



# Mineral stress: the missing link in understanding how global climate change will affect plants in real world soils

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## Abstract

Many natural and agricultural ecosystems are characterized by sub-optimal availability of mineral nutrients and ion toxicities. Mineral stresses are likely to have important, complex, and poorly understood interactions with global climate change variables. For example, most terrestrial vegetation is supported by weathered soils with some combination of low P, low Ca, Al toxicity, and Mn toxicity. Each of these stresses has complex, yet distinct, interactions with global change variables, making it very difficult to predict how plants in these environments will respond to future climate scenarios. Important, yet poorly understood, interactions include the effects of transpiration on root acquisition of soluble nutrients, particularly Ca and Si, the effects of altered root architecture on the acquisition of immobile nutrients, particularly P, the effects of altered root exudate production on Al toxicity and transition metal acquisition, and the interaction of photochemical processes with transition metal availability. The interaction of Mn toxicity with light intensity and other global change variables is discussed as an example of the complexity and potential importance of these relationships. Current conceptual models of plant response to multiple resource limitations are inadequate. Furthermore, substantial genetic variation exists in plant responses to mineral stress, and traits improving adaptation to one stress may incur tradeoffs for adaptation to other stresses. Root traits under quantitative genetic control are of central importance in adaptation to many mineral stresses. An integration of quantitative genetics with mechanistic and conceptual models of plant response to mineral stresses is needed if we are to understand plant response to global change in real-world soils.

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## 1. Introduction

Mineral stress, defined as sub-optimal availability of essential nutrients or toxicity of nutrient or

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Table 1

Database survey conducted in October 2003 (Web of Science, ISI) for journal articles dealing with elevated CO<sub>2</sub> as well as minerals of importance to plant nutrition

Key words	Number of journal articles
Elevated CO <sub>2</sub> , plants	1658
Elevated CO <sub>2</sub> , plants + N	685
Elevated CO <sub>2</sub> , plants + P	82
Elevated CO <sub>2</sub> , plants + K	10
Elevated CO <sub>2</sub> , plants + Ca	15
Elevated CO <sub>2</sub> , plants + Mg	7
Elevated CO <sub>2</sub> , plants + Fe	2
Elevated CO <sub>2</sub> , plants + Mn	3
Elevated CO <sub>2</sub> , plants + Cu	0
Elevated CO <sub>2</sub> , plants + Zn	1
Elevated CO <sub>2</sub> , plants + B	1
Elevated CO <sub>2</sub> , plants + Al	2
Elevated CO <sub>2</sub> , plants + Si	1

Note that mention of an element in an article often resulted from routine tissue analysis rather than specific study of the interaction of elevated CO<sub>2</sub> with mineral stress.

non-nutrient minerals (especially Al, Na, Cl, Mn, and other heavy metals), is a primary constraint to plant growth over the majority of the earth's land surface. Natural ecosystems, managed forests and rangelands, and agriculture in less developed countries (LDCs) are largely characterized by multiple mineral stresses. This being the case, we will not be able to understand or predict ecosystem responses to global change variables without understanding how these variables interact with mineral stresses. Unfortunately, apart from N, this topic has received relatively little research attention (Table 1). The goal of this article is to provide a brief overview of some edaphic stresses of global importance, plant adaptations to edaphic stress (focusing on organismic processes), and ideas about how these adaptations might be affected by global change. This paper results from a workshop on genomics in global change research, and so we also discuss the role that genomics could play in research on this topic. Because of the scope of issues addressed, the restricted length of this article, and the scant empirical data for many interactions of interest, our discussion will, by necessity, highlight specific issues and ideas and will not attempt a comprehensive literature review (although where possible, recent representative articles and overviews are cited).

## 2. Mineral stresses of global importance

Edaphic stresses include physical factors such as soil shallowness, poor drainage, and poor water retention, as well as chemical factors such as sub-optimal availability of mineral nutrients, acidity, alkalinity, salinity, and metal toxicity. Chemical factors are more important limitations to plant growth than physical factors on a global basis.

