbuscular mycorrhizae in a sandstone grassland increased 180%, but did not increase in a serpentine grassland under elevated compared to ambient $CO_2$. A second reason why mycorrhizal mass may not be a good index of mycorrhizal benefit to plants is that there is no relationship between mycorrhizal mass and either plant mass or nutrient uptake. McGonigle (1988) showed that there was no relationship between percent of arbuscular mycorrhizal roots and plant mass in a review of 78 field trials. Further, Wallander et al. (1999) showed that there may be a decrease in ectomycorrhizal sheath mass with increasing availability of N.

A second index of mycorrhizal benefit is greater increase in whole-plant P or N than in whole-plant mass under elevated than ambient $CO_2$. There is some evidence to support the value of this index. Stribley et al. (1980), for example, surveyed 13 studies of arbuscular mycorrhizas and found that shoot P increased more than shoot mass of plants with and without mycorrhizas. O'Neill et al. (1987) suggested that the same pattern should occur with ectomycorrhizas under elevated $CO_2$. They reasoned that if mycorrhizae are more beneficial under elevated than ambient $CO_2$, then P or N should increase more than plant mass in mycorrhizal than non-mycorrhizal plants. Seven plant species have been grown under elevated $CO_2$ with mycorrhizal inoculum present or absent (Table 2). In six of eight cases whole-plant P increased more than plant mass when plants grown under elevated $CO_2$ with and without mycorrhizas were compared. In four of six cases whole-plant N increased more than plant mass when plants grown under elevated $CO_2$ with and without mycorrhizas were compared. The greater increase in nutrients than in mass when mycorrhizas were present suggests increased mycorrhizal benefit under elevated compared with ambient $CO_2$.

In sum, pot experiments suggest that in mycorrhizal plants nutrients increased relatively more than plant mass under elevated compared with ambient $CO_2$. This relative increase was greater for P than for N. The increase in ectomycorrhizal mass relative to plant mass under elevated $CO_2$ is a poor index of benefit, and might indicate parasitism rather than mutualism.

## Increased root-to-shoot ratio and changes in morphology and architecture

Intuitively, increased root growth is another strategy for plants to cope with conditions of low nutrient availability, by either directly increasing the volume of soil explored or indirectly by providing a more extensive platform for mycorrhizal growth (Norby et al. 1986). Our functional balance model (see Modeling synthesis) quantifies two effects of increased root allocation, expressed as root-to-shoot ratio, $r$. For a fixed rate of nutrient uptake per mass of root, $\bar{v}$, whole-plant uptake per mass of plant scales as $r \times \bar{v}$. This gain is compensated by lower allocation to photosynthetic structures, in the proportion $(1+r)$. In functional balance, RGR is proportional to $\sqrt{r \times \bar{v}}/(1+r)$, which is a very weak function of $r$. The greater benefit of increased $r$ may be allocation selectively to support of MRF, which have higher uptake rates, $\bar{v}$ than do roots.

There is a considerable debate as to whether high $CO_2$ stimulates root biomass allocation (Stulen and den Hertog 1993). Although earlier literature indicated that elevated $CO_2$ almost universally increased root-to-shoot ratio (Eamus and Jarvis 1989; Bazzaz 1990; Poorter 1993), more recent literature reveals a less pronounced effect (Norby 1994; Rogers et al. 1994). Ceulemans and Mousseau (1994) reviewed the literature between 1989 and 1993 for woody plants and confirmed the earlier conclusions that more biomass is allocated to roots in response to high $CO_2$ but such a shift in biomass was less likely when supplemental N was added to the experi-

mental plants. In contrast, in a survey of 224 observations of woody plants grown at high $CO_2$, Wullschleger et al. (1995) found a significant increase in root-to-shoot ratio in only 6% of cases. Norby (1994) also concluded that elevated $CO_2$ does not lead to a significant shift in biomass allocation regardless of soil N availability. The conclusion that elevated $CO_2$ will not alter biomass allocation to roots is further confirmed by results of a meta analysis by Curtis and Wang (1998) and the earlier review by McGuire et al. (1995).

Obviously the task of reliably comparing results from the literature is confounded by differences in experimental protocols. When experimental conditions are similar, it is often observed that changes in root-to-shoot ratio in response to $CO_2$ enrichment depend on soil nutrient availability, i.e., increased root-to-shoot ratio is often associated with nutrient limitation (Ericsson et al. 1992; McDonald et al. 1991) a response that could be suppressed when nutrient limitation is avoided (Bazzaz 1990; Pettersson and McDonald 1992; Ceulemans and Mousseau 1994). In a survey of more than 40 tree species, McGuire et al. (1995) found that as N availability increased, the $CO_2$-induced increase in biomass allocation to roots was substantially decreased and overall the effect was not statistically significant. However, they attributed the lack of a statistical difference in root-to-shoot ratio at high versus low N availability to an inadequate sample size.

In addressing the effects of elevated $CO_2$ on root growth, particularly as it relates to plant nutrient uptake, caution must be exercised. For example, a mere increase in root-to-shoot ratio may not be important in terms of plant nutrient acquisition, though it is an important parameter in terms of plant C allocation, particularly if biomass is allocated into tap roots or other highly suberized components of the root system not involved in nutrient uptake. Even when it is used to evaluate C partitioning in response to $CO_2$, root-to-shoot ratio may be a poor indicator of root carbon allocation since it does not take into account biomass lost by fine root turnover (Pregitzer et al. 1995) or root exudation. Therefore, a more relevant indicator of root characteristics that could potentially enhance plant nutrient capture is the proportion of biomass allocated to fine roots (BassiriRad et al. 1996a, 1997a, 1997b). Fine root ratio, defined as fine roots relative to total plant biomass, is sensitive to nutrient availability (Körner and Renhardt 1987), but depending upon the species, it may or may not be sensitive to growth at elevated $CO_2$ (BassiriRad et al. 1997b).

Changes in biomass allocation to fine roots in response to $CO_2$ enrichment must also be viewed in the context of root turnover. In many deciduous forest species fine root turnover can account for as much as 80% of annual NPP (Ceulemans and Mousseau 1994). Pregitzer et al. (1995) showed that growth in high $CO_2$ increased root turnover in *Populus tremuloides*. Elevated $CO_2$ has also been shown to increase root turnover in a number of grassland species (Fitter et al. 1996, 1997; Hungate et al. 1997). Therefore evaluation of biomass allocation to fine roots based on a single or infrequent harvests of standing roots will not be useful to assess the long term impact of $CO_2$ on nutrient uptake. Root turnover must also be evaluated relative to nutrients provided to the shoot; a higher ratio of nutrients to turnover is adaptive.

Alterations in root morphology (e.g., root length and radius) and architecture (e.g., branching pattern) are also effective mechanisms that influence plant nutrient acquisition (Barber 1984; Caldwell 1987; Fitter and Hay 1987). Finer roots can confer greater nutrient uptake per unit root mass, as discussed earlier for mycorrhizal fungi. Quantitative assessment of such root characteristics, particularly in natural ecosystems, are difficult, which is perhaps why very little information is available as to how these parameters change in response to high $CO_2$. In a growth-chamber study, Rogers et al. (1992) demonstrated that elevated $CO_2$ doubled root length and increased root diameter by 27% but had no effect on the number of the first-order laterals. Ferris and Taylor (1995) found that elevated $CO_2$ had contrasting effects on root morphological and architectural characteristics among four native chalk grassland species. After 100 days of treatment, root-to-shoot ratio was unchanged but root length was significantly higher in three out of four species grown at high versus ambient $CO_2$. In contrast, specific root length (m $g^{-1}$) significantly increased in response to $CO_2$ enrichment in only one of the four species. Berntson and Woodward (1992) examined root branching pattern of *Senecio vulgaris*, a common fast-growing annual in Britain, and found that elevated $CO_2$ resulted in longer roots and increased root branching. However, they found that root density (root length per volume of soil) was unaffected by growth at high $CO_2$. More recently Berntson and Bazzaz (1997) examined a number of architectural parameters in roots of yellow birch and found no elevated $CO_2$ effects on specific root length and specific root number.

The growth and morphological characteristics discussed here are all important factors in plant nutrient acquisition and many of them appear to respond to $CO_2$ enrichment. However, studies of root morphology and architecture have seldom, if ever, shown a direct link between these structural characteristics and nutrient uptake responses to high $CO_2$. Future studies must make such linkages in order to establish a clear cause and effect relationship between form and function. Such a linkage is also necessary to build more robust mechanistic models designed to predict whole-plant and ecosystem responses to $CO_2$.

## Enhanced root physiological uptake capacity

Another potentially important mechanism that could influence plant nutrient uptake is root physiological uptake capacity (Nye and Tinker 1977; Barber 1984; Chapin 1988). In general, Michaelis-Menten kinetics describe uptake well at realistic soil concentrations, so that physi-

ological uptake capacity, $\bar{v}$, is expressible in terms of maximal uptake capacity, $V_{max}$, and the affinity, $1/K_m$, where $K_m$ is the Michaelis-Menten constant. Consequently, achieved uptake rate is simply

$$\bar{v} = \frac{V_{\max} c_a}{(c_a + K_m)} \quad (1)$$

where $c_a$ is the nutrient concentration at the root surface. In real soils, diffusion kinetics cause $c_a$ to decline as $V_{max}$ increases, such that increases in $V_{max}$ are quite ineffective in increasing RGR over wide ranges of soil nutrient concentrations and diffusivities (see Modeling synthesis). One may ask why increases in $V_{max}$ are expressed; the answer is often elusive (see, e.g., Gutschick 1993).

While kinetic parameters may have a (weak or strong) regulatory role in plant nutrient budgets, changes in $V_{max}$ and $K_m$ in response to elevated $CO_2$ have rarely been examined. Root uptake and assimilation of N and P are energy demanding processes (Lambers et al. 1991; Bloom et al. 1992; Pilbeam and Kirkby 1990) with carbohydrates derived from photosynthesis providing the required energy (ATP) and reductants (NADH, NADPH). Because $CO_2$ enrichment increases the availability of root respiratory substrates (Tschaplinski et al. 1993; BassiriRad et al. 1996b), metabolically regulated processes such as active nutrient uptake might be stimulated under high $CO_2$.

