11 Nutrient Acquisition of Terrestrial Plants in a Changing Climate

D.G. Bielenberg and H. BassiriRad

11.1 Introduction

The previous chapters highlighted the many ways by which nutrient acquisition can regulate plant response to the environment. Today, ecosystems and ecological processes are impacted by a suite of anthropogenic agents that will define plant ecology in ways that were not imagined even as little as five decades ago. Changes in land use and anthropogenic production of environmental pollutants have all but devastated many native systems of the world and will remain a growing danger to the health of the remaining native systems. Ecologists, particularly those working with plants and ecosystems, bear the intellectual task of reliably predicting the potential consequences of global change. Such knowledge will be critical in management and policy measures designed to halt further deterioration of native systems. In this chapter, we argue that reliable predictions of the fate of terrestrial plant communities, and thereby the policy and management choices of the future, will require a clear understanding of plant nutrient uptake in a changing climate.

By the end of this century, most of the globe will be experiencing atmospheric CO_2 concentrations twice as high as those encountered during the mid-20th century, while the global temperature is likely to rise by as much as 5 °C during the same period. In addition to their direct effects, the higher concentration of CO_2 and other greenhouse gasses will impact terrestrial ecosystems via dramatic changes in climate pattern, including the occurrence of extreme drought and flooding. Major biomes of the earth will also experience above-average input of atmospheric N, ozone (stratospheric ozone will decrease and tropospheric levels increase), and UV-B radiation. Either individually or collectively, alterations in these environmental factors will change plant nutrient demand. Unless these demands are met via adjustments in nutrient availability and/or uptake, the productivity and composition of plant communities may change irreversibly.

Ecological Studies, Vol. 181
H. BassiriRad (Ed.) Nutrient Acquisition by Plants
An Ecological Perspective

Obviously, we will not be able to cover all the components of global change in this chapter. Chapter 10 (this Vol.) has covered soil temperature as a component of global change. Here, we will focus on the impacts of three major components of global change, and examine the state of the knowledge on how these factors affect plant nutrient uptake. The components of global change focused on here are elevated tropospheric ozone, increased incident UV-B radiation, and elevated atmospheric CO_2 concentration.

11.2 Elevated Tropospheric Ozone or Elevated UV-B Radiation

11.2.1 Extent of the Problem and Relevance to Nutrient Uptake

At first consideration, elevated levels of tropospheric ozone (O_3) and elevated levels of UV-B solar radiation would appear to have little similarity. Nonetheless, these topics will be considered together because of the shared themes that emerge from the literature: both have direct effects upon aboveground plant organs, both have the potential to generate oxidative damage, and both have the potential to alter biomass accumulation and partitioning. Fundamentally, however, little is known about the effect of either of these stresses on nutrient acquisition from the soil environment.

Tropospheric O_3 is the major phytotoxic constituent of photochemical smog, and was first identified as damaging to plants in the 1950s (Richards et al. 1958). Large areas of Asia, Africa, Australia, and the Americas have high potential for the production of elevated tropospheric O_3, based on predicted energy use patterns and global solar radiation patterns (Kickert and Krupa 1990). Ozone reduces photosynthesis, growth, and yield, increases respiration, causes accelerated foliar senescence, reduces root:shoot ratios, and can increase plant susceptibility to pathogens (Runeckles and Krupa 1994).

Elevated UV-B, resulting from stratospheric O_3 depletion, has the potential to affect a wide range of ecosystems and plant types. In some sensitive species, laboratory experiments have demonstrated that UV-B can reduce photosynthesis, leaf area, water use efficiency, growth, and yield as well as altering many aspects of plant morphology (Runeckles and Krupa 1994). However, these impacts of UV-B exposure are minimal in many plant species, and by and large the evidence available to date predicts no impact for most species at UV-B levels that reflect realistic environmental dosages (Searles et al. 2001).

11.2.2 Direct Effects on Nutrient Uptake

11.2.2.1 Changes in Root-to-Shoot Ratios, Morphology and Architecture

A shift in biomass allocation to the shoots (a decrease in root-to-shoot ratios, RSR) has been observed in a wide range of plant species in response to O_3 exposure (Cooley and Manning 1987). The shift in partitioning to the shoot is generally ascribed to increased use of carbohydrates for repair of O_3-induced damage in the leaves, and O_3-induced disruption of phloem loading (Cooley and Manning 1987). However, when assessing the effects of environmental treatments upon RSR shifts, it is important to evaluate the impact of changes in plant size as a causal factor in altered RSR (Ledig et al. 1970; Coleman et al. 1994). Coleman and McConnaughay (1995) emphasized the need for caution with their reexamination of a study of biomass partitioning involving the air pollutant SO_2. When they accounted for treatment-induced changes in plant size, they eliminated differences in RSR that previously appeared to support a conclusion of altered biomass partitioning. Similarly, when Bielenberg et al. (2002) investigated the effects of O_3 on biomass partitioning in hybrid poplar, shifts in RSR occurred as a result of treatment-induced changes in plant size, and not from specific alterations in biomass partitioning.

