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## Root system adjustments: regulation of plant nutrient uptake and growth responses to elevated CO<sub>2</sub>

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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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>. Here we examine the literature to assess the extent to which these mechanisms have been shown to respond to high CO<sub>2</sub>. The literature survey reveals no consistent pattern either in direction or magnitude of responses of these mechanisms to high CO<sub>2</sub>. 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<sub>2</sub> most investigators have examined these mechanisms in isolation. Because such mechanisms can potentially counterbalance one another, a more reliable prediction of elevated CO<sub>2</sub> 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 effi-

ciency can be integrated to assess growth responses to high CO<sub>2</sub>. The FB model suggests that the mechanisms of increased N uptake highlighted here have different weights in determining overall plant responses to high CO<sub>2</sub>. 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<sub>2</sub> except when relative growth rate (RGR) reaches its developmental limit, maximum RGR (RGR<sub>max</sub>).

**Keywords** Elevated CO<sub>2</sub> · Nutrients · Root system adjustments · Mycorrhizae

### Introduction

As the debate about the potential impact of high CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>.

During the initial stages of acclimation to high CO<sub>2</sub>, 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

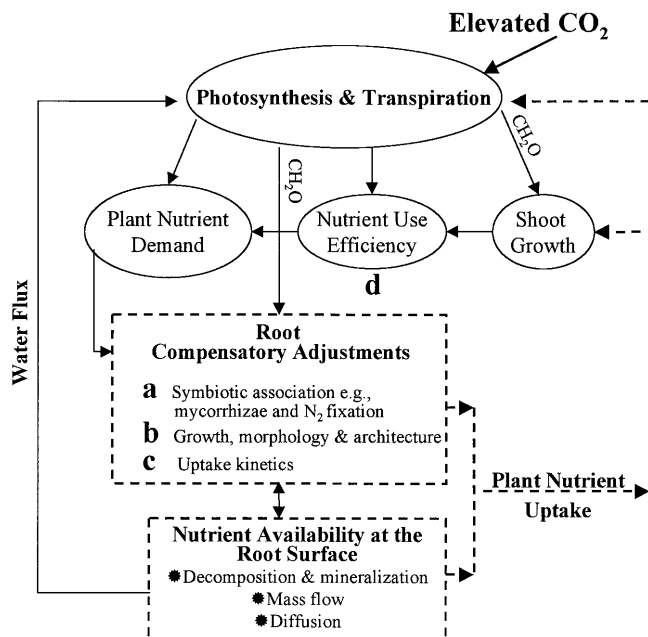
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al. 1994; Newbery et al. 1995), there is no evidence that such a positive response to elevated  $\text{CO}_2$  can be sustained over the long term without a concomitant increase in availability and/or acquisition of growth limiting nutrients. There are several ecosystem- and plant-level mechanisms that could compensate for the greater nutrient demand under high  $\text{CO}_2$ . 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  $\text{CO}_2$  may result in increased microbial activity (Dhillon 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  $\text{CO}_2$ , but this enhancement was caused by reduced transpiration and improved soil moisture rather than improved C supply to the soil. Because elevated  $\text{CO}_2$  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  $\text{CO}_2$  suppressed water use in wheat and improved soil water availability. They suggested that the reduced water use observed in plants grown under high  $\text{CO}_2$  decreased mass flow of  $\text{K}^+$  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  $\text{CO}_2$  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  $\text{CO}_2$  responses in natural ecosystems.

The main focus of this paper is to evaluate plant-level processes that influence nutrient acquisition under high  $\text{CO}_2$ . We discuss here specifically the relative growth rate (RGR) and net primary productivity (PP; gross or net) as two primary measures of performance. Plants possess 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  $\text{N}_2$ -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  $\text{CO}_2$ . 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  $\text{CO}_2$  enrichment is reviewed in the following section. Because very few  $\text{CO}_2$  studies have addressed nutrients other than



**Fig. 1** A conceptual model depicting various mechanisms by which plants can meet increased nitrogen demand under elevated  $\text{CO}_2$  levels. Dashed and solid lines represent supply and demand components of plant nutrient status, respectively

N, this review is largely focused on the role of these mechanisms in N uptake and growth responses to high  $\text{CO}_2$ .