In many nutrient-limited habitats, however, carbohydrate availability seldom limits nutrient uptake (Chapin et al. 1995). Furthermore, although an adequate supply of carbohydrates is often required for root nutrient uptake capacity, C supply does not necessarily regulate changes in ion uptake: the nutrient flow to root re-circulating from the shoot is a stronger controller (Glass 1989). In fact, BassiriRad et al. (1996a) found that kinetics of root $NH_4^+$ uptake in field grown loblolly pine saplings was unaffected by growth $CO_2$ concentration even though total non-structural carbohydrates were significantly higher in fine roots of the high $CO_2$ saplings. Similarly, in pot-grown cotton grass seedlings, root carbohydrate status increased significantly in response to high $CO_2$ without a significant effect on kinetics of root $PO_4^{3-}$ uptake (BassiriRad et al. 1996a). Even more contrary to the energetic expectation is the finding by BassiriRad et al. (1996b) showing a marked decrease in the rate of root $NH_4^+$ uptake of both loblolly and ponderosa pine seedlings in response to $CO_2$ enrichment.

Studies by BassiriRad et al. (1996a, 1996b, 1997a) are based on determining root kinetic parameters using a Michaelis-Menten model. In this approach, root uptake rate of the target ion was determined at a minimum of six external concentrations in the high affinity uptake range. Jackson and Reynolds (1996) used an excised root technique to examine the rate of either $NH_4^+$ or $NO_3^-$ uptake of six annual grassland species at a single concentration of the inorganic N forms. They found no significant effect of high $CO_2$ on $NH_4^+$ uptake whereas $NO_3^-$ uptake rate significantly decreased in response to $CO_2$ enrichment. In intact roots of loblolly and ponderosa pine seedlings, a single uptake technique showed that elevated $CO_2$ significantly increased $NO_3^-$ uptake rate but decreased the uptake rates for $NH_4^+$ (BassiriRad et al. 1997a) leading to no significant effect on total N uptake rate. Newbery et al. (1995) examined the effect of $CO_2$ on root physiological uptake capacity for N, P, and K in *Agrostis capallaris*. They used three different concentrations in the uptake medium and found that elevated $CO_2$ did not significantly affect the rate of root N, P and K uptake.

Luo et al. (1999) highlighted the fact that a wide range of kinetic responses to high $CO_2$ have been reported and warned against generalization in this area until more data become available. The contradictory responses reported in this area (Fig. 2) may have several origins, some of which may represent differences in the assay techniques. However, a larger portion of the variation may represent true differences among species. Such species differences will have significant ecological consequences, but as Norby et al. (1999) pointed, "without a rigorous demonstration that species were responsible for differences in observed $CO_2$ responses in a controlled experiment, this common reliance on 'species differences' to account for disparate responses should be avoided". In a recent study, Zerihun and BassiriRad (2000) examined this question using seedlings of six tree species and showed that under identical experimental conditions kinetics of root $NH_4^+$ uptake responses to elevated $CO_2$ were highly species specific. BassiriRad et al. (1997b) also found that, depending on species, root $NO_3^-$ absorption rate doubled or halved in response to doubling of the atmospheric $CO_2$ concentration. Inter-specific differences in responses in root physiological characteristics may explain why some species do not exhibit a commonly observed decline in tissue nutrient concentration at high $CO_2$. In a study of three desert species, BassiriRad et al. (1997b) showed that elevated $CO_2$ decreased foliar N and P concentration in *Larrea tridentata* and *Prosopis glandulosa*, but not in *Bouteloua eriopoda*, which was the only species that had up-regulated its root uptake rate for both N and P. Contrasting nutrient uptake responses to high $CO_2$ might represent genetically fixed characteristics of different species (Mengel and Kirkby 1978). In habitats of low nutrient concentration and/or diffusibility, up-regulation offers little increase in RGR; little selection pressure may exist to express up-regulation. In the case of $NO_3^-$ uptake species differences in responses to elevated $CO_2$ may represent differences in the predominant site of $NO_3^-$ reduction. Nitrate can be assimilated in root and shoot or both, and the assimilation rate is directly correlated with $NO_3^-$ uptake (Smirnoff and Stewart 1985; Pate 1973; Andrews 1986). Under optimal light conditions, shoot $NO_3^-$ may be photoassimilated with very little demand for carbohydrates whereas root assimilation is almost exclusively dependent on respiratory energy supplied by carbohydrates (Pate and Layzell 1990; Sechley et al. 1992). It is therefore expected that the projected rise in atmospheric $CO_2$ concentration would disproportionately benefit $NO_3^-$ uptake in root- versus shoot-reducing species. In any event, the en-

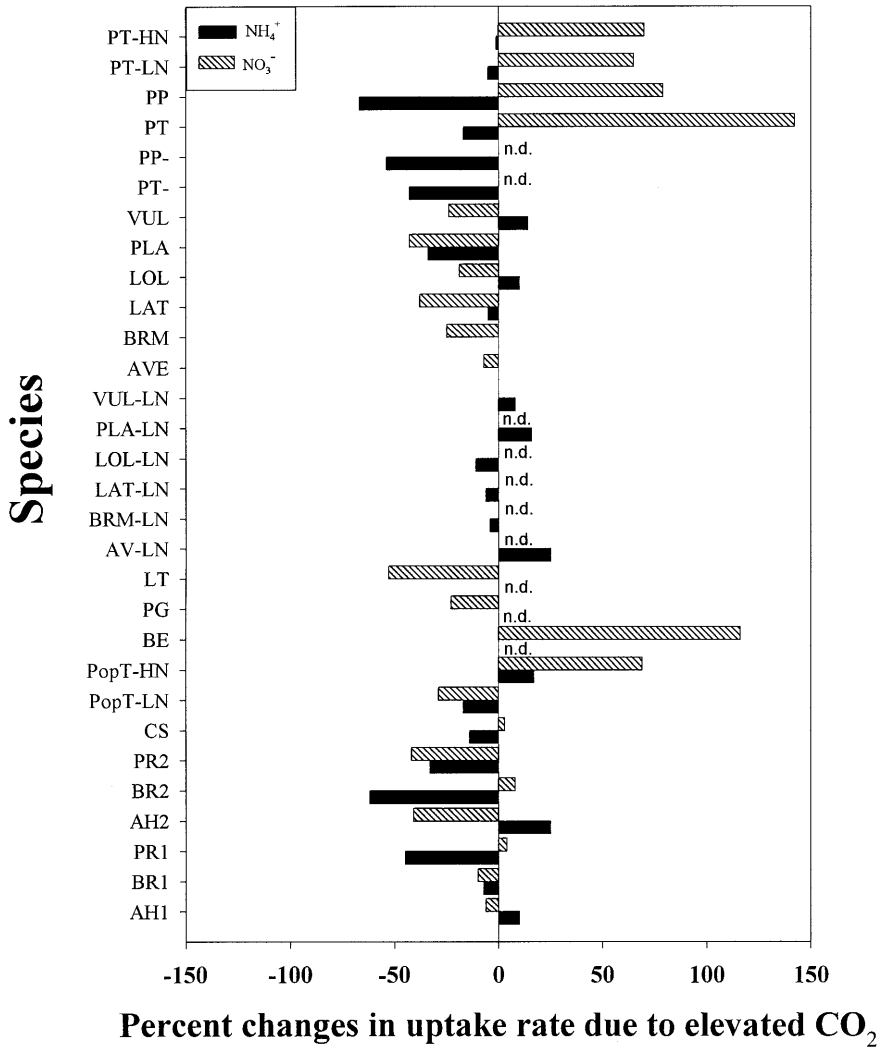


**Fig. 2** Percent changes in rates of uptake of $NH_4^+$ and $NO_3^-$ in response to elevated compared to ambient $CO_2$ grown plants. Data have been compiled from the literature. Species listed on the *y*-axis and the corresponding references: *PT-HN, PT-LN Pinus tadeda* high- and low-nitrogen treatments, respectively (BassiriRad et al. 1996b); *PT, PP, P. taeda* and *P. ponderosa*, respectively (BassiriRad et al. 1997a); *VUL, PLA, LOL, LAT, BRM, AVE Vulpia microrstachys, Plantago erecta, Lolium multiflorum, Lasthenia californica, Bromus hordeaceus, Avena fatua*, respectively (Jackson and Reynolds 1996). In this study *species name followed by LN* refers to low-nutrient treatment and those *without N treatment designation* refer to supplemental N,P,K treatment. *LT, PG, BE Prosopis glandulosa, Larrea tridentata, Bouteloua eriopoda*, respectively (BassiriRad et al. 1997b); *PopT Populus tremuloides* either in low-nitrogen (*LN*) or high-nitrogen (*HN*) treatments (Rothstein and Zak 2000); *CS Ceratonia siliqua* (Cruz et al. 1997); *PR, BR, AH Pleuraphis rigida, Bromus madritensis, Achnatherum hymenoides*, respectively, either at harvest *1* or harvest *2* (Yoder et al. 2000); *n.d.* not determined

ergy demand for N assimilation, while significant, remains modest. Even a 50% change in energy demand for N assimilation per unit mass of tissue, which is an extreme scenario, may only represent a 5% change in total energy demanded for growth and thus in biosynthetic efficiency of growth, $\beta$ (mass increment per unit carbohydrate metabolized). In our functional-balance model below, we offer evidence that RGR responds as the square root of $\beta$, which further dilutes the adaptive value of shifts in N-assimilation energetics.