The root:shoot ratio can also be affected by UV-B exposure (Sullivan 1997), although the results from different experiments have been variable. Increased, decreased and unchanged RSR have all been reported in response to UV-B exposure (Sullivan 1997; Weih et al. 1998). Alterations in RSR induced by UV-B can be subtle and sometimes transient. UV-B increased RSR in the first year of a 2-year study by Sullivan et al. (1994). No differences in RSR were detected in the second year of the study (Sullivan et al. 1994). Ziska et al. (1993) reported a strong reduction of RSR in cassava by UV-B, without changes in whole-plant biomass. Reduced biomass allocation to roots may decrease nutrient uptake, as well as reducing the yield of economically important plant parts (Ziska et al. 1993). It remains to be determined whether most UV-B-induced changes in RSR result from altered ontogeny or from altered partitioning priorities.

Root system architecture is also affected by exposure to O_3, although specific changes in architecture appear variable and highly species-specific. In an O_3-sensitive loblolly pine selection, O_3 was shown to decrease both total root surface area and root surface area per unit root mass (Qiu et al. 1992). Reduced root surface area may limit nutrient uptake. However, Taylor and Davies (1990) noted an increase in specific root length (length per unit mass) in response to O_3 in beech seedlings. Temple et al. (1993) reported an increase in fine root mass, and a decrease in coarse root mass in a field study with ponderosa pine. Nutrient acquisition is facilitated by increased specific root length and increased fine root numbers. Finally, no impact of

O_3 on the proportion of coarse and fine root biomass, or the specific root length of the coarse and fine fractions was reported in birch (Maurer and Matyssek 1997).

11.2.2.2 Changes in Root Respiration and Carbohydrate Supply to the Roots

Root respiration is generally reduced by O_3 stress. Theoretically, such reduction can limit the energy supply required for active nutrient uptake. In some cases, decreases in total root system respiration are attributable to decreases in total root mass (Coleman et al. 1996), while in other cases a reduction in respiration on a specific root mass basis has been suggested (Edwards 1991). A large fraction of total root respiration is related to nutrient uptake (Lambers 1987), but nutrient uptake was not measured in either of these studies.

A number of studies using isotopic tracers have shown that proportionately less photosynthate is translocated from leaves to roots in O_3-stressed plants (Nouchi et al. 1995; Pausch et al. 1996a; Samuelson and Kelly 1996). The decrease in translocation of C to the roots is viewed as the cause of decreased root mass (Cooley and Manning 1987). By decreasing both root growth and root respiration, it is likely that O_3 also limits nutrient acquisition from the soil environment.

11.2.2.3 Changes in Root Uptake Kinetics

The preceding sections indicate O_3 has the potential to alter nutrient uptake by reducing carbohydrate availability, decreasing root biomass, and altering root architecture. Direct investigations of the effect of O_3 on nutrient uptake are few, and indicate species-specific differences in response. Nouchi et al. (1991) reported a specific reduction in ammonium uptake in roots excised from O_3-treated rice plants. Pausch et al. (1996b) showed a shift in N acquisition away from N-fixing nodules to N acquisition from the root zone in O_3-exposed soybean, and ascribed this reduction to reduced photosynthate translocation to roots from the shoots (Pausch et al. 1996a). However, Bielenberg et al. (2002) showed no O_3 impact on labeled N uptake by hybrid poplars on a whole-plant basis at two levels of N availability. Similarly, in one of the few studies that included other mineral nutrients besides N, chronic O_3 exposure did not affect tissue concentrations or shoot uptake of a number of these (N, P, K, S, Ca, Mg, Fe, Mn, and Zn) in spring wheat (Fangmeier et al. 1997). However, a later study in potato found that tuber concentrations of N and Mg significantly increased in response to O_3 exposure, but this effect may be attributable to reduced biomass, rather than increased nutrient uptake (Fangmeier et al. 2002).

Few studies to date have addressed the effect of UV-B exposure on root system uptake of nutrients from the soil environment (Baker and Allen 1994; Sullivan 1997; Caldwell et al. 1998; Zepp et al. 1998). A small number of studies have investigated the effect of UV-B on whole-plant accumulation of nutrients. These studies have used nutrient content (mass nutrient per plant or plant part; Murali and Teramura 1985; Yue et al. 1998) or concentration (mass nutrient per dry weight of plant or plant part; Elawad et al. 1985; Larsson et al. 1998; Moorthy and Kathiresan 1998; de la Rosa et al. 2001; Shukula and Kakkar 2002) in the standing biomass (shoot, leaves, or whole plant) as an indication of whole-plant uptake. Nutrients increase in concentration (Larsson et al. 1998), or remain unchanged (de la Rosa et al. 2001) in plant tissues in response to UV-B exposure. In the studies where nutrient content was measured along with concentration (Murali and Teramura 1985; Yue et al. 1998), plant content was usually unaffected or very slightly reduced in response to UV-B exposure. Therefore, UV-B appears to have very little or no affect on nutrient accumulation on a whole-plant basis. Plant nutrient concentration changes appear to result from UV-B-induced biomass reductions, rather than changes in the physiology of nutrient acquisition.