### 2.1. Nutrient deficiency

Nutrient deficiency is the norm in native soils. The most inherently fertile soils such as Mollisols generally support dense plant communities characterized by intense nutrient competition, so even in these soils plants can be nutrient deficient. Sub-optimal availability of N and P are nearly universal. Imbalances of base cations (K, Ca, and Mg) and micronutrient deficiencies affect large areas. Intensive agriculture in developed nations has alleviated nutrient deficiencies, but the majority of world agriculture occurs with low fertility inputs on soils with poor availability of P and other nutrients (Conway, 1997; Lynch, 1998; Bank, 2002).

### 2.2. Soil acidity

Soil acidity (i.e., pH below 5.5) is characteristic of weathered soils of the tropics and subtropics, and many temperate forest systems (Fig. 1, Table 2). These soils, including most Oxisols and Ultisols, as well as many Spodosols and Inceptisols, support most of the global vegetation as well as much of the earth's population. Acid soils are characterized by Al toxicity (below pH 5), P deficiency, poor availability of bases, especially Ca, and Mn toxicity. Negative effects of global change on these systems would have disproportionate effects on human welfare, since Third World agriculture (the single largest human occupation, (Bank, 2002)) is characterized by poor access to soil fertility amendments.

### 2.3. Soil alkalinity

Soil alkalinity (i.e., pH above 7.5) is characteristic of arid and semi-arid regions, and highly calcareous soils. These soils, including many Aridisols and some

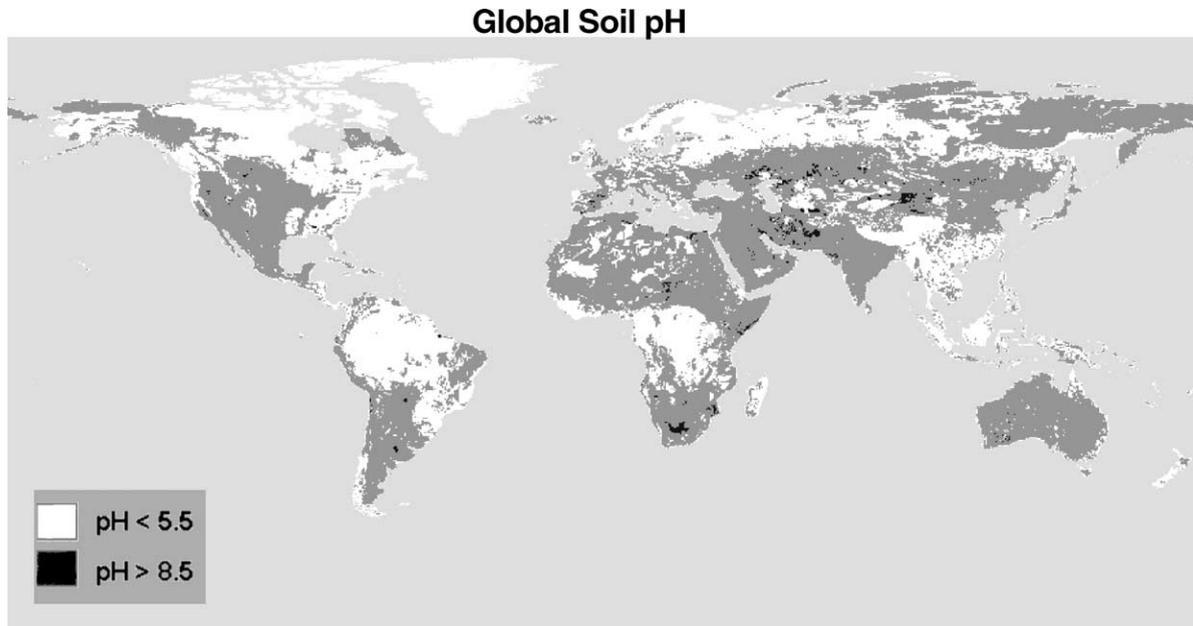


Fig. 1. Distribution of soils having acidic (<5.5) and alkaline (>8.5) pH based on interpretation of data from the FAO soils database. Distribution of acidic (pH < 5.5, white area) and alkaline (pH >8.5, black area) soils.

Entisols, are extensive but usually too dry to support dense vegetation. Alkaline soils are characterized by poor availability of P and micronutrient transition metals (Fe, Cu, Mn, and Zn).