In considering the relationship between high $CO_2$, root energy supply, and inorganic nitrogen uptake, other complexities must also be considered. Plant N is primarily supplied from the available soil $NO_3^-$ and $NH_4^+$ solution, but the relative preference for each form may largely depend on the ability of roots to absorb, assimilate, and translocate that form. Although uptake and assimilation of both N forms require expenditure of energy, considerably more energy is associated with the uptake and assimilation of $NO_3^-$ than $NH_4^+$, because $NO_3^-$ must be metabolically reduced to ammonia before it can be assimilated (Haynes and Goh 1978; Blacquière 1987). In barley seedlings, uptake and assimilation of $NH_4^+$ consumes 14% of root carbon catabolism whereas uptake and assimilation of $NO_3^-$ requires 23% of root carbon catabolism (Bloom et al. 1992). It is suggested that when the rate of carbohydrate supply to the root and hence its energy production is limiting, $NO_3^-$ is a less favorable form of N (Turpin et al. 1985). Uptake and utilization of $NO_3^-$ may therefore, be disproportionately enhanced compared to $NH_4^+$ with improved photosynthate and energy status of the root (BassiriRad et al. 1997a) although this effect is not universally observed (Cruz et al. 1993; Jackson and Reynolds 1996). Again, energetic shifts in N assimilation have much-diluted effects on RGR and perhaps on seasonal PP. This is especially true if PP is more limited by soil nutrient mobilization than by light usage for photosynthesis.

Nutrient uptake is largely driven by demand (Glass 1989), and, considering that plant demand fluctuates during the growing season, one may expect a strong interaction between time of the season and $CO_2$ effect on nutrient uptake. For example, Larigauderie et al. (1988) showed that in *Bromus mollis*, elevated $CO_2$ significantly

decreased leaf N content at the beginning of the growing season, but by the end of the growing season there were no differences in foliar N content between $CO_2$ treatment. Therefore, a more reliable evaluation of $CO_2$ effects on nutrient uptake must be based on more than a single measurement during the growing season. Furthermore, considering that elevated $CO_2$ often accelerates growth and development (Coleman et al. 1993, 1994), it is important to assess if potential changes in nutrient uptake are related to intrinsic changes in active uptake properties or simply due to changes in ontogeny.

### Increase nutrient use efficiency or decreased physiological demand

In most $C_3$ species, short-term $CO_2$ exposure results in a greater biomass production despite a concomitant decrease in foliar and plant concentration of many essential elements (Hocking and Meyer 1985; Norby et al. 1986; Sage et al. 1989; Conroy 1992; Baxter et al. 1994; Curtis et al. 1994; Reeves et al. 1994; Newbery et al. 1995). The arguments of functional balance, presented shortly, readily explain how plants may achieve both higher relative growth rate and lower fractional nutrient content, $f_n$; RGR is proportional to the square root of photosynthetic nutrient-use efficiency, while $f_n$ is inversely proportional. The concepts are often invoked with respect to N nutrition of plants but its role in regulation of uptake of other nutrients under elevated $CO_2$ is rarely considered. Rubisco activity and concentration often decline significantly in response to $CO_2$ enrichment (Sage et al. 1989; Tissue et al. 1993; Sage 1994; Drake et al. 1997; Stitt and Krapp 1999). Nutrients such as N may then be diverted away from Rubisco for other metabolic processes (Sage 1994; Xu et al. 1994; Stitt 1991). Reallocation of N within the plant would concur with the models of maximum resource-use efficiency (Bloom et al. 1985; Johnson 1985; Robinson 1986) and if operative it may ameliorate N limitation of growth.

While the concept of increased N use efficiency and decreased N demand can be theoretically justified based on the tight linkage between N and Rubisco, increased nutrient use efficiency for other nutrients such as P, K, and Ca (Baxter et al. 1994) cannot be explained by the same mechanism. These essential elements are also important for proper functioning of photosynthesis but they are not represented in Rubisco as prominently as N (30–60% of foliar N can be allocated to Rubisco). Therefore, it should not be expected that a substantial amount of these nutrients will be repartitioned away from Rubisco or any other photosynthetic compartment when plants are grown under high $CO_2$.

## Modeling synthesis

So far, we have conceptually evaluated the role of major root system mechanisms that can adjust to varying degrees in response to elevated $CO_2$. More accurate prediction of growth response to $CO_2$ (or whether such adjustments would adequately meet increased plant N demand under high $CO_2$) would require a better understanding of these mechanisms evaluated collectively rather than singly. The root system adjustments discussed in this review can be successfully integrated into a mechanistic model designed to predict the overall growth responses to high $CO_2$. We are particularly interested in a modeling synthesis that quantifies the relative contribution (leverage) of each mechanism in regulating growth responses to $CO_2$. Synthetic models combine the knowledge of how distinct processes act in concert. The functional balance (FB) model (Gutschick 1993; Gutschick and Kay 1995) is a synthetic model seeking to understand how individual compensatory processes in N nutrition contribute to upholding relative growth rate (RGR) under N limitation. The model equates $RGR_{nl}$ determined by N acquisition with $RGR_{pl}$ determined by photosynthesis (nl, nutrient-limited; pl, photosynthesis-limited):

$$RGR_{nl}=RGR_{pl} \tag{2}$$

or

$$\frac{r\bar{v}}{(1+r)f_{n,w}}=\frac{\beta\alpha_L f_{n,L}p^*}{(1+r)} \tag{3}$$

The full derivations are in the references cited. Here, $r$ is the root-to-shoot mass ratio, $\bar{v}$ is the maximum N uptake rate per gram dry mass of roots, $f_{n,w}$ is the fraction of whole-plant tissue N, $\beta$ is the biosynthetic conversion efficiency from photosynthate to final biomass, $\alpha_L$ is the fraction of shoot mass as leaf mass, and $p^*$ is the photosynthetic utility of the N (as, say, grams of photosynthate made per gram of nutrient per day). The parameters can be resolved further, such as by specifying $\bar{v}$ in a Michaelis-Menten form (Eq. 1). In equating the two relative growth rates, the model predicts that the tissue N concentration is not independently regulated but reflects the balance of acquisition and photosynthetic utility of N:

$$f_{n,w}=\sqrt{\frac{r\bar{v}}{\beta\alpha_L\alpha_n p^*}} \tag{4}$$

and it predicts a final value of RGR,

$$RGR=\left[\frac{\sqrt{r}}{1+r}\right]\sqrt{\beta\alpha_L\alpha_n P^*\bar{v}} \tag{5}$$

This functional balance (FB) model is one of a continuum of such models involving a balance between nutrient and carbon uptake (e.g., Bouwer 1962; Davidson 1969; Orians and Solbrig 1977; Givnish 1987; Luo et al. 1994; and recent purely numerical models that lack closed-form mathematical solutions, such as the CENTURY model, Parton 1996). It is admittedly somewhat restrictive in form: it assumes relatively steady growth with little dependence on internal reserves, and thus is better suited for annuals, or for perennials only at longer time scales; it assumes that nutrients are used for photosynthesis rather than defense or storage; resource availabili-

ty must be definable, as by defining $p^*$ in terms of photosynthetic physiology and uptake rate $\bar{v}$ in terms of root geometry and soil-solution conditions. However, the FB model directly illustrates sensitivity to uptake compensation, i.e., RGR is (1) predicted to vary as the square root of $\bar{v}$ and (2) predicted to vary as the square root of $p^*$, which can be formulated with the model of Farquhar et al. (1980) and estimates of partitioning of nutrients into carboxylation or electron-transport components. For the latter exercise, consider $p^*$ (carboxylation rate per unit mass of N) and the light-saturated carboxylation rate. The rise in $C_i$ with a rise in external $CO_2$ gives a robust prediction of how $p^*$ and thus RGR vary with $CO_2$ (Luo et al. 1994). Note that the model predicts that the co-occurring changes in root-to-shoot allocation ratio, $r$, have very modest effects on RGR, readily overwhelmed by the effects of changes in $p^*$ and $\bar{v}$. Note also that the model was developed for early growth (Zerihun et al. 2000), in which self-shading or competitor shading of leaves is negligible, so that $p^*$ is a function of plant mass, declining as the integrated light interception declines with mass {approximately as $[1\text{-}\exp(\text{-}m/m^*)]/m$}.

## Extension of the model to include mycorrhizal metabolism and nutrient uptake

Whether for plant tissue or mycorrhizal fungi (MRF), photosynthate is used for carbon skeletons, ATP and reductant generation for growth (biosynthesis), and ATP generation for maintenance. The implicit assumption in the original model is that the biosynthetic conversion efficiency includes the first two uses, but not maintenance (e.g., functions such as ion uptake, as defined by Gutschick 1987). Thus, $\beta$ is formulated only in terms of current tissue mass, and rate of C use proportional to rate of growth. An accurate accounting of maintenance is complex and it is not strictly logical to separate maintenace from growth (Hansen et al. 1998). At the least, we must account for maintenance rates of respiration as roughly proportional to growth potential (leaf N content and photosynthetic capacity, for example; Cannell and Thornley 2000). Then, maintenance respiration integrated over time is proportional to integrated growth, that is, to say, maintenance respiration rate is proportional to the rate of mass increase, d$m$/d$t$, just as is biosynthetic respiration rate. We define a new, inclusive biosynthetic conversion efficiency, while retaining the symbol $\beta$. Its value is closer to 0.4–0.5 $g_{DM}\ g^{-1}$ photosynthate than the old value of 0.67. We admit that $\beta$ may differ between plant tissue and fungal tissue, so that $\beta$(MRF) is defined as a multiple of that for plant tissue [i.e., G×β(plant)]. We must also describe the amount of mycorrhizal biomass. We choose to express it as a multiplier of root biomass (i.e., $m_{MRF}=\alpha_M m_r$). The carbon-limited growth rate is changed correspondingly. Actually, on both the C-limited and nutrient-limited sides of Eq. 3, the factor $r$) in the denominator becomes $r\ (1+G\alpha_M)$].