11.2.2.4 Changes in Foliar Uptake/Leaching

Solutes, particularly cations and small-molecular weight molecules, can be taken up by the leaf through the waxy cuticle that forms the outer boundary of the leaf surface. Atmospheric deposition of nitrogen and sulfur onto leaf surfaces can result in significant foliar uptake of these nutrients (Lambers et al. 1998). The ease with which uptake occurs is inversely related to cuticle thickness. UV-B has been shown to increase the thickness of the cuticle layer surrounding the leaf (Grammatikopoulos et al. 1998), potentially limiting the uptake of nutrients such as N and S deposited from the atmosphere.

Similarly, UV-B-induced thickening of leaf cuticles may reduce leaching of foliar nutrients. Foliar leaching can result in considerable loss of nutrients, particularly Ca and Mg, in moist climates (Marschner 1995). Foliar leaching may negatively impact the plant by removing essential nutrients, but also may increase the soil availability of nutrients for new growth that are inefficiently remobilized from older leaves (Marschner 1995). In areas of acidic deposition, however, foliar leaching and pH-induced soil leaching may result in significant losses of cations from the plant–soil system (Edwards et al. 1995).

11.2.3 Indirect Effects on Nutrient Uptake

Chronic O_3 stress has been demonstrated to cause accelerated senescence of leaves in many species of plants (Reich and Lassoie 1985; Sanders et al. 1992;

Wiltshire et al. 1993; Sicher and Bunce 1998; Pell et al. 1999). UV-B has also been shown to trigger early senescence of cotyledons and leaves (Ambler et al. 1975; Ernst et al. 1997). Additionally, UV-B impaired remobilization of Zn (Ambler et al. 1975), and Fe, Mg, and Mn (Ernst et al. 1997) from cotyledons of seedlings. Early leaf loss will alter the schedule of litter-fall availability to the decomposer community, and may change temporal patterns of soil nutrient cycling and availability.

In addition to altering the timing of leaf fall, O_3 affects the tissue quality and decomposition of abscised foliage (Kickert and Krupa 1990). In a study of the effect of O_3 on leaf loss and decomposition in poplar, Jones et al. (1994) demonstrated that leaf litter resulting from O_3-induced accelerated senescence contained greater amounts of N and bound phenolic compounds. Contrary to the expectation that increased N would speed decomposition, this change in litter quality resulted in slowed decomposition, presumably as a result of phenolic-N complexation. Additionally, naturally senescing leaves from the same O_3-exposed plants had reduced N content, compared to leaves abscised from non-O_3-exposed plants (Jones et al. 1994).

UV-B exposure frequently induces the synthesis of UV-absorbing phenylpropanoid compounds (Zepp et al. 1998). Grammatikopoulos et al. (1998) reported increased phenolics and tannins, and decreased N content in leaves of *Laurus nobilis* and *Ceratonia siliqua*. In contrast, no effects of UV-B exposure upon leaf litter quality (nutrient or phenolic contents) were found in a study of *Quercus robur* (Newsham et al. 2001). These compounds can affect nutrient cycling by retarding the rate of decomposition and/or affecting the availability of other nutrients in leaf litter (Zepp et al. 1998). A slowed rate of decomposition could result in lower turnover of organic matter and mineral nutrients in the soil, potentially reducing productivity as more and more nutrients are sequestered. However, no direct effects of UV-B exposure on litter decomposition were found in a dune grassland system (Verhoef et al. 2000).

Far more attention has been paid to the effects of O_3 than of UV-B on root characteristics and function. Much of the O_3 literature is contradictory and indicates that, depending upon species, there may be a wide range of responses to elevated tropospheric O_3. Additional studies involving a wider range of functional types are needed to predict possible community and ecosystem alterations resulting from O_3-impaired nutrient acquisition. The little UV-B literature that exists indicates that only limited, if any, effects on direct nutrient uptake can be expected. Both stresses have potential for indirect effects upon ecosystem nutrient cycling in the long term. More studies are needed to assess the potential for species- and community-level feedbacks of elevated O_3 or UV-B on nutrient cycling that result from alterations in phenology, litter quality, or decomposition processes.