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  $\text{CO}_2$ .

## Plant-level responses to $\text{CO}_2$ enrichment

### Increased symbiotic association with mycorrhizal fungi

Increased association with  $\text{N}_2$  fixing organisms and mycorrhizal fungi is an effective mechanism by which plants could increase their nutrient uptake per mass of root under high  $\text{CO}_2$ , thereby increasing RGR and PP. Several studies have shown that elevated  $\text{CO}_2$  stimulates  $\text{N}_2$  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  $\text{N}_2$  fixers. In contrast, roots of the majority of terrestrial plants form mycorrhizal associations. Furthermore, unlike  $\text{N}_2$ -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<sub>2</sub>. 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	<i>Quercus alba</i>	Norby et al. 1986
1.26	3.07	<i>Pinus echinata</i>	O'Neill et al. 1987
1.35	1.24	<i>P. sylvestris</i>	Perez-Soba et al. 1995
0.96	2.44	<i>P. ponderosa</i> , low soil P	Walker et al. 1995
1.49	2.66	<i>P. ponderosa</i> , medium soil P	Walker et al. 1995
1.46	1.58	<i>P. ponderosa</i> , high soil P	Walker et al. 1995
1.14	1.80	<i>Betula alleghaniensis</i>	Berntson and Bazzaz 1997
1.11	1.74	<i>B. papyrifera</i>	Godbold et al. 1997
1.31	2.10	<i>P. strobus</i>	Godbold et al. 1997
Arbuscular mycorrhizas			
1.35	1.02	<i>Tsuga canadensis</i>	Godbold et al. 1997
1.25	3.50	<i>Populus euroamericana</i>	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<sub>2</sub> is attractive because it is easy to assume that under elevated CO<sub>2</sub> 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<sub>2</sub>, 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<sub>2</sub>, 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<sub>2</sub>, 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<sub>2</sub> 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<sub>2</sub>, 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<sub>2</sub>. 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<sub>2</sub>. Although there have been many reports of arbuscular mycorrhizal percent infection under elevated CO<sub>2</sub>, 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<sub>2</sub>. A second component of mycorrhizal mass that could increase under elevated CO<sub>2</sub> is

**Table 2** Whole-plant N and P status under elevated CO<sub>2</sub> 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			
<b>Ectomycorrhizas</b>				
1.19	n.d.	1.19	<i>Pinus taeda</i> + <i>Pisolithus tinctorius</i> ; low P	Lewis and Strain 1996; Lewis et al. 1994
1.15	0.96	0.78	<i>Pinus sylvestris</i> + <i>Paxillus involutus</i>	Rouhier and Read 1998a
1.22	1.17	0.68	<i>Pinus sylvestris</i> + <i>Suillus bovinus</i>	Rouhier and Read 1998a
<b>Arbuscular mycorrhizas</b>				
1.22	1.55	1.28	<i>Trifolium repens</i> + <i>Glomus mosseae</i>	Jongen et al. 1996
1.98	1.50	1.32	<i>Beilschmiedia pendula</i> +indigenous inoculum	Lovelock et al. 1996
12.16	n.d.	4.00	<i>Plantago lanceolata</i> +indigenous inoculum	Rouhier and Read 1998b
3.08	1.38	1.6	<i>Citrus aurantium</i> + <i>Glomus intraradices</i> ; low soil P	Syvertsen and Graham 1999
2.33	1.09	1.49	<i>Citrus sinensis</i> + <i>Glomus intraradices</i> ; 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<sub>2</sub>. 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<sub>2</sub>. 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<sub>2</sub>. 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<sub>2</sub>. They reasoned that if mycorrhizae are more beneficial under elevated than ambient CO<sub>2</sub>, 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>.