Mycorrhizal fungal uptake of nutrient is added to that by the root tissue proper. The rate per unit of mycorrhizal biomass may be denoted as $\bar{v}_M$, or as $g\bar{v}$, that is, a factor $g$ (usually >1) relative to root-tissue uptake. The rate per unit mass of plant, formerly just $r\bar{v}$, becomes $r(\bar{v}+\alpha_M v_M)$. We may write this as $r\ \bar{v}\ (1+g\alpha_M)$. Consequent to both modifications, RGR for mycorrhizal roots ($RGR_{MR}^{FB}$) at functional balance becomes:

$$RGR_{MR}^{FB} = \sqrt{\frac{\beta A_L p* r\bar{v}p(1+g\alpha_M)}{[1+r(1+G\alpha_M)][1+r(1+\alpha_M)]}} \qquad (6)$$

Immediately, one may compare this to $RGR^{FB}$ in a plant lacking mycorrhizal infection, but otherwise physiologically identical. The ratio of RGRs is:

$$\frac{RGR_{MR}^{FB}}{RGR^{FB}} = (1+r)\sqrt{\frac{(1+g\alpha_M)}{[1+r(q+G\alpha_M)][1+r(1+\alpha_M)]}} \qquad (7)$$

Consider the case that mycorrhiza are more active in both uptake and metabolism than is plant tissue – say, $g$=$G$=3. For a typical root-to-shoot ratio, $r$=0.5, the ratio of RGRs is 1.15, or a 15% gain in RGR for the mycorrhizal plant. One can show that, for any $g$=$G$ both greater than 1, the plant benefits, as if it had additional roots more active than its own.

## Extension of the model to consider source-sink balance and product inhibition of photosynthesis

Product inhibition appears strongly related to hexose fluxes (Moore et al. 1999). In some cases, it reduces to a dependence on accumulated carbohydrates (see also Krapp and Stitt 1995). We can modify the assimilation rate per mass of shoot, which was the factor $\beta\alpha_L f_n$,$Lp^*$ on the right-hand side of Eq. 3. Simply, we multiply it by a factor $1/(1+k_C f_C)$ , where $k_C$ is an inhibition constant and $f_C$ is a measure of average plant carbohydrate status, similar to molar concentration of sucrose in phloem. This is the most parsimonious form to express how elevated $f_C$ inhibits photosynthesis in a smooth fashion. The sink for carbohydrates must also respond to carbohydrate status. Sink activity may be limited by meristematic activity (meristem number or density and activity per meristem). The net effect may be expressed approximately as a limitation on RGR to the value $RGR_{max}\ f_C/(f_C+K_e)$. Here, $K_e$ is an empirical constant in a mathematical form that allows RGR to reach saturation in response to achieved carbohydrate status. We thereby introduce then the concept of maximal RGR (e.g., Poorter and Remkes 1990; Garnier 1992). Some plants undergo ontogenic shifts in sink distribution, as between roots and shoots (Fonseca et al. 1996) and thus $RGR_{max}$ and its responsiveness to elevated $CO_2$. We obtain then a second, separate functional-balance equation for carbohydrates. This must be solved for $f_C$. The simultaneous solution of the nutrient and carbohydrate FB equations does not lend itself to analytical solutions (closed mathematical forms) but is readily solved by simple binary searches (James et

al. 1977) over intervals in $f_C$ and $f_n$ that are physiologically plausible. Such a solution method has been programmed in FORTRAN 77 and is available on the web site mvar.nmsu.edu/vince. Shortly, we plan to have the program executable from this Web site.

### Extension to calculate uptake rates in realistic soil conditions

The modified model with MRF biomass, $k_c$, and $K_e$ all set to zero reproduces correctly the predictions of the unmodified model. However, the model, modified or not, relies on a knowledge of nutrient uptake rate $\bar{v}$ at the root surface or the estimation of $\bar{v}$ as $V_{max}\, c_a/(c_a+K_m)$ , with $c_a$ defined as nutrient concentration at the root surface. The latter form displays the control exerted by root physiology as $V_{max}$ and $K_m$, but the prediction of $c_a$ from concentration in bulk soil ($c_b$) is complicated by soil. The model has thus been extended also to calculate $\bar{v}$ from $V_{max}$, $K_m$, $c_b$, and soil diffusion properties: the diffusivity $D$ of the ion, the mean root radius $a$, and the mean spacing between roots $b$. This is in the spirit of many verified models (Barber 1984; Nye and Tinker 1997).

One more feature added to the model is calculation of RGR sensitivity to any one parameter, when other physiological and soil parameters are fixed. Simply, one can readily alter a single parameter (using a keyword to identify it). The program automatically reports the logarithmic sensitivity, $R=(\mathrm{d}RGR/RGR)/(\mathrm{d}param/param)=(\mathrm{d}\ \ln RGR)/(\mathrm{d}\ \ln param)$ where $R$ is closely related to control coefficients (Schulze 1994) and has intuitive significance. For example, in the original model, RGR varied not as $\bar{v}$, but as the square root of $\bar{v}$: RGR=(constant) $\bar{v}^{0.5}$, or ln(RGR)=ln(constant)+0.5 ln ($\bar{v}$). Thus, $R(\bar{v})=0.5$. Other factors such as $r$ had much lower control over RGR. In the case $r$=0.5, $R(r)=0.5\ (1\text{-}r)/(1+r)=0.17$. That is, RGR increases relatively only 17% as fast as does $r$.

Any physiological or soil parameter can affect $f_N$ quite differently from how it affects RGR. For example, $f_N$ is predicted to vary in the simple model as $\sqrt{r}$, yielding $S(r)=0.5$ in the control of $f_N$ by $r$. That is, tissue "quality" as $f_N$ is much more sensitive to $r$; the effects on susceptibility to herbivory may be significant in some conditions (e.g., Gutschick 1999).

## Some predictions of the model

### Importance of uptake capacity $V_{max}$ in growth

In the Michaelis-Menten form for uptake rate (per mass or per area of root), the saturated rate $V_{max}$ exerts an apparent direct control over realized uptake rate, $\bar{v}$. However, in real soils with diffusional limitations on ion movement, changes in $V_{max}$ are compensated by changes in root-surface concentration, $c_a$ ("drawdown"). Measurements and simulations of the drawdown effect have long been available (e.g., Nye and Tinker 1977). We present a specific simulation in Fig. 3 that reinforces some key interpretations of phenomena, particularly in combination with later figures here. The plant being simulated has relatively high growth potential. Its maximal RGR is 0.3 $d^{-1}$, matched by (or, one may say, conferred by) a high leaf: shoot mass ratio ($\alpha_L$=0.5, appropriate for an herbaceous plant) and a moderately high photosynthetic NUE (34 g PSate $g_N^{-1}$ $d^{-1}$; PSate, photosynthate). The root-to-shoot ratio is 0.8, appropriate to early growth and

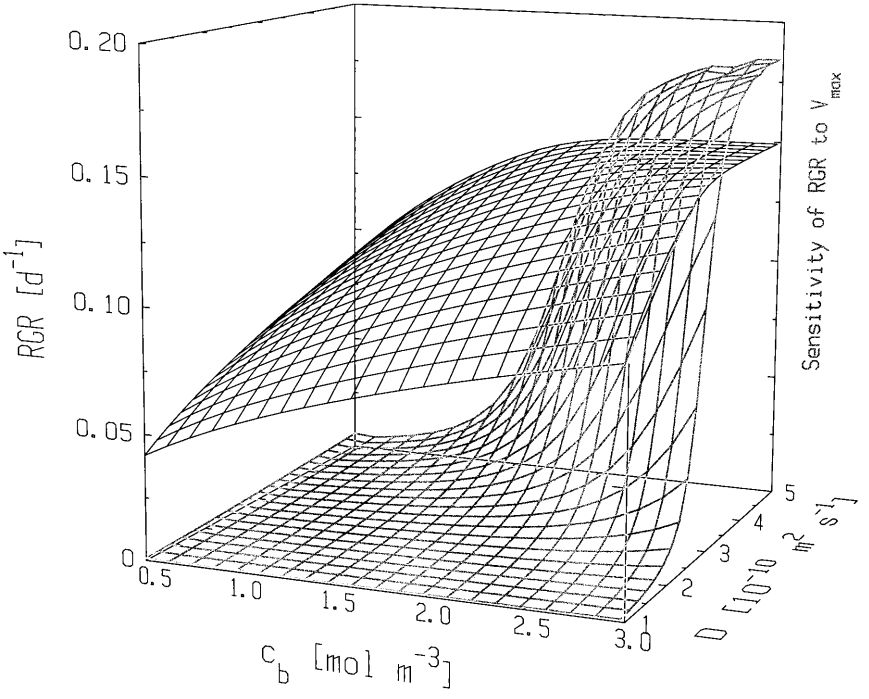


**Fig. 3** Role of diffusional limitation on root uptake rate: simulation of relative growth rate (RGR) itself (*solid-shaded contour lines*), and $S_{RGR}$ to $V_{max}$ (*dotted-shaded contour lines*), i.e., the sensitivity of RGR to changes in uptake capacity per unit root surface area. Here, $c_b$ is concentration in bulk soil solution and $D$ is diffusivity of inorganic nitrogen in soil. Plant physiological parameters are described in the text

near the model-predicted optimum of unity. Note that results are qualitatively very similar over wide ranges of $r$. Biosynthetic efficiency, $\beta$, is 0.5 $g_{DM}$ $g^{-1}$ PSate, in a range typical of most plants, and the photosynthetic inhibition parameters are also estimated in the normal range $k_c$=1, $K_e$=0.5). The value of $V_{max}$ is fixed at a moderately high value, $10^{-6}$ mol $m^{-2}$ $s^{-1}$. Note that RGR rises monotonically as either bulk soil concentration of N ($c_b$) or N ion diffusivity ($D$) increase. Only after diffusion limitations have been much reduced (Fig. 3, right corner) is RGR able to respond significantly to increases in $V_{max}$ (shaded surface for logarithmic derivative of RGR with respect to $V_{max}$). The same qualitative trends occur for slower-growing plants, such as saplings of woody species, which have lower leaf to shoot ratios, lower mass fraction of fine roots, lower $RGR_{max}$, etc. The principal change is that the flattening of RGR begins at smaller values of $c_b$ and $D$.