11.3 Elevated Atmospheric CO2 Concentration

11.3.1 Extent of the Problem and Relevance to Nutrient Uptake

The advent of the industrial revolution, increased combustion of fossil fuel, and deforestation have substantially accelerated the rate of CO_2 production on earth, and thereby its accumulation in the atmosphere. Data from ice-core gasses indicate that between 1750 and the pre-industrial revolution, the atmospheric CO_2 concentration remained constant at roughly 280 ppm (Houghton et al. 2001). Since then, however, the average CO_2 concentration has risen to 370 ppm. More importantly, direct atmospheric CO_2 measurements from Mauna Loa, Hawaii, indicate that more than 60 % of this dramatic rise in CO_2 has occurred in the last 40 years (Keeling and Whorf 2002). At this rate, it is expected that by the end of this century, the CO_2 concentration of the atmosphere will be double the current levels.

One of the most common plant responses to increased CO_2 concentration is the reduction in foliage N and many other nutrients (BassiriRad et al. 2001). This is perhaps why most researchers in this field suggest that while short-term exposure to CO_2 enrichment 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 the availability and uptake of nutrients are critical in determining plant and ecosystem responses to high CO_2. Here, we distinguish between responses in plant ability to take up nutrients (direct effects), as opposed to ecosystem availability of nutrients (indirect effects).

11.3.2 Direct Effects of CO2 on Plant Nutrient Uptake

11.3.2.1 Changes in Root-to-Shoot Ratios

Most of the early work in this area was based on the assumption that plant responses to high CO_2 would be driven by the functional balanced model. Such theoretical underpinning predicts that at high availability of C, biomass allocation to the roots should increase. Over the past three decades, considerable debate has emerged 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 ratios (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 experimental 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 the 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). More recently, Poorter and Nagel (2000) reviewed 170 observations from 80 publications, and concluded that there would be no significant changes in response to a doubling of CO_2 concentration.

The survey by Poorter and Nagel (2000) is particularly relevant to our discussion here, because they highlighted the importance of other environmental factors, e.g., light, water and nutrients, in regulating plant biomass allocation responses to CO_2. Therefore, caution must be exercised when the results of experiments with dissimilar protocols are compared. When comparable experiments are considered, 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 (McDonald et al. 1991; Ericsson et al. 1992) – a response that could be suppressed when nutrient limitation is avoided (Bazzaz 1990; Pettersson and McDonald 1992; Ceulemans and Mousseau 1994). In their survey of more than 40 tree species, McGuire et al. (1995) reported 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 vs. 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, the relative distribution of biomass between fine and coarse roots may be particularly important. For example, a mere increase in root-to-shoot ratio may not be highly informative in terms of plant nutrient acquisition, although it is an important parameter in terms of plant C allocation, particularly if biomass is allocated into taproots 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, b). The 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 CO_2 levels (BassiriRad et al. 1997b).

Fine root biomass allocation responses to high CO_2 provide a robust estimate of plant nutrient acquisition only if it is complimented with information about 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). Matamala and Schlesinger (2000) distinguished between live fine root (LFR) and dead fine root (DFR) in a loblolly pine stand under ambient and elevated CO_2, and found that after one season of fumigation LFR increased by 86 % in response to CO_2 enrichment, but DFR was relatively unaffected by the CO_2 treatment. In the same system, Pritchard et al. (2001) used mini-rhizotron observations and reported only modest changes in root turnover, but found a significant CO_2 by depth interaction on root mortality. It is therefore necessary that biomass allocation studies consider spatial and temporal dynamics of root growth responses to elevated CO_2.

11.3.2.2 Changes in Root Morphology and Architecture

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 (Caldwell 1987; Fitter and Hay 1987). Finer roots can confer greater nutrient uptake per unit root mass. Quantitative assessments 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 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, the root-to-shoot ratio was unchanged but root length was significantly higher in three out of four species grown at high vs. ambient CO_2. In contrast, specific root length (m/g) significantly increased in response to CO_2 enrichment in only one of the four species. Berntson and Woodward (1992) examined the 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.

It is also clear that mycorrhizal associations will be an important component of the root system responses to CO_2 that may regulate nutrient acquisition capacity of the whole plant. We have not discussed this topic here, but the reader is encouraged to consult the following works for a more comprehensive treatment of that topic: O'Neill (1994), Fitter et al. (2000), and BassiriRad et al. (2001). 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 in this field must make such linkages in order to establish a clear cause-and-effect relationship between form and function.

11.3.2.3 Changes in Root Uptake Kinetics

There are at least three theoretical reasons why kinetics of root nutrient uptake should respond to changes in atmospheric CO_2 concentration. First, given the energy requirement for the active transport of nutrients, one would expect that higher availability of carbohydrates under CO_2 would result in up-regulation of root nutrient transporters. Second, elevated CO_2, at least in the short term, has been shown to accelerate growth. Higher growth rate should then increase plant nutrient demand and uptake capacity (Lee 1982; Clarkson 1985). Third, models of whole-plant carbon nutrient balance (Bloom et al. 1985; Johnson 1985; Robinson 1986; Luo et al. 1994; Gutschick and Kay 1995) predict that resources of abundant availability – C – must be allocated to increase the uptake of the most limiting resource – nutrients. A large number of CO_2 studies have demonstrated both a short-term stimulation of growth and an increased supply of root respiratory substrates (Cruz et al. 1993; Tschplinski et al. 1993; Norby et al. 1995). Yet to date, the data on root uptake kinetics show no consistent pattern of uptake response to high CO_2.