#### 2.4. Salinity

Salinity (i.e., electrical conductivity greater than  $4 \text{ dS m}^{-1}$ ) is characteristic of arid and semi-arid regions, and irrigated agriculture. Salinity stress is an important constraint to world agriculture, affecting 7% of the land surface of the earth and over 50% of

irrigated land (Flowers et al., 1997). Saline soils present an array of problems for plant growth, including poor water availability, toxic amounts of Na and Cl, and low availability of Ca (Marschner, 1995).

#### 2.5. Metal toxicity

Metal toxicity is most commonly found as Al and Mn toxicity in acid soils (Adams, 1984), although localized regions have excessive amounts of heavy metals (Pb, Cd, Cu, Zn, Mn) due to unusual soil parent

Table 2

Soil pH ranges in relation to land use. Land use categories are simplified from the Anderson Land Use/Land Cover classification of the globe (USGS Global Land Cover Classification data set)

Land use	Percentage of total area	Land use within soil pH range				
		Percentage with pH < 4.5	Percentage with pH > 4.5 to <5.5	Percentage with pH > 5.5 to <7.2	Percentage with pH > 7.2 to < 8.5	Percentage with pH > 8.5
Agriculture	19.6	8.6	16.9	22.7	23.2	13.3
Forest	26.8	43.7	47.3	18.9	3.8	1.9
Grass/savanna	41.8	38.2	20.6	44.4	71.4	84.55
Tundra	11.9	9.5	15.2	14.0	1.6	0.2

The total area used in this assessment was  $199,492,637 \text{ km}^2$ . Water and some non-soil areas are not included in the total area (Warner and Lynch, unpublished data).

material (e.g., ultramafic rock) or industrial activity. Manganese toxicity can be found in volcanic soils (Andosols) even at neutral pH. Volcanic soils typically support dense human populations such as the Pacific rim and Africa's Rift Valley.

Humans have alleviated the inherent edaphic limitations of native soils used for intensive agriculture in developed nations, but in most areas of the globe, human activity has significantly degraded soil fertility. A large portion of cropland in developing countries is degraded (65% in Africa, 50% in Latin America, and 40% in Asia, (Bank, 2002)). Soil erosion is a massive problem in the humid tropics, deforestation has degraded the fertility of many tropical forest soils (Chazdon, 2003), acid precipitation has accelerated base leaching and forest decline in Northern Europe and the Eastern US (Tomlinson, 2003), crop irrigation without adequate drainage and leaching has created serious salinity problems in semi-arid regions, especially in the former Soviet Republics, the Mideast and the Western US, rising water tables have salinized croplands in Australia, and poor fertilizer policies have contributed to soil acidification in China. In general, these trends are worsening, driven by the pressure of burgeoning human populations in less developed countries and by excessive resource consumption in developed countries.

### 3. Plant adaptations to edaphic stress

Plants display a remarkable array of physiological adaptations to edaphic stress (Marschner, 1995). Some traits permit conservative use of all nutrients such as slow growth (Aerts and Chapin, 2000), while other traits represent adaptations to specific stresses such as the induction of organic acid exudation to protect root tips exposed to Al stress (Kochian, 1995), the induction of strategy 1 and strategy 2 mechanisms to mobilize rhizosphere Fe in response to Fe deficiency (Marschner and Romheld, 1994), and the regulation of root architecture to optimize soil exploration in response to P deficiency (Lynch and Brown, 2001). Root traits are particularly important adaptations to edaphic stress, since roots explore the soil, acquire nutrients and water, and interact with symbionts and soil biota.

Adaptations to edaphic stress, especially root adaptations, often entail ecological or physiological tradeoffs. For example, in annual crop plants, low P availability induces alterations in root architecture that enhance topsoil foraging, since the topsoil is the region of greatest P availability (Lynch and Brown, 2001). A tradeoff to enhanced topsoil foraging is greater sensitivity to drought stress (Ho et al., 2004). A tradeoff to increased specific root length, a common response to nutrient stress, is reduced root lifespan (Eissenstat, 1997). A tradeoff with greater root growth may be reduced photosynthate allocation to shoot growth and reproduction (Poorter et al., 1990). Although such tradeoffs are poorly understood, they are likely to have important ecophysiological repercussions on plant fitness in future environmental scenarios.