## Influence of root-to-shoot ratio and of achieved uptake rate, $\bar{v}$, on RGR, moderated by inherent growth potential

Figure 4A shows simulations of RGR for plants with physiological parameters similar to those in Fig. 3, while $r$ and $\bar{v}$ are varied (by genotype or environment). The response of RGR is, of course, strongest when RGR is not constrained by inherent RGR limitations. These limitations are expressed as low $RGR_{max}$ and correspondingly low values of the inhibition parameters, $k_c$ and $K_e$ introduced earlier. The RGR response surfaces for a plant unaffected by photosynthetic inhibition were generated with both $k_c$ and $K_e$ set to zero. Progressively greater growth constraint in the two other cases arose from setting $K_c$=1 and $K_e$=0.5, with $RGR_{max}$=0.3 $d^{-1}$ ("moderate") or the same $k_c$ and $K_e$ but $RGR_{max}$=0.15 $day^{-1}$ ("strong"). This constraint compresses RGR to a narrow range, while tissue N fraction continues to respond strongly (Fig. 4B). Essentially, N is taken up, but is not readily used for growth; it accumulates in luxury amounts. Simulation of the readily-inhibited plant is terminated at intermediate uptake rates (0.02 $g_N$ $(g_{DM\ root})^{-1}$ $d^{-1}$), because such plants never possess high uptake capacity. The ability of $r$ to influence RGR is predicted to be limited, much as in the original model. The sensitivity of RGR to $r$, $S_{RGR}(r)$, vanishes as $r$ approaches 1, the nominal optimum. The sensitivity to $\bar{v}$, $S_{RGR}(\bar{v})$, remains moderately high (0.3–0.5; simulation data not shown), only decreasing strongly as RGR approaches $RGR_{max}$.

## Growth responses directly to elevated CO2

Figure 5 shows RGR at double ambient $CO_2$ (doubled $p^*$), for the same physiological constitution as in Fig. 4. All the responses to $r$ and $\bar{v}$ are expanded by the approximate factor $\sqrt{2}$, appropriate to even the simple model, in which RGR is proportional to $\sqrt{p^*}$. That is, elevated $CO_2$ does not change the nature of any response, in this model. The increase in $p^*$ at high $CO_2$ is predicted to enhance RGR always, without any requirement for compensatory increase in uptake rate $\bar{v}$, expressed per root mass or per root area. In such cases, tissue N content decreases while RGR increases.

## Mycorrhizae affect RGR and $f_N$ modestly, but with significant effects over a season

Figure 6 presents the results of simulations with varied mycorrhizal activity. Plant physiological parameters are similar to those in Fig. 3, except $r$=0.5, for a more mature plant. Uptake rate is fixed at a moderate value for fast-growing plants, 0.015 $g_N(g_{DM}$ $root)^{-1}$ $d^{-1}$. In all cases, mycorrhizae have 20% the biomass of roots alone ($\alpha_M$=0.20). In the base case, mycorrhizal fungi act similarly to roots; their specific uptake rate equals that for plants ($g$=1, or $\bar{v}_M=\bar{v}_{plant}$), and their metabolic rate is the same as for roots ($G$=1). The mycorrhizal fungi are more active in uptake in a second scenario ($g$=3) but have the

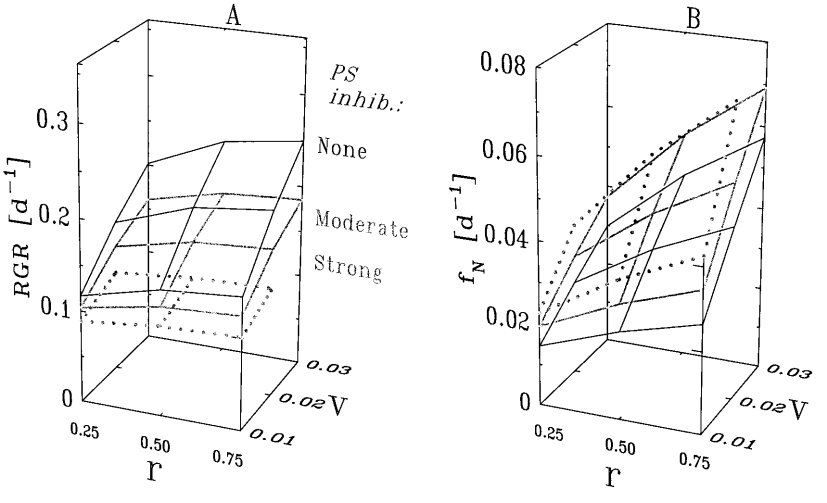


**Fig. 4** Role of root:shoot ratio ($r$) and of uptake rate ($V$) in determining **A** RGR and **B** tissue N content ($f_N$) under ambient $CO_2$ concentration: simulation for three different degrees of susceptibility to photosynthetic inhibition (*PS inhib*)

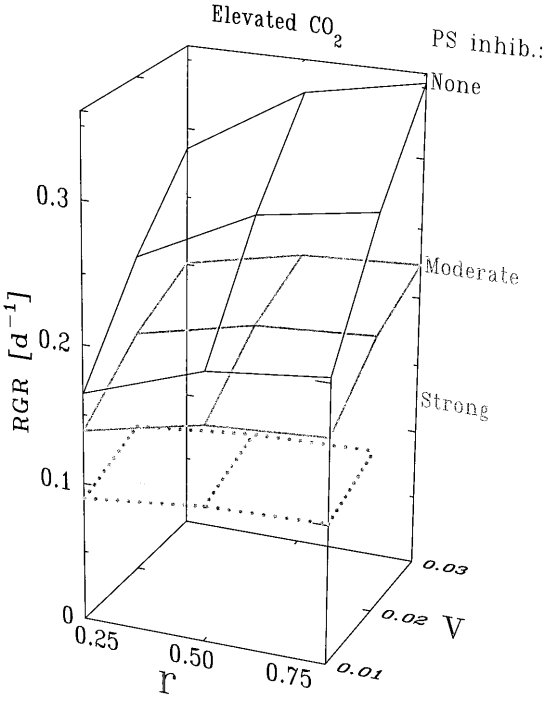


**Fig. 5A–C**. Role of root:shoot ratio and root uptake rate in determining RGR at elevated $CO_2$ level. All parameters are the same as Fig. 4, except that $p^*$ is doubled to 68 g PSate $g_N^{-1}$ $d^{-1}$ (*PSate* photosynthate)

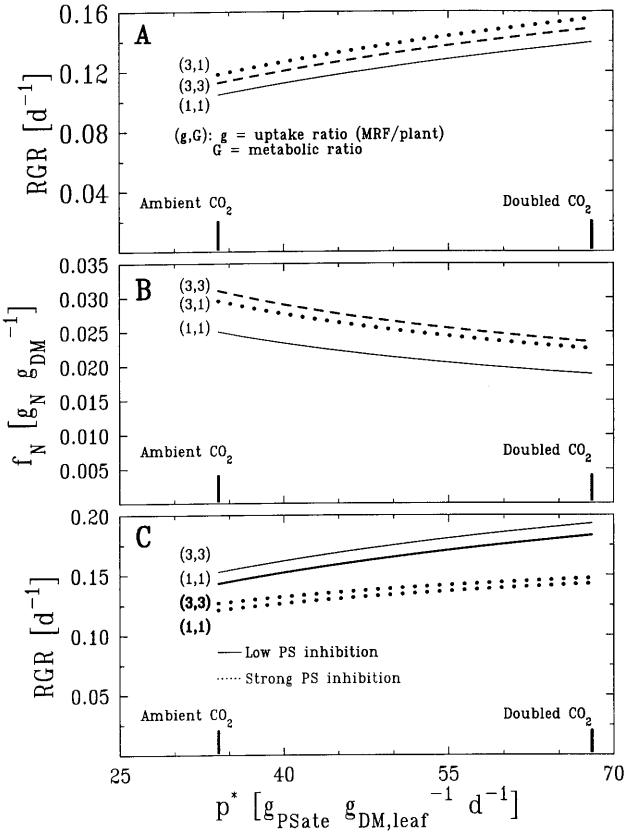


**Fig. 6A–C**. Simulation of the effects of mycorrhizal (MR) fungal activity on RGR and tissue N content ($f_N$), as a function of photosynthetic N-use efficiency ($p^*$); the latter changes with $CO_2$ concentration. **A** Differences in response of RGR to $p^*$ as dependent on the uptake advantage of MR fungi ($g$) and the metabolic ratio ($G$). All other parameters are described in the text; note that the growth potential is high and MR fungi account for 20% of the total root system biomass. **B** Differences in response of tissue N content, for the same three cases as in **A**. **C** Dependence of RGR response upon susceptibility to photosynthetic inhibition; *solid lines* represent $RGR_{max}$ of 0.3 $day^{-1}$ and *dotted lines* represent $RGR_{max}$ of 0.18 $d^{-1}$

same metabolic rate as roots ($G$=1). In a third scenario, the mycorrhiza are more active both metabolically and in uptake ($g$=3=$G$). Graph A presents results with fixed parameters of growth constraint, appropriate again to a fast-growing plant ($RGR_{max}$=0.3 $day^{-1}$, $k_c$ =1, $K_e$=0.5). Over the range of $CO_2$ that doubles $p^*$ (doubling the $CO_2$, approximately), the three cases retain almost invariant differences in RGR. One might expect differences in RGR to be proportional to original RGR, instead, given that RGR varies approximately as the square root of $p^*$, which is the only parameter that is varying. If so, the differences in RGR would increase as $p^*$ increases. However, the plants with higher mycorrhizal uptake (both cases with $g$=3) incur increased carbohydrate accumulation. This increases the degree of product inhibition of photosynthesis. Additionally, the plant with higher MRF metabolism ($G$=3) loses carbon directly to such metabolism. Only the higher nutrient content (resulting from lower dilution of N by total growth) upholds RGR, so that it parallels RGR of the base case ($g$=1, $G$=1). The differences in RGR are modest, about 0.015 $day^{-1}$ between the extreme cases ($g$,$G$)=(1,1) and ($g$,$G$)=(3,1). This is about 12% of RGR, such that if the plant in the base case increased in biomass 32-fold (5 doubling times), the plant with $G$=3=$g$ would undergo 1.12×5=5.6 doublings. Consequently, its biomass would be $2^{0.6}$=1.5-fold greater. The effect on $f_N$ (graph B) are relatively larger than on RGR. The case ($g$,$G$)=(3,3) is now at the extreme from the base case, because N content relative to C content is increased both by greater uptake and by the loss of carbon in respiration. The increase in $f_N$ is almost uniformly 1.25-fold across all values of $p^*$.