The earliest direct measurements of root uptake responses to CO_2 enrichment were reported by Newbery et al. (1995) who examined the rates of N, P and K uptake in *Agrostis capallaris*, at three different external concentrations, and found no significant CO_2 effect. Using field-grown loblolly pine saplings that had been exposed to 18 months of CO_2 treatment, BassiriRad et al. (1996b) found no significant changes in V_{max} of NH_4^+ uptake, but elevated CO_2 significantly enhanced V_{max} for NO_3^- uptake. Jackson and Reynolds (1996) also found no effect of elevated CO_2 on NH_4^+ uptake rates of six grassland annuals, but NO_3^- uptake rate was inhibited in response to CO_2 enrichment. Other studies (see BassiriRad 2000; BassiriRad et al. 2001) also produced equally inconsistent patterns. Even in cases where similar species are examined, the effect of CO_2 on the kinetics of NH_4^+ varies from one experiment to the other (BassiriRad et al. 1996a, b).

The observed variability in root nutrient uptake responses to high CO_2 is consistent with that observed in other plant characteristics such as root growth (Tingey et al. 2000), shoot growth (Norby et al. 1999) as well as water use efficiency, photosynthetic rate, tissue N concentration, and nonstructural carbohydrates (Luo et al. 1999). Until we find a unified mechanism to explain such variability, our predictive capacity for plant and ecosystem responses to elevated CO_2 will remain limited. Some of the variations in response to high CO_2 may simply result from differences in experimental protocols. However, Zerihun and BassiriRad (2001) examined NH_4^+ and NO_3^- uptake kinetic responses of six broad-leaf and conifer tree species grown under identical conditions, and found that root NH_4^+ uptake kinetic responses to high CO_2 are clearly species-dependent.

Interspecific variation 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 concentrations in *Larrea tridentata* and *Prosopis glandulosa*, but not in *Bouteloua eriopoda* that was the only species that had up-regulated its root uptake rate for both N and P. Species-specific responses of N uptake kinetics can also be one of the potential mechanisms by which elevated CO_2 may affect competitive balance among co-occurring species, thereby affecting ecosystem productivity and composition (Berntson et al. 1998).

It is important to note that on their own, changes in root uptake kinetics will not be a meaningful index of plant nutrient acquisition responses to elevated CO_2. Often, in cases where kinetics of uptake are severely down-regulated, the overall plant growth response to CO_2 is still positive. This is partly because root uptake kinetic response is only one potential mechanism that can lead to changes in nutrient uptake. Compensatory adjustments in other root characteristics, such as morphology and life span, along with increased nutrient use efficiency, can prevent the need for a positive adjustment in uptake kinetics. Jackson and Reynolds (1996) examined root physiological uptake capacity for N, and root biomass responses of a mixed community of annual grasses and forbs. They reported that N uptake responses to elevated CO_2 were more closely correlated with root physiological capacity under low N availability, but correlated more strongly with root biomass under relatively high N availability. Zerihun et al. (2000) reported that the relative contribution of root physiological uptake capacity in determining the overall plant responses to CO_2 enrichment must be evaluated in conjunction with other root mechanisms that can also influence nutrient acquisition. Therefore, future studies addressing the relative contribution of active ion uptake to plant nutrient status and growth responses to high CO_2 will require experimental designs that monitor changes in these mechanisms simultaneously (Berntson and Bazzaz 1996, 1997; Berntson et al. 1998).

11.3.3 Indirect Effects of CO2 on Nutrient Availability at the Root Surface

Indirectly, elevated CO_2 can alter nutrient availability at the root surface via a number of mechanisms. Increased C supply to the soil can enhance microbial activities (Dhillion et al. 1996), accompanied by higher mineralization and plant uptake (Zak et al. 1993; Rice et al. 1994), although this effect is not universally observed (Diaz et al. 1993). A higher microbial activity was also reported for a grassland system by Hungate et al. (1997), but they argued that this enhancement was caused by reduced transpiration and improved soil moisture, rather than improved C supply to the soil. Reduced transpiration response to high CO_2 has also been invoked as a possible indirect mechanism that suppressed mass flow of K^+ to the root surface in wheat, but this effect was offset by a higher diffusion rate (Van Vuuren et al. 1997). Finally, 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 is not the focus of this chapter. However, such information is important for models designed to reliably predict CO_2 responses in natural ecosystems.