There are two general conceptual models of the response of individual plants to resource availability: the 'Law of the Minimum', which postulates that overall plant growth is limited by the single most limiting resource (van der Ploeg et al., 1999), and the Microeconomic Paradigm, that postulates that plants are optimizing entities that allocate internal resources so that no single external resource is limiting (Bloom et al., 1985). Increasing atmospheric CO<sub>2</sub> is reducing the importance of carbon as a limiting external resource. If the Law of the Minimum is correct, this will have no effect on the growth of the majority of plants on earth, which are faced with edaphic constraints and nutrient limitations. In contrast, the Microeconomic Paradigm would predict that increased carbon availability will permit (for example) greater root growth, alleviation of nutrient stresses, and greater overall plant growth. A recent empirical study of growth responses to multiple nutrient limitations found that in some cases plants followed the Law of the Minimum, in other cases the Microeconomic Paradigm, and in some cases showed complex behavior that followed neither model (Rubio et al., 2003). These models must be reconciled or improved if we are to predict plant response to global change.

An important feature of plant adaptations to edaphic stress is that they typically display substantial interspecific and intraspecific variation, as well as substantial phenotypic plasticity. In crop plants, it is not uncommon to find differences of 200–300% in the ability to tolerate edaphic stress, and concomitant

large variation in specific traits such as root hairs, root architecture, and root exudates (Baligar and Duncan, 1990). This variation will facilitate natural and human selection for genotypes adapted to future environments.

#### 4. Potential interactions of global change with mineral stress

Global change variables (GCVs) of interest here include elevated atmospheric CO<sub>2</sub>, ozone, and UV radiation, and changes in spatial and temporal patterns of precipitation, temperature, humidity, and photosynthetically active radiation. The extensive (and often inconclusive) literature concerning plant responses to these factors will not be reviewed here. Rather, we will attempt to briefly highlight noteworthy issues regarding the interaction of these factors with mineral stresses.

Table 3 lists potential interactions of GCVs with mineral stresses. Some interactions shown are supported by experimental data, but many are supported only by theory, inference, or a few research reports.

##### 4.1. Transpiration-driven mass flow

Acquisition of water-soluble nutrients such as nitrate, sulfate, Ca, Mg, and Si is primarily determined by mass flow of soil water to roots as a result of shoot transpiration (Barber, 1995). GCVs that affect transpiration should, therefore, also affect the acquisition of these nutrients. Elevated CO<sub>2</sub> normally reduces leaf level transpiration in C3 plants, and appears to reduce stand level transpiration in annual crops (Ainsworth

et al., 2002; Wullschleger et al., 2002), and has significant but more muted effects on transpiration of forest canopies (Wullschleger et al., 2002). This interaction may be particularly important for Ca and Si, two nutrients that are especially dependent on transpiration in most plant species (Marschner, 1995). Elevated CO<sub>2</sub> significantly reduced Ca uptake in wheat (*Triticum aestivum* L.) plants (Fangmeier et al., 1997). Low Ca availability is prevalent in acid soils that encompass most terrestrial forests (Table 2). Logging and acid deposition have reduced Ca pools in temperate forests of Northeastern America and Western Europe, a factor associated with forest decline (Tomlinson, 2003). Further reductions in Ca transport by elevated CO<sub>2</sub>, if not offset by higher temperatures and longer warm seasons, could be detrimental. Silicon is an essential element for monocots and gymnosperms, and in dicots, it is an important component of plant resistance to insect and fungal attack (Epstein, 1999). Effects of GCVs on Si transport to leaves are unknown but could have important ecological consequences.

##### 4.2. Root growth and architecture

Elevated atmospheric CO<sub>2</sub> generally increases plant carbon allocation to belowground processes, including root growth, respiration, and exudation (Gorissen, 1996; Gregory et al., 1996; Rogers et al., 1996). Belowground effects of elevated CO<sub>2</sub> could have positive or negative feedbacks on plant productivity depending on nutrient availability and other belowground processes (Zak et al., 1993; Berntson and Bazzaz, 1996), including sequestration of carbon into soil pools. Although data are scarce, several studies indicate that