In sum, pot experiments suggest that in mycorrhizal plants nutrients increased relatively more than plant mass under elevated compared with ambient CO<sub>2</sub>. This relative increase was greater for P than for N. The increase in ectomycorrhizal mass relative to plant mass under elevated CO<sub>2</sub> 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<sub>2</sub> stimulates root biomass allocation (Stulen and den Hertog 1993). Although earlier literature indicated that elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>, Wullschlegel et al. (1995) found a significant increase in root-to-shoot ratio in only 6% of cases. Norby (1994) also concluded that elevated CO<sub>2</sub> does not lead to a significant shift in biomass allocation regardless of soil N availability. The conclusion that elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>-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<sub>2</sub> 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<sub>2</sub>, 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<sub>2</sub> (BassiriRad et al. 1997b).

Changes in biomass allocation to fine roots in response to CO<sub>2</sub> 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<sub>2</sub> increased root turnover in *Populus tremuloides*. Elevated CO<sub>2</sub> 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 al-

location 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<sub>2</sub> 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<sub>2</sub>. In a growth-chamber study, Rogers et al. (1992) demonstrated that elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>. In contrast, specific root length (m g<sup>-1</sup>) significantly increased in response to CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>. More recently Berntson and Bazzaz (1997) examined a number of architectural parameters in roots of yellow birch and found no elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>. 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<sub>2</sub>.

#### 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  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$ .

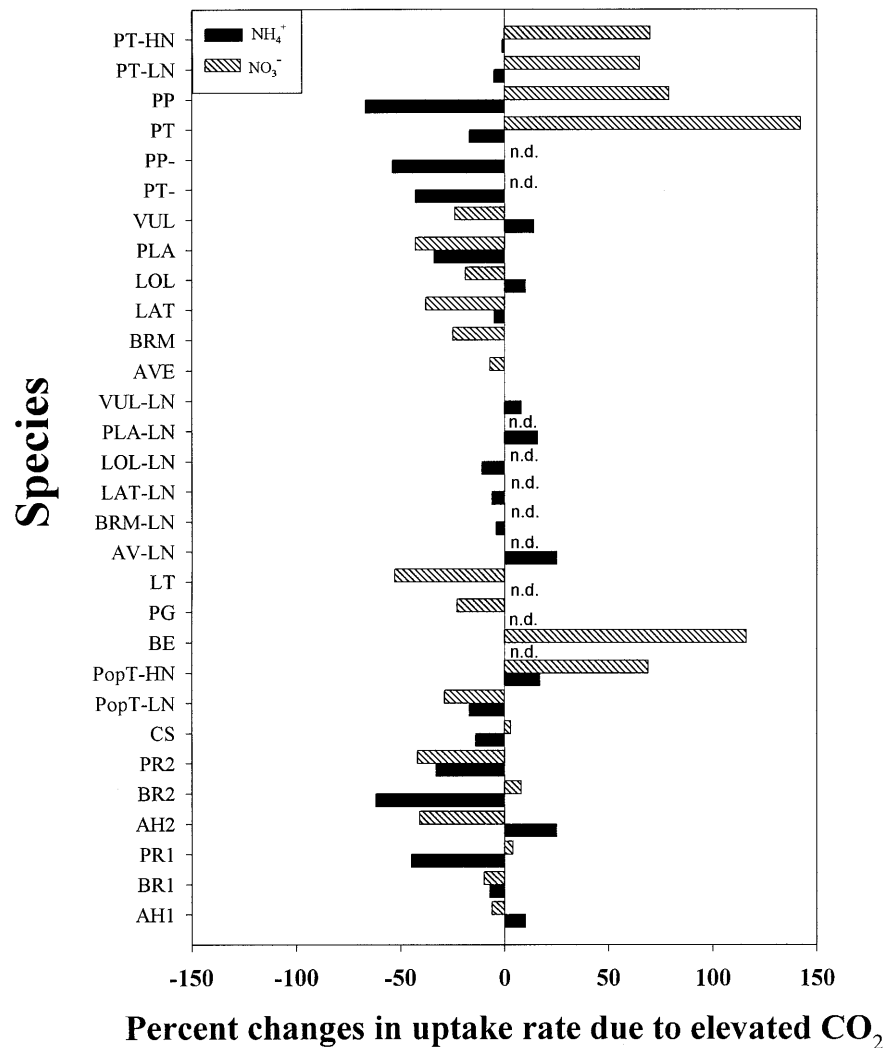
In many nutrient-limited habitats, however, carbohydrate availability seldom limits nutrient uptake (Chapin et al. 1995). Furthermore, although an adequate supply of carbohydrates is often required for root nutrient uptake capacity, C supply does not necessarily regulate changes in ion uptake: the nutrient 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  $\text{NH}_4^+$  uptake in field grown loblolly pine saplings was unaffected by growth  $\text{CO}_2$  concentration even though total non-structural carbohydrates were significantly higher in fine roots of the high  $\text{CO}_2$  saplings. Similarly, in pot-grown cotton grass seedlings, root carbohydrate status increased significantly in response to high  $\text{CO}_2$  without a significant effect on kinetics of root  $\text{PO}_4^{3-}$  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  $\text{NH}_4^+$  uptake of both loblolly and ponderosa pine seedlings in response to  $\text{CO}_2$  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  $\text{NH}_4^+$  or  $\text{NO}_3^-$  uptake of six annual grassland species at a single concentration of the inorganic N forms. They found no significant effect of high  $\text{CO}_2$  on  $\text{NH}_4^+$  uptake whereas  $\text{NO}_3^-$  uptake rate significantly decreased in response to  $\text{CO}_2$  enrichment. In intact roots of loblolly and ponderosa pine seed-