11.4 Summary

There are many facets of global climate change that could synergistically affect native vegetation. Whenever possible, experimental approaches must consider the consequences for plants under realistic, multiple stress conditions. Models designed to predict plant and ecosystem responses to global change should integrate more thoroughly the role of plant nutrient acquisition, and how it may respond to a changing climate. Our current mechanistic models are largely based on plant gas-exchange parameters. We can significantly improve the robustness of these models by incorporating parameters of nutrient uptake, e.g., root system characteristics. We also highlight the need to examine the root system controllers of nutrient uptake collectively, rather than individually. It is not reasonable to assume that the knowledge of changes in just one parameter, e.g., root-to-shoot ratio, can elucidate the mechanism and/or the extent of the effects of global change on plant nutrient uptake, much the same way that we do not expect that the knowledge of changes in leaf area alone will be sufficient to reliably predict canopy gas-exchange in response to climate change. Within this context, we recommend that future studies should pay more attention to the collective effects of root morphology, mycorrhizal association (Chap. 9, this Vol.), kinetics (Chap. 6, this Vol.) and architecture (Chap. 7, this Vol.), as well as life span (Chap. 8, this Vol.) in determining whole-plant nutrient responses to global change.

Acknowledgments. The corresponding author, H. BassiriRad, would like to acknowledge support from the National Science Foundation for this project.

References

Ambler JE, Krizek DT, Semeniuk P (1975) Influence of UV-B radiation on early seedling growth and translocation of ^{65}Zn from cotyledons in cotton. Physiol Plant 34:177–181

Baker JT, Allen LH (1994) Assessment of the impact of rising carbon-dioxide and other potential climate changes on vegetation. Environ Pollut 83:223–235

BassiriRad H (2000) Kinetics of nutrient uptake by roots: responses to global change. New Phytol 147:150–169

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 and 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 and 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 and PO_4^{-3} uptake capacity of three desert species in response to atmospheric CO_2 enrichment. Aust J Plant Physiol 24:353–358

BassiriRad H, Gutschick V, Lussenhop J (2001) Root system adjustments: regulation of plant nutrient uptake and its control of growth responses to elevated CO_2. Oecologia 126:305–320

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 (1996) Belowground positive and negative feedbacks on CO_2 growth enhancement. Plant Soil 187:119–131

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 *Senicio vulgaris* in elevated carbon dioxide and drought. Funct Ecol 6:324–333

Berntson GM, Rajakaruna N, Bazzaz FA (1998) Species-level and community-level growth and nitrogen uptake in elevated CO_2 atmospheres in an experimental annual community. Global Change Biol 4:101–120

Bielenberg DG, Lynch JP, Pell EJ (2002) Nitrogen dynamics during O_3-induced accelerated senescence and related compensation in hybrid poplar. Plant Cell Environ 25(4):501–512

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

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

Caldwell MM, Bjorn LO, Bornman JF, Flint SD, Kulandaivelu G, Teramura AH, Tevini M (1998) Effects of increased solar ultraviolet radiation on terrestrial ecosystems. J Photochem Photobiol B Biol 46:40–52

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

Clarkson DT (1985) Factors affecting mineral nutrient acquisition by plants. Annu Rev Plant Physiol 36:77–115

Coleman JS, McConnaughay KDM (1995) A non-functional interpretation of a classical optimal-partitioning example. Funct Ecol 9:951–954

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

Coleman MD, Dickson RE, Isebrands JG, Karnosky DF (1996) Root growth and physiology of potted and field-grown trembling aspen exposed to trophospheric ozone. Tree Physiol 16:145–152

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

Cooley DR, Manning WJ (1987) The impact of ozone on assimilate partitioning in plants: a review. Environ Pollut 47:95–113

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

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

de la Rosa TM, Julkunen-Tiitto R, Lehto T, Aphalo PJ (2001) Secondary metabolites and nutrient concentrations in silver birch seedlings under five levels of daily UV-B exposure and two relative nutrient addition rates. New Phytol 150:121–131

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

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 19:5l–55

Edwards NT (1991) Root and soil respiration responses to ozone in *Pinus taeda* L. seedlings. New Phytol 118:315–321

Edwards GS, Sherman RE, Kelly JM (1995) Red spruce and loblolly-pine nutritional responses to acidic precipitation and ozone. Environ Pollut 89:9–15

Elawad SH, Allen LH, Gascho GJ (1985) Influence of UV-B radiation and soluble silicates on the growth and nutrient concentration of sugarcane. Soil Crop Sci Soc Fla Proc 44:134–141

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

Ernst WHO, van de Staaij JWM, Nelissen HJM (1997) Reaction of savanna plants from Botswana on UV-B radiation. Plant Ecol 128:162–170

Fangmeier A, Gruters U, Hogy P, Vermehren B, Jager HJ (1997) Effects of elevated CO_2, nitrogen supply and tropospheric ozone on spring wheat. II. Nutrients (N, P, K, S, Ca, Mg, Fe, Mn, Zn). Environ Pollut 96:43–59