Responsiveness of RGR to mycorrhizal activity depends upon inherent growth potential of the plant, as expected. This is expressed quantitatively in the simulation of graph C in Fig. 6. Here, we have retained the two scenarios (1,1 and 3,3) differing most in carbon dynamics (photosynthetic gain minus respiratory loss), while simulating for each of these two different degrees of growth constraint. The case of low photosynthetic inhibition uses the same parameters as earlier, $RGR_{max}$=0.3 $d^{-1}$, $k_c$=1, and $K_e$=0.5. The case of strong inhibition uses $RGR_{max}$=0.18 $d^{-1}$. As expected, high carbohydrate use by the fungi cannot remove the limitation on RGR posed by feedback inhibition of photosynthesis. For any values of $G$ and $g$, a high susceptibility to inhibition (especially summarized in low $RGR_{max}$) makes RGR almost insensitive to mycorrhizal uptake or metabolism (the two lower curves are only minimally separated). Additionally, RGR

becomes rather insensitive to photosynthetic ability which is proportional to $p^*$.

## Concluding remarks

According to models of whole-plant carbon-nutrient balance, resources of abundant availability should be allocated to optimize the acquisition of the most limiting resources. Elevated $CO_2$ improves whole-plant and root C status yet it is still unclear if plants can exchange this additional carbon for nutrients. Increased symbiotic association, changes in root growth, morphology and architecture as well as active nutrient uptake all represent mechanisms with which plant nutrient capture can be optimized. The ability to reliably predict plant and ecosystem responses to high $CO_2$ may largely depend on the balance between C and nutrient uptake. Mechanisms of leaf and canopy adjustment in C uptake responses to high $CO_2$ levels have been extensively utilized in formulating predictive models of plant and ecosystem responses to high $CO_2$. Yet little is known about the root system mechanisms which are causally related to nutrient relations of plants grown under high $CO_2$.

The proposed conceptual model (Fig. 1) suggests that in predicting the whole-plant nutrient uptake, root system adjustments reviewed here must be considered collectively. Examination of each mechanism in isolation is likely to lead to false prediction of how nutrient acquisition may be impacted by high $CO_2$. For example, an increase in fine root production under high $CO_2$ does not automatically translate into greater nutrient uptake if the fine roots produced under high $CO_2$ have substantially lower physiological capacity to take up nutrients. Similarly, with respect to mycorrhizae, an increase in percent infection (which is commonly used as a measure of response to $CO_2$) does not necessarily mean an increase in external hyphae or N and P uptake. The fungal symbionts should be capable of affecting whole-plant nutrient uptake much more significantly than the fractional biomass allocated to them. Their carbon metabolism is likely to be of less importance, positively or negatively. We suggest that the mechanisms of increased nitrogen uptake highlighted here have different weights in determining overall plant responses to high $CO_2$. For example, root-to-shoot biomass allocation should have a minor effect on RGR. This allocation is, however, expected to affect tissue nutrient content significantly, altering as well the risks of herbivory and the mineralization of litter. Increases in nutrient uptake per unit root mass, $\overline{v}$, should always affect RGR and tissue $f_n$ strongly. The ability to increase $\overline{v}$ by physiological adjustments in kinetic parameters is highly suppressible by soil diffusional limitation in most, but not all, ecosystems. On the other hand, photosynthetic nitrogen use efficiency should always have a strong effect on RGR, except when RGR approaches its developmental limit, $RGR_{max}$. The latter may be an important parameter to measure. Product inhibition of photosynthesis and its changes with $CO_2$ and nutrient treatments are expected to have only modest effects for most plants.

Even when one focuses on a single mechanism, responses to high $CO_2$ vary from positive to no change to negative. Some of those inconsistencies are attributable to differences in experimental protocols. A larger part of those inconsistencies may, however, be attributed to genetic differences among species. These adjustments could be elicited by $CO_2$ to a different extent depending on the species which, perhaps, could explain why there is a wide range of inter-species variation in growth responses to $CO_2$. Obviously this has enormous implications for net primary productivity. However, such inter-species variation may also explain why elevated $CO_2$ can decrease nutrient concentration in some species, but not in others. If the genetic potentials for expressing these root system compensatory adjustments are, indeed, different among species then it is abundantly plausible that high $CO_2$ may lead to changes in species composition and biodiversity via a shift in competitive ability in nutrient acquisition. Future conceptual and quantitative models designed to predict plant and ecosystem responses to rising $CO_2$ would require a better understanding of the factors that regulate plant nutrient status and how these factors may change in response to $CO_2$. The FB model presented here is one such attempt.

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## References

Allen LH Jr, Vu JCV, Valle RR, Boote KJ (1988) Nonstructural carbohydrates and nitrogen of soybean grown under carbon dioxide enrichment. Crop Sci 28:84–94

Andrews M (1986) The partitioning of nitrate assimilation between roots and shoot of higher plants. Plant Cell Environ 9:511–519

Arnone JA III, Gordon JC (1990) Effect of nodulation, nitrogen fixation and $CO_2$ enrichment on the physiology, growth and dry mass allocation of seedlings of *Alnus rubra* Bong. New Phytol 116:55–66

Barber SA (1984) Soil nutrient bioavailability: a mechanistic approach. Wiley, New York, pp 55–89

BassiriRad H, Griffin KL, Strain BR, Reynolds JF (1996a) Effects of $CO_2$ enrichment on root $^{15}NH_4$ uptake kinetics and growth in seedlings of loblolly and ponderosa pine. Tree Physiol 16:957–962

BassiriRad H, Thomas RB, Reynolds JF, Strain BR (1996b) Differential responses of root uptake kinetics of $NH_4^+$ and $NO_3^-$ to enriched atmospheric $CO_2$ in field grown loblolly pine. Plant Cell Environ 19:367–371

BassiriRad H, Griffin KL, Reynolds JF, Strain BR (1997a) Changes in root $NH_4^+$ and $NO_3^-$ absorption rates of loblolly and ponderosa pine in response to $CO_2$ enrichment. Plant Soil 190:1–9

BassiriRad H, Reynolds JF, Virginia RA, Brunelle MH (1997b) Growth and root $NO_3^-$ and $PO^{3+}_4$ uptake capacity of three desert species in response to atmospheric $CO_2$ enrichment. Aust J Plant Physiol 24:353–358

Baxter R, Gantley M, Ashenden TW, Farrar IF (1994) Effects of elevated carbon dioxide on three grass species from mountain pasture. II. Nutrient uptake, allocation and efficiency of use. J Exp Bot 278:1267–1278

Bazzaz FA (1990) The response to natural ecosystems to the rising global $CO_2$ levels. Annu Rev Ecol Syst 21:167–196

Berntson GM, Bazzaz FA (1997) Nitrogen cycling in microcosms of yellow birch exposed to elevated $CO_2$: simultaneous positive and negative below-ground feedbacks. Global Change Biol 3:247–258

Berntson GM, Woodward FI (1992) The root system architecture and development of *Senecio vulgaris* in elevated carbon dioxide and drought. Funct Ecol 6:324–333

Blacquière T (1987) Ammonium and nitrate nutrition in *Plantago lanceolata* and *P. major*. II. Efficiency of root respiration and growth. Comparison of measured and theoretical values of growth respiration. Plant Physiol Biochem 25:1775–1785

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants – an economic analogy. Annu Rev Ecol Syst 16:363–392

Bloom AJ, Sukrapanna SS, Warner RL (1992) Root respiration associated with ammonium and nitrate absorption and assimilation by barley. Plant Physiol 99:1294–1301

Bouwer R (1962) Distribution of dry matter in the plant. Neth J Agric Sci 10:361–376

Caldwell MM (1987) Plant architecture and resource competition. In: Schulze E-D, Zwolfer H (eds) Ecological studies, vol 61. Springer, Berlin Heidelberg New York, pp 164–179

Cannell MGR, Thornley JHM (2000) Modelling the components of plant respiration: some guiding principles. Ann Bot 85: 45–54

Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric $CO_2$ on woody plants. New Phytol 127:425–446

Chapin FS III (1988) Ecological aspects of plant mineral nutrition. In: Tinker B, Lauchli A (eds) Advances in plant nutrition, vol 3. Praeger, New York, pp 161–191

Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KG, Laundre JA (1995) Responses of arctic tundra to experimental and observed changes in climate. Ecology 76:694–711

Coleman JS, McConnaughay KDM, Bazzaz FA (1993) Elevated $CO_2$ and plant nitrogen use – is reduced tissue nitrogen concentration size-dependent? Oecologia 93:195–200

Coleman JS, McConnaughay KDM, Ackerly DD (1994) Interpreting phenotypic variation in plants. Trends Ecol Evol 9(5):187–191

Conroy JP (1992) Influence of elevated atmospheric $CO_2$ concentrations on plant nutrition. Aust J Bot 40:445–456

Conroy J, Hocking P (1993) Nitrogen nutrition of $C_3$ plants at elevated atmospheric $CO_2$ concentrations. Physiol Plant 89:570–576

Conroy JP, Milham PJ, Barlow EWR (1992) Effect of nitrogen and phosphorus availability on the growth response of *Eucalyptus grandis* to high $CO_2$. Plant Cell Environ 15:843–847

Cruz C, Lips SH, Martins-Loução MA (1993) The effect of nitrogen source on photo-synthesis of carob at high $CO_2$ concentrations. Physiol Plant 89:552–556