lings, a single uptake technique showed that elevated  $\text{CO}_2$  significantly increased  $\text{NO}_3^-$  uptake rate but decreased the uptake rates for  $\text{NH}_4^+$  (BassiriRad et al. 1997a) leading to no significant effect on total N uptake rate. Newbery et al. (1995) examined the effect of  $\text{CO}_2$  on root physiological uptake capacity for N, P, and K in *Agrostis capillaris*. They used three different concentrations in the uptake medium and found that elevated  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{NH}_4^+$  uptake responses to elevated  $\text{CO}_2$  were highly species specific. BassiriRad et al. (1997b) also found that, depending on species, root  $\text{NO}_3^-$  absorption rate doubled or halved in response to doubling of the atmospheric  $\text{CO}_2$  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  $\text{CO}_2$ . In a study of three desert species, BassiriRad et al. (1997b) showed that elevated  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{NO}_3^-$  uptake species differences in responses to elevated  $\text{CO}_2$  may represent differences in the predominant site of  $\text{NO}_3^-$  reduction. Nitrate can be assimilated in root and shoot or both, and the assimilation rate is directly correlated with  $\text{NO}_3^-$  uptake (Smirnov and Stewart 1985; Pate 1973; Andrews 1986). Under optimal light conditions, shoot  $\text{NO}_3^-$  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  $\text{CO}_2$  concentration would disproportionately benefit  $\text{NO}_3^-$  uptake in root- versus shoot-reducing species. In any event, the en-

**Fig. 2** Percent changes in rates of uptake of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in response to elevated compared to ambient  $\text{CO}_2$  grown plants. Data have been compiled from the literature. Species listed on the y-axis and the corresponding references: *PT-HN*, *PT-LN* *Pinus taeda* 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-nitrogen 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  $\text{CO}_2$ , root energy supply, and inorganic nitrogen uptake, other complexities must also be considered. Plant N is primarily supplied from the available soil  $\text{NO}_3^-$  and  $\text{NH}_4^+$  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  $\text{NO}_3^-$  than  $\text{NH}_4^+$ , because  $\text{NO}_3^-$  must be metabolically reduced to ammonia before it can be assimilated (Haynes and Goh 1978; Blacqui re 1987). In