Fangmeier A, De Temmerman L, Black C, Persson K, Vorne V (2002) Effects of elevated CO_2 and/or ozone on nutrient concentrations and nutrient uptake of potatoes. Eur J Agron 17(4):353–368

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

Fitter AH, Heinemeyer A, Staddon PL (2000) Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO_2 and nitrogen deposition. New Phytol 147:189–200

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

Grammatikopoulos G, Kyparissis A, Drilias P, Petropoulou Y, Manetas Y (1998) Effects of UV-B radiation on cuticle thickness and nutritional value of leaves in two Mediterranean evergreen sclerophylls. J Plant Physiol 153:506–512

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

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosu D (eds) (2001) Climate change 2001. The scientific basis. Cambridge University Press, Cambridge

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

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

Jones CG, Coleman JS, Findlay S (1994) Effects of ozone on interactions between plants, consumers and decomposers. In: Alscher RG, Wellburn AR (eds) Plant responses to the gaseous environment: molecular, metabolic and physiological aspects. Chapman & Hall, New York, pp 339–363

Keeling CD, Whorf TP (2002) Atmospheric CO_2 records from sites in the SIO air sampling network. In: Trends: a compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, TN (http://cdiac.ornl.gov/trends/CO_2/sio-mlo.htm)

Kickert RN, Krupa SV (1990) Forest responses to tropospheric ozone and global climate change – an analysis. Environ Pollut 68:29–65

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

Lambers H (1987) Growth, respiration, exudation and symbiotic association: the fate of carbon translocated to roots. In: Gregory PJ, Lake JV, Rose DA (eds) Root development and function. Cambridge University Press, London, pp 125–143

Lambers H, Pons TL, Chapin FS (1998) Plant physiological ecology. Springer, Berlin Heidelberg New York

Larsson EH, Bornman JF, Asp H (1998) Influence of UV-B radiation and Cd^{2+} on chlorophyll fluorescence, growth and nutrient content in *Brassica napus*. J Exp Bot 49:1031–1039

Ledig FT, Bormann FH, Wenger KF (1970) The distribution of dry matter growth between shoot and roots in loblolly pine. Bot Gaz 131:349–359

Lee RB (1982) Selectivity and kinetics of ion uptake by barley plants following nutrient deficiency. Ann Bot 50:429–449

Llyod 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

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

Marschner H (1995) Mineral nutrition of higher plants. Academic Press, San Diego

Matamala R, Schlesinger W (2000) Effects of elevated atmospheric CO_2 on fine root production and activity in a temperate forest ecosystem. Global Change Biol 6:967–980

Maurer S, Matyssek R (1997) Nutrition and the ozone sensitivity of birch (*Betula pendula*) 2. Carbon balance, water-use efficiency and nutritional statue of the whole plant. Trees Struct Funct 12:11–20

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

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

Moorthy P, Kathiresan K (1998) Effects of UV-B irradiance on biomass and uptake of nutrients in mangrove seedlings of *Rhizophora apiculata* (Rhizophorales: Rhizophoraceae). Indian J Mar Sci 27:239–242

Murali NS, Teramura AH (1985) Effects of ultraviolet-B irradiance on soybean. 7. Biomass and concentration and uptake of nutrients at varying P-supply. J Plant Nutr 8:177–192

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

Newsham KK, Splatt P, Coward PA, Greenslade PD, McLeod AR, Anderson JM (2001) Negligible influence of elevated UV-B radiation on leaf litter quality of *Quercus robur.* Soil Biol Biochem 33:659–665

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, 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

Nouchi I, Ito O, Harazono Y, Kobayashi K (1991) Effects of chronic ozone exposure on growth, root respiration and nutrient uptake of rice plants. Environ Pollut 74:149–164

Nouchi I, Ito O, Harazono Y, Kouchi H (1995) Acceleration of ^{13}C-labelled photosynthate partitioning from leaves to panicles in rice plants exposed to chronic ozone at the reproductive stage. Environ Pollut 88:253–260

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

Pausch RC, Mulchi CL, Lee EH, Forseth IN, Slaughter LH (1996a) Use of ^{13}C and ^{15}N isotopes to investigate O_3 effects on C and N metabolism in soybeans. I. C fixation and translocation. Agric Ecosyst Environ 59:69–80

Pausch RC, Mulchi CL, Lee EH, Meisinger JJ (1996b) Use of ^{13}C and ^{15}N isotopes to investigate O_3 effects on C and N metabolism in soybeans. II. Nitrogen uptake, fixation, and partitioning. Agric Ecosyst Environ 60:61–69

Pell EJ, Sinn JP, Brendley BW, Samuelson L, Vinten-Johansen C, Tien M, Skillman J (1999) Differential response of four tree species to ozone-induced acceleration of foliar senescence. Plant Cell Environ 22:779–790