Cruz C, Lips SH, Martins-Loução MA (1997) Changes in the morphology of roots and leaves of carob seedlings induced by nitrogen source and atmospheric carbon dioxide. Ann Bot 80:817–823

Curtis PS, Wang X (1998) A meta-analysis of elevated $CO_2$ effects on woody plant mass, form and physiology. Oecologia 113:299–313

Curtis PS, Zak DR, Pregitzer KS, Teeri JA (1994) Above- and belowground response of *Populus grandidentata* to elevated atmospheric $CO_2$ and soil N availability. Plant Soil 165:45–51

Davidson RL (1969) Effect of root/shoot ratio in some pasture grasses and clover. Ann Bot 33:571–577

Dhillion SS, Roy J, Abrams M (1996) Assessing the impact of elevated $CO_2$ on soil microbial activity in a Mediterranean model ecosystem. Plant Soil 187:333–342

Diaz S, Grime JP, Harris J, McPherson E (1993) Evidence of a feedback mechanism limiting plant response to elevated carbon dioxide. Nature 364: 616–617

Drake BG, Gonzàles-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric $CO_2$? Annu Rev Plant Physiol Plant Mol Biol 48:609–639

Eamus D, Jarvis PG (1989) The direct effects of increase in the global atmospheric $CO_2$ concentration on natural and commercial temperate trees and forests. Adv Ecol Res 19:l-55

Ericsson T, Rytter L, Linder S (1992) Nutritional dynamics and requirements of short rotation forests. In: Mitchel CP, Ford-Robertson JB, Hinckley T, Sennerby-Forsse L (eds) Ecophysiology of short rotation forest crops. Elsevier, London, pp 35–65

Farquhar GD, Caemmerer S von, Berry JA (1980) A biochemical model of photosynthetic $CO_2$ assimilation in leaves of $C_3$ species. Planta 149:78–90

Ferris R, Taylor G (1995) Contrasting effects of elevated $CO_2$ on the root and shoot growth of four native herbs commonly found in chalk grassland. New Phytol 125:855–866

Fitter AH, Hay RKM (1987) Environmental physiology of plants, 2nd edn. Academic Press, New York, pp 99–106

Fitter AH, Self GK, Wolfenden J, Vuuren MMI van, Brown TK, Williamson L, Graves JD, Robinson D (1996) Root production and mortality under elevated atmospheric carbon dioxide. Plant Soil 187:299–306

Fitter AH, Graves JD, Wolfenden J, Self GK, Brown TK, Bogie D, Mansfield TA (1997) Root production and turnover and carbon budgets of two contrasting grasslands under ambient and elevated atmospheric carbon dioxide concentrations. New Phytol 137:247–256

Fonseca F, Den Hertog J, Stulen I (1996) The response of *Plantago majo*r ssp. *pleiosperma* to elevated $CO_2$ is modulated by the formation of secondary shoots. New Phytol 133:627–635

Galloway JN, Schlesinger WH, Levy H II, Michaels A, Schnoor JL (1995) Nitrogen fixation: anthropogenic enhancement-environmental response. Global Biogeochem Cycles 9:235–252

Garnier E (1992) Growth analysis of congeneric annual and perennial grass species. J Ecol 80:665–675

Givnish TJ (1987) Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. In: TJ Givnish (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp 171–213

Glass ADM (1989) Plant nutrition: an introduction to current concepts. Jones and Barlett, Boston

Godbold DL, Berntson GM, Bazzaz FA (1997) Growth and mycorrhizal colonization of three North American tree species under elevated atmospheric $CO_2$. New Phytol 137:433–440

Gutschick VP (1987) A functional biology of crop plants. Croom Helm, London

Gutschick VP (1993) Nutrient-limited growth rates: roles of nutrient-use efficiency and of adaptations to increase uptake rate. J Exp Bot 44:41–51

Gutschick VP (1999) Biotic and abiotic consequences of differences in leaf structure. New Phytol 143:3–18

Gutschick VP, Kay LE (1995) Nutrient-limited growth rates: quantitative benefits of stress responses and some aspects of regulation. J Exp Bot 46:995–1009

Hansen LD, Breidenbach RW, Smith BN, Hansen JR, Criddle RS (1998) Misconceptions about the relation between plant growth and respiration. Bot Acta 111:255–260

Haynes RJ, Goh KM (1978) Ammonium and nitrate nutrition of plants. Biol Rev 53:465–510

Hocking PJ, Meyer CP (1985) Responses of Noogoora burr (*Xanthium occidentale* Bertol.) to nitrogen supply and carbon dioxide enrichment. Ann Bot 55:835–844

Hungate BA, Holland EA, Jackson RB, Chapin FS III, Mooney HA, Field CB (1997) The fate of carbon in grasslands under carbon dioxide enrichment. Nature 388:576–579

Jackson RB, Reynolds HL (1996) Nitrate and ammonium uptake for single-and mixed-species communities grown at elevated $CO_2$. Oecologia 105:74–80

James ML, Smith GM, Wolford JC (1977) Applied numerical methods for digital computation with Fortran and CSMP. Harper and Row, New York

Johnson IR (1985) A model of the partitioning of growth between the shoots and the roots of vegetative plants. Ann Bot 55:421–431

Jongen M, Fay P, Jones MB (1996) Effects of elevated carbon dioxide and arbuscular mycorrhizal infection on *Trifolium repens*. New Phytol 132:413–423

Klironomos JN, Rillig MC, Allen MF, Zak DR, Kubiske M, Pregitzer KS (1997) Soil fungal-arthropod responses to *Populus tremuloides* grown under enriched atmospheric $CO_2$ under field conditions. Global Change Biol 3:473–478

Körner CH, Renhardt U (1987) Dry matter partitioning and root length/leaf area ratios in herbaceous perennial plants with diverse altitudinal distribution. Oecologia 74:411–418

Kramer PJ (1981) Carbon dioxide concentration, photosynthesis, and dry matter production. BioScience 31:29–33

Krapp A, Stitt M (1995) An evaluation of direct and indirect mechanisms for the sink-regulation of photosynthesis in spinach: changes in gas exchange, carbohydrates, metabolites, enzyme activities and steady-state transcript levels after cold-girdling source leaves. Planta 195:313–323

Lambers H, Van Der Werf A, Konings H (1991) Respiratory patterns in roots in relation to their functioning. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. Marcel Dekker, New York, pp 229–263

Larigauderie A, Hilbert DW, Oechel WC (1988) Effect of $CO_2$ enrichment and nitrogen availability on resource acquisition and resource allocation in a grass, *Bromus mollis*. Oecologia 77:544–549

Lewis JD, Strain BR (1996) The role of mycorrhizas in the response of *Pinus taeda* seedlings to elevated $CO_2$. New Phytol 133:431–443

Lewis JD, Thomas RB, Strain BR (1994) Effect of elevated $CO_2$ on mycorrhizal colonization of loblolly pine (*Pinus taeda* L.) seedlings. Plant Soil 165:81–88

Lloyd J, Farquhar GD (1996) The $CO_2$ dependence of photosynthesis, plant growth responses to elevated atmospheric $CO_2$ concentrations and their interaction with soil nutrient status. I. General principles and forest ecosystems. Funct Ecol 10:4–32

Lovelock CE, Kyllo D, Winter K (1996) Growth responses to vesicular-arbuscular mycorrhizae and elevated $CO_2$ in seedlings of a tropical tree, *Beilschmiedia pendula*. Funct Ecol 10:662–667

Lovett GM (1994) Atmospheric deposition of nutrients and pollutants in North America: an ecological perspective. Ecol Appl 4:629–650

Luo Y, Field CB, Mooney HA (1994) Predicting responses of photosynthesis and root fraction to elevated carbon dioxide. Interactions among carbon, nitrogen and growth. Plant Cell Environ 17:1195–1204

Luo Y, Reynolds J, Wang Y, Wolfe D (1999) A search for predictive understanding of plant responses to elevated [$CO_2$]. Global Change Biol 5:143–156

Lussenhop J, Treonis A, Curtis PS, Teeri JA, Vogel CS (1998) Response of soil biota to elevated atmospheric $CO_2$ in poplar model systems. Oecologia 113:247–251

McDonald AJS, Ericsson T, Ingestad T (1991) Growth and nutrition of tree seedlings. In: Raghavendra AS (ed) Physiology of trees. Wiley, New York, pp 199–220

McGonigle TP (1988) A numerical analysis of published field trials with vesicular-arbuscular mycorrhizal fungi. Funct Ecol 2:473–478

McGuire AD, Melillo JM, Joyce LA (1995) The role of nitrogen in the response of forest net primary production to elevated atmospheric carbon dioxide. Annu Rev Ecol Syst 26:473–503

McKee IF, Woodward FI (1994) $CO_2$ enrichment responses of wheat: interactions with temperature, nitrate and phosphate. New Phytol 127:447–453

Mengel K, Kirkby EA (1978) Principles of plant nutrition. International Polish Institute, Berne, pp 347–366

Moore BD, Cheng SH, Sims D, Seemann JR (1999) The biochemical and molecular basis for photosynthetic acclimation to elevated atmospheric $CO_2$. Plant Cell Environ 22:567–582

Newbery RM, Wolfenden J, Mansfield TA, Harrison AF (1995) Nitrogen, phosphorus and potassium uptake and demand in *Agrostis capillaris*: the influence of elevated $CO_2$ and nutrient supply. New Phytol 130:565–574

Norby RJ (1994) Issues and perspectives for investigating root responses to elevated atmospheric carbon dioxide. Plant Soil 165:9–20

Norby RJ (1998) Nitrogen deposition: a component of global change analysis. New Phytol 139:189–200

Norby RJ, O'Neill EG, Luxmoore RL (1986) Effects of atmospheric $CO_2$ enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. Plant Physiol 82:83–89

Norby RJ, Wullschleger SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree responses to rising $CO_2$ in field experiments: implications for the future forests. Plant Cell Environ 22:683–714