barley seedlings, uptake and assimilation of  $\text{NH}_4^+$  consumes 14% of root carbon catabolism whereas uptake and assimilation of  $\text{NO}_3^-$  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,  $\text{NO}_3^-$  is a less favorable form of N (Turpin et al. 1985). Uptake and utilization of  $\text{NO}_3^-$  may therefore, be disproportionately enhanced compared to  $\text{NH}_4^+$  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  $\text{CO}_2$  effect on nutrient uptake. For example, Larigauderie et al. (1988) showed that in *Bromus mollis*, elevated  $\text{CO}_2$  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<sub>2</sub> treatment. Therefore, a more reliable evaluation of CO<sub>2</sub> effects on nutrient uptake must be based on more than a single measurement during the growing season. Furthermore, considering that elevated CO<sub>2</sub> 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<sub>3</sub> species, short-term CO<sub>2</sub> 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<sub>2</sub> is rarely considered. Rubisco activity and concentration often decline significantly in response to CO<sub>2</sub> 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<sub>2</sub>.

#### Modeling synthesis

So far, we have conceptually evaluated the role of major root system mechanisms that can adjust to varying de-

grees in response to elevated CO<sub>2</sub>. More accurate prediction of growth response to CO<sub>2</sub> (or whether such adjustments would adequately meet increased plant N demand under high CO<sub>2</sub>) 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<sub>2</sub>. We are particularly interested in a modeling synthesis that quantifies the relative contribution (leverage) of each mechanism in regulating growth responses to CO<sub>2</sub>. 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<sub>nl</sub> determined by N acquisition with RGR<sub>pl</sub> determined by photosynthesis (nl, nutrient-limited; pl, photosynthesis-limited):

$$RGR_{nl} = RGR_{pl} \quad (2)$$

or

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

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:

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

and it predicts a final value of RGR,

$$RGR = \left[ \frac{\sqrt{r}}{1+r} \right] \sqrt{\beta\alpha_L\alpha_n p^* \bar{v}} \quad (5)$$

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  $\text{CO}_2$  gives a robust prediction of how  $p^*$  and thus RGR vary with  $\text{CO}_2$  (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  $[1-\exp(-m/m^*)]/m$ }.

#### 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 maintenance 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,  $dm/dt$ , 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  $\text{g}_{\text{DM}} \text{g}^{-1}$  photosynthate than the old value of 0.67. We admit that  $\beta$  may differ between plant tissue and fungal tissue, so that  $\beta(\text{MRF})$  is defined as a multiple of that for plant tissue [i.e.,  $G \times \beta(\text{plant})$ ]. We must also describe the amount of mycorrhizal biomass. We choose to express it as a multiplier of root biomass (i.e.,  $m_{\text{MRF}} = \alpha_M m_r$ ). 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  $r(\bar{v} + \alpha_M \bar{v}_M)$ . We may write this as  $r\bar{v}(1+g\alpha_M)$ . Consequent to both modifications, RGR for mycorrhizal roots ( $\text{RGR}_{\text{MR}}^{\text{FB}}$ ) at functional balance becomes:

$$\text{RGR}_{\text{MR}}^{\text{FB}} = \sqrt{\frac{\beta \alpha_L p^* r \bar{v} p (1 + g \alpha_M)}{[1 + r(1 + G \alpha_M)][1 + r(1 + \alpha_M)]}} \quad (6)$$

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

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

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  $\beta \alpha_L f_n L p^*$  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  $\text{RGR}_{\text{max}} f_C / (f_C + K_e)$ . 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  $\text{RGR}_{\text{max}}$  and its responsiveness to elevated  $\text{CO}_2$ . 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](http://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,  $R = (dRGR/RGR) / (dparam/param) = (d \ln RGR) / (d \ln param)$  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  $\bar{v}$ :  $RGR = (\text{constant}) \bar{v}^{0.5}$ ,

or  $\ln(RGR) = \ln(\text{constant}) + 0.5 \ln(\bar{v})$ . Thus,  $R(\bar{v}) = 0.5$ . Other factors such as  $r$  had much lower control over RGR. In the case  $r = 0.5$ ,  $R(r) = 0.5 (1-r)/(1+r) = 0.17$ . That is, RGR increases relatively only 17% as fast as does  $r$ .