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

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, Nagel O (2000) The role of biomass allocation in growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Aust J Plant Physiol 27:595–607

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

Pritchard S, Rogers H, Davis M, Van Santen E, Prior S, Schlesinger W (2001) The influence of elevated atmospheric CO_2 on fine root dynamics in an intact temperate forest. Global Change Biol 7:829–837

Qiu Z, Chappelka AH, Somers GL, Lockaby BG, Meldahl RS (1992) Effects of ozone and simulated acidic precipitation on above- and below-ground growth of loblolly pine (*Pinus taeda*). Can J For Res 22:582–587

Reich PB, Lassoie JP (1985) Influence of low concentrations of ozone on growth, biomass partitioning and leaf senescence in young hybrid poplar plants. Environ Pollut 39:39–51

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

Richards BL, Middleton JT, Hewitt WB (1958) Air pollution with relation to agronomic crops. V. Oxidant stipple of grape. Agron J 50:559–561

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

Runeckles VC, Krupa SV (1994) The impact of UV-B radiation and ozone on terrestrial vegetation. Environ Pollut 83:191–213

Samuelson LJ, Kelly JM (1996) Carbon partitioning and allocation in northern red oak seedlings and mature trees in response to ozone. Tree Physiol 16:853–858

Sanders GE, Colls JJ, Clark AG (1992) Physiological changes in *Phaseolus vulgaris* in response to long-term ozone exposure. Ann Bot 69:123–133

Searles PS, Flint SD, Caldwell MM (2001) A meta analysis of plant field studies simulating stratospheric ozone depletion Oecologia 127:1–10

Shukula UC, Kakkar P (2002) Effect of dual stress of ultraviolet-B radiation and cadmium on nutrient uptake of wheat seedlings. Commun Soil Sci Plant Anal 33(11/12):1737–1749

Sicher RC, Bunce JA (1998) Evidence that premature senescence affects photosynthetic decline of wheat flag leaves during growth in elevated carbon dioxide. Int J Plant Sci 159:798–804

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

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

Sullivan JH (1997) Effects of increasing UV-B radiation and atmospheric CO_2 on photosynthesis and growth: implications for terrestrial ecosystems. Plant Ecol 128:194–206

Sullivan JH, Teramura AH, Dillenburg LR (1994) Growth and photosynthetic responses of field-grown sweetgum (*Liquidambar Styraciflua* Hamamelidaceae) seedlings to UV-B radiation. Am J Bot 81:826–832

Taylor G, Davies WJ (1990) Root growth of *Fagus sylvatica*: impact of air quality and drought at a site in southern Britain. New Phytol 116:457–464

Temple PJ, Riechers GH, Miller PR, Lennox RW (1993) Growth responses of ponderosa pine to long-term exposure to ozone, wet and dry acidic deposition, and drought. Can J For Res 23:59–66

Tingy DT, Phillips DL, Johnson MG (2000) Elevated CO_2 and conifer roots: effects on growth, life span and turnover. New Phytol 147:87–104

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

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

Verhoef HA, Verspagen JMH, Zoomer HR (2000) Direct and indirect effects of ultraviolet-B radiation on soil biota, decomposition and nutrient fluxes in dune grassland soil systems. Biol Fertil Soils 31:366–371

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

Weih M, Johanson U, Gwynn-Jones D (1998) Growth and nitrogen utilization in seedlings of mountain birch (*Betula pubescens* ssp. *tortuosa*) as affected by ultraviolet radiation (UV-A and UV-B) under laboratory and outdoor conditions. Trees Struct Funct 12:201–207

Wiltshire JJJ, Wright CJ, Unsworth MH, Craigon J (1993) The effects of ozone episodes on autumn leaf fall in apple. New Phytol 124:433–437

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

Yue M, Li Y, Wang XL (1998) Effects of enhanced ultraviolet-B radiation on plant nutrients and decomposition of spring wheat under field conditions. Environ Exp Bot 40:187–196

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

Zepp RG, Callaghan TV, Erickson DJ (1998) Effects of enhanced solar ultraviolet radiation on biogeochemical cycles. J Photochem Photobiol B Biol 46:69–82

Zerihun A, BassiriRad H (2001) Interspecific variation in nitrogen uptake kinetic responses of temperate forest species to elevated CO_2: potential causes and consequences. Global Change Biol 7:211–222

Zerihun A, Gutschick VP, BassiriRad H (2000) Relative roles of photosynthetic N-use efficiency and N uptake in determining plant growth response to elevated CO_2: evaluation using the functional balance model approach. Ann Bot 86:723–730

Ziska LH, Teramura AH, Sullivan JH, McCoy A (1993) Influence of ultraviolet-B (UV-B) radiation on photosynthetic and growth-characteristics in field-grown cassava (*Manihot-Esculentum* Crantz). Plant Cell Environ 16:73–79