Nye PH, Tinker PB (1977) Solute movement in the soil-root system. University of California Press, Berkeley

Ollinger SV, Aber JD, Lovett GM, Millham SE, Lathrop RG, Ellis JM (1993) A spatial model of atmospheric deposition for the northeastern United States. Ecol Appl 3:459–472

O'Neill EG (1994) Responses of soil biota to elevated atmospheric carbon dioxide. Plant Soil 165:55–65

O'Neill EG, Luxmore RJ, Norby RJ (1987) Increases in mycorrhizal colonization and seedling growth in *Pinus echinata* and *Quercus alba* in an enriched $CO_2$ atmosphere. Can J For Res 17:878–883

Orians GH, Solbrig OT (1977) A cost-income model of leaves and roots with special reference to arid and semiarid areas. Am Nat 111:677–690

Parton WJ (1996) The CENTURY model. In: Poulson DS, Smith P, Smith JU (eds) Evaluation of soil organic matter models using existing long-term datasets (NATO ASI-series I-38). Springer, Berlin Heidelberg New York, pp 283–293

Pate JS (1973) Uptake, assimilation and transport of nitrogen compounds by plants. Soil Biol Biochem 5:109–119

Pate JS, Layzell DB (1990) Energetic and biological cost of nitrogen assimilation. In: Biochemistry of plants, vol 16. Intermediary nitrogen metabolism. Academic Press, San Diego, pp 1–42

Perez-Soba M, Dueck TA, Puppi G, Kuiper PJC (1995) Interactions of elevated $CO_2$, $NH_3$, and $O_3$ on mycorrhizal infection, gas exchange and N metabolism in saplings of Scots pine. Plant Soil 176:107–116

Pettersson R, McDonald AIS (1992) Effects of elevated carbon dioxide concentration on photosynthesis and growth of small birch plants (*Betula pendula* Roth.) at optimal nutrition. Plant Cell Environ 15:911–919

Phillips DA, Newell KD, Hassell SA, Felling EC (1976) The effect of $CO_2$ enrichment on root nodule development and symbiotic $N_2$ reduction in *Pisum sativum L.* Am J Bot 63:356–362

Pilbeam DJ, Kirkby EA (1990) The physiology of nitrate uptake. In: Abrol YP (ed) Nitrogen in higher plants. Wiley, New York, pp 39–64

Poorter H (1993) Interspecific variation in the growth response of plants to an elevated ambient $CO_2$ concentration. Vegetatio 104/105:77–97

Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83:553–559

Pregitzer KS, Zak DR, Curtis PS, Kubiske ME, Teeri JA, Vogel CS (1995) Atmospheric $CO_2$, soil nitrogen and turnover of fine roots. New Phytol 129:579–585

Reeves DW, Rogers HH, Prior SA (1994) Elevated atmospheric carbon dioxide effects on sorghum and soybean nutrient status. I. Plant Nutr 17:1939–1954

Rice CW, Garcia FO, Hampton CO, Owensby CE (1994) Soil microbial response in tallgrass prairie to elevated $CO_2$. Plant Soil 165:67–74

Rillig MC, Allen MF, Klironomos JN, Field CB (1998) Arbuscular mycorrhizal percent root infection and infection intensity *of Bromus hordeacus* grown in elevated atmospheric $CO_2$. Mycologia 90:199–205

Robinson D (1986) Compensatory changes in the partitioning of dry matter in relation to nitrogen uptake and optimal variations in growth. Ann Bot 58:841–848

Rogers HH, Peterson CM, McCrimmon JN, Cure JD (1992) Response of plant roots to elevated atmospheric carbon dioxide. Plant Cell Environ 15:749–752

Rogers HH, Runion GB, Krupa SV (1994) Plant responses to atmospheric $CO_2$ enrichment with emphasis on roots and the rhizosphere. Environ Pollut 83:155–189

Rothstein DE, Zak DR (2000) Kinetics of nitrogen uptake by *Populus tremuloides* in relation to atmospheric $CO_2$ and soil nitrogen availability. Tree Physiol 20:265–270

Rouhier H, Read DJ (1998a) Plant and fungal responses to elevated atmospheric carbon dioxide in mycorrhizal seedlings of *Pinus sylvestris*. Environ Exp Bot 40:237–246

Rouhier H, Read DJ (1998b) The role of mycorrhiza in determining the response of *Plantago lanceolata* to $CO_2$ enrichment. New Phytol 139:367–373

Sage RF (1994) Acclimation of photosynthesis to increasing atmospheric $CO_2$: the gas exchange perspective. Photosynth Res 39:351–368

Sage RF, Sharkey TD, Seemann JR (1989) Acclimation of photosynthesis to elevated $CO_2$ in five $C_3$ species. Plant Physiol 89:590–596

Schulze E-D (1994) Flux control in biological systems. Academic Press, San Diego

Sechley KA, Yamaya T, Oaks A (1992) Compartmentation of nitrogen assimilation in higher plants. Int Rev Cytol 134:85–163

Sinclair TR (1992) Mineral nutrition and plant growth response to climate change. J Exp Bot 253:1141–1146

Smirnoff N, Stewart GR (1985) Nitrate assimilation and translocation by higher plants-comparative physiology and ecological consequences. Physiol Plant 64:133–140

Smith SE, Read DJ (1997) Mycorrizal symbiosis. Academic Press, San Diego. pp 605

Soussana JF, Hartwig UA (1996) The effects of elevated $CO_2$ on symbiotic $N_2$ fixation: a link between the carbon and nitrogen cycles in grassland ecosystems. Plant Soil 187:321–332

Stitt M (1991) Rising $CO_2$ levels and their potential significance for carbon flow in photosynthetic cell. Plant Cell Environ 14:741–762

Stitt M, Krapp A (1999) The interaction between elevated carbon dioxide and nitrogen nutrition: The physiological and molecular background. Plant Cell Environ 22:583–621

Stribley DP, Tinker PB, Rayner JH (1980) Relation of internal phosphorus concentration and plant weight in plants infected by vesicular-arbuscular mycorrhizas. New Phytol 86:261–266

Stulen I, Hertog J den (1993) Root growth and functioning under atmospheric $CO_2$ enrichment. Vegetatio 104/105:99–115

Syvertsen JP, Graham JH (1999) Phosphorus supply and arbuscular mycorrhizas increase growth and net gas exchange responses of two *Citrus* spp. grown at elevated $CO_2$. Plant Soil 208:209–219

Thomas RB, Richter DD, Ye H, Heine PR, Strain BR (1991) Nitrogen dynamics and growth of seedlings of an N-fixing tree (*Gliricidia sepium* (Jacq.) Walp.) exposed to elevated atmospheric carbon dioxide. Oecologia 88:415 –421

Tissue DT, Thomas RB, Strain BR (1993) Long-term effects of elevated $CO_2$ and nutrients on photosynthesis and rubisco in loblolly pine seedlings. Plant Cell Environ 16:859–865

Tschaplinski TJ, Norby RJ, Wullschleger SD (1993) Responses of loblolly pine seedlings to elevated $CO_2$ and fluctuating water supply. Tree Physiol 13:283–296

Turpin DH, Layzell DB, Elrift IR (1985) Modeling the C-economy of *Anabena flos-aquae* – estimates of establishment, maintenance and active costs associated with growth on $NH_4^+$, $NO_3^-$ and $N_2$. Plant Physiol 78:746–752

Van Vuuren MMI, Robinson D, Fitter AH, Chasalow SD, Williamson L, Raven JA (1997) Effects of elevated carbon dioxide and soil water availability on root biomass, root length and N, P and K uptake in wheat. New Phytol 135:455–465

Vitousek PM, Aber J, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman GD (1997) Human alteration of the global nitorgen cycle: sources and consequences. Ecol Appl 7:737–750

Vogel CS, Curtis PS, Thomas RB (1997) Growth and nitrogen accretion of dinitrogen-fixing *Alnus glutinosa* (L) Gaertin under elevated carbon dioxide. Plant Ecol 130:63–70

Walker RF, Geisinger DR, Johnson DT, Ball JT (1995) Enriched atmsopheric $CO_2$ and soil P effects on growth and ectomycorrhizal colonization of juvenile ponderosa pine. Forest Ecol Manage 78:207–215

Wallander H, Arnebrant K, Dahlberg A (1999) Relationships between fungal uptake of ammonium, fungal growth, and nitrogen availability in ectomycorrhizal *Pinus sylvestris* seedlings. Mycorrhiza 8:215–223

Wolfenden J, Diggle PJ (1995) Canopy gas exchange and growth of upland pasture swards in elevated $CO_2$. New Phytol 130:369–380

Wullschleger SD, Post WM, King AW (1995) On the potential for a $CO_2$ fertilization effect in forests: estimates of the biotic growth factor based on 58 controlled-exposure studies. In: Woodwell GM, Mackenzie FT (eds) Biotic feedbacks in the global climatic system: will warming feed the warming? Oxford University Press, New York, pp 85–107

Xu DQ, Gifford RM, Chow WJ (1994) Photosynthetic acclimation in pea and soybean to high atmospheric $CO_2$ partial pressure. Plant Physiol 100:661–671

Yoder CK, Vivin P, DeFalco LA, Seemann JR, Nowak RS (2000) Root growth and function of three Mojave Desert grasses in response to elevated atmosphric $CO_2$ concentration. New Phytol 145:245–256

Zak DR, Pregitzer KS, Curtis PS, Teeri JA, Fogel R, Randlett RL (1993) Elevated atmospheric $CO_2$ and feedback between carbon and nitrogen cycles. Plant Soil 51:105–117

Zerihun A, BassiriRad H (2000) Interspecific variation in nitrogen uptake kinetic responses of temperate forest species to elevated $CO_2$: potential causes and consequences. Global Change Biol (in press)

Zerihun A, Gutschick VP, BassiriRad H (2000) Compensatory role of nitrogen uptake and photosynthetic nitrogen use efficiency in determining plant growth response to elevated $CO_2$: evaluation using a functional balanced model. Ann Bot 86:723–730