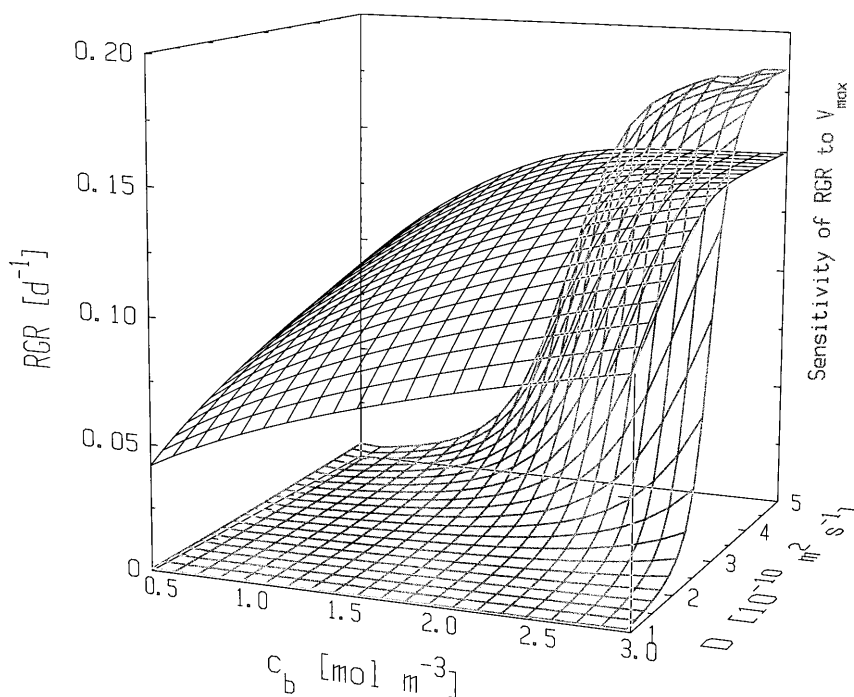
Any physiological or soil parameter can affect  $f_N$  quite differently from how it affects RGR. For example,  $f_N$  is predicted to vary in the simple model as  $\sqrt{r}$ , yielding  $S(r) = 0.5$  in the control of  $f_N$  by  $r$ . That is, tissue "quality" as  $f_N$  is much more sensitive to  $r$ ; 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  $0.3 \text{ d}^{-1}$ , 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 ( $34 \text{ g PSate g}_N^{-1} \text{ d}^{-1}$ ; 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  $0.5 \text{ g}_{\text{DM}} \text{ g}^{-1} \text{ PSate}$ , 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  $V_{\text{max}}$  is fixed at a moderately high value,  $10^{-6} \text{ mol m}^{-2} \text{ s}^{-1}$ . 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  $V_{\text{max}}$  (shaded surface for logarithmic derivative of RGR with respect to  $V_{\text{max}}$ ). 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  $\text{RGR}_{\text{max}}$ , 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  $\text{RGR}_{\text{max}}$  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  $\text{RGR}_{\text{max}}=0.3 \text{ d}^{-1}$  ("moderate") or the same  $k_c$  and  $K_e$  but  $\text{RGR}_{\text{max}}=0.15 \text{ day}^{-1}$  ("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 ( $0.02 \text{ g}_{\text{N}} (\text{g}_{\text{DM root}})^{-1} \text{ d}^{-1}$ ), 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  $r$ ,  $S_{\text{RGR}}(r)$ , vanishes as  $r$  approaches 1, the nominal optimum. The sensitivity to  $\bar{v}$ ,  $S_{\text{RGR}}(\bar{v})$ , remains moderately high (0.3–0.5; simulation data not shown), only decreasing strongly as RGR approaches  $\text{RGR}_{\text{max}}$ .

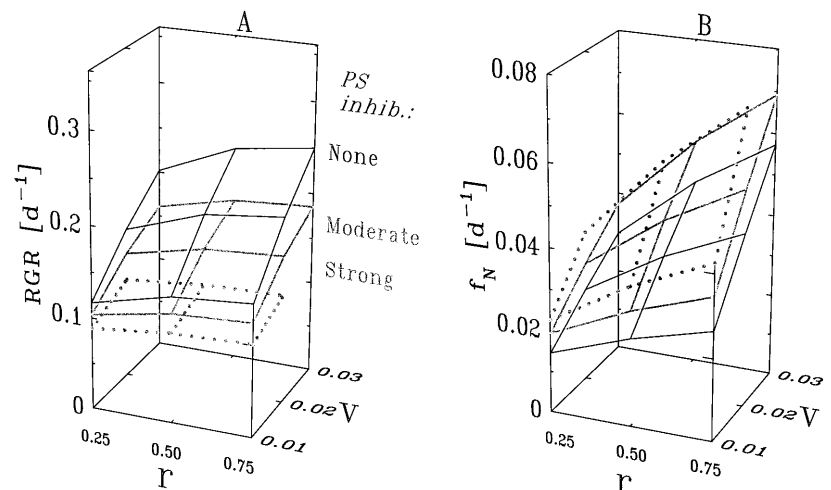
#### Growth responses directly to elevated CO<sub>2</sub>

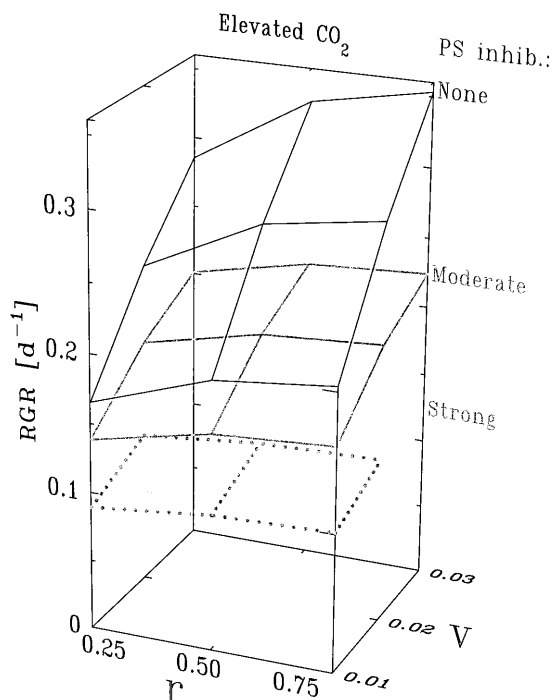
Figure 5 shows RGR at double ambient CO<sub>2</sub> (doubled  $p^*$ ), for the same physiological constitution as in Fig. 4. All the responses to  $r$  and  $\bar{v}$  are expanded by the approximate factor  $\sqrt{2}$ , appropriate to even the simple model, in which RGR is proportional to  $\sqrt{p^*}$ . That is, elevated CO<sub>2</sub> does not change the nature of any response, in this model. The increase in  $p^*$  at high CO<sub>2</sub> 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 $f_{\text{N}}$ 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,  $0.015 \text{ g}_{\text{N}} (\text{g}_{\text{DM root}})^{-1} \text{ d}^{-1}$ . 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  $\bar{v}_M=\bar{v}_{\text{plant}}$ ), 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

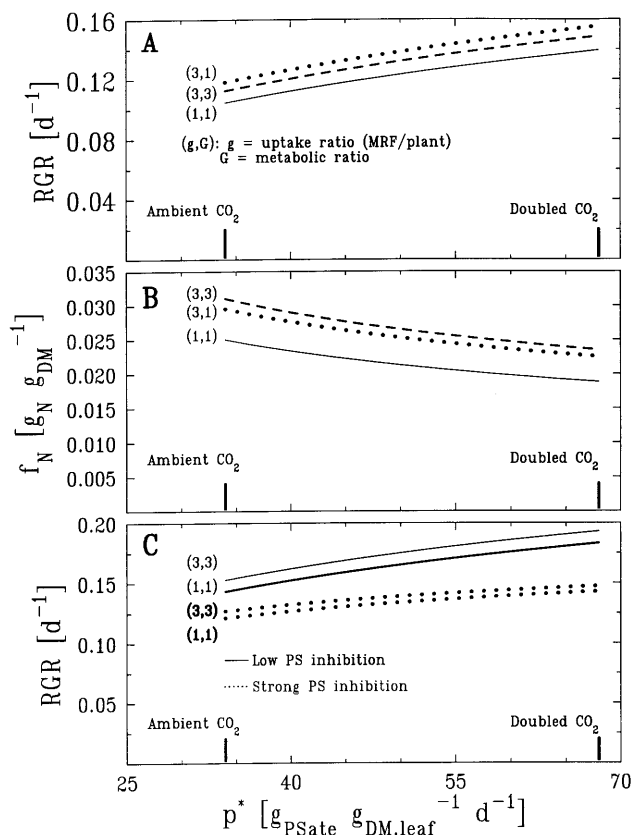
**Fig. 4** Role of root:shoot ratio ( $r$ ) and of uptake rate ( $V$ ) in determining **A** RGR and **B** tissue N content ( $f_{\text{N}}$ ) under ambient CO<sub>2</sub> concentration: simulation for three different degrees of susceptibility to photosynthetic inhibition (*PS inhib*)





**Fig. 5A–C.** Role of root:shoot ratio and root uptake rate in determining RGR at elevated  $\text{CO}_2$  level. All parameters are the same as Fig. 4, except that  $p^*$  is doubled to  $68 \text{ g PSate g}_N^{-1} \text{ d}^{-1}$  (PSate photosynthate)

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 ( $\text{RGR}_{\text{max}}=0.3 \text{ day}^{-1}$ ,  $k_c=1$ ,  $K_e=0.5$ ). Over the range of  $\text{CO}_2$  that doubles  $p^*$  (doubling the  $\text{CO}_2$ , 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  $0.015 \text{ day}^{-1}$  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  $1.12 \times 5 = 5.6$  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



**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  $\text{CO}_2$  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  $\text{RGR}_{\text{max}}$  of  $0.3 \text{ day}^{-1}$  and *dotted lines* represent  $\text{RGR}_{\text{max}}$  of  $0.18 \text{ d}^{-1}$

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,  $\text{RGR}_{\text{max}}=0.3 \text{ d}^{-1}$ ,  $k_c=1$ , and  $K_e=0.5$ . The case of strong inhibition uses  $\text{RGR}_{\text{max}}=0.18 \text{ d}^{-1}$ . 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  $\text{RGR}_{\text{max}}$ ) 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  $\text{CO}_2$  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  $\text{CO}_2$  may largely depend on the balance between C and nutrient uptake. Mechanisms of leaf and canopy adjustment in C uptake responses to high  $\text{CO}_2$  levels have been extensively utilized in formulating predictive models of plant and ecosystem responses to high  $\text{CO}_2$ . Yet little is known about the root system mechanisms which are causally related to nutrient relations of plants grown under high  $\text{CO}_2$ .

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  $\text{CO}_2$ . For example, an increase in fine root production under high  $\text{CO}_2$  does not automatically translate into greater nutrient uptake if the fine roots produced under high  $\text{CO}_2$  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  $\text{CO}_2$ ) 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  $\text{CO}_2$ . 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,  $\bar{v}$ , should always affect RGR and tissue  $f_n$  strongly. The ability to increase  $\bar{v}$  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,  $\text{RGR}_{\text{max}}$ . The latter may be an important parameter to measure. Product inhibition of photosynthesis and its changes with  $\text{CO}_2$  and

nutrient treatments are expected to have only modest effects for most plants.

Even when one focuses on a single mechanism, responses to high  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$ . Obviously this has enormous implications for net primary productivity. However, such inter-species variation may also explain why elevated  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  would require a better understanding of the factors that regulate plant nutrient status and how these factors may change in response to  $\text{CO}_2$ . The FB model presented here is one such attempt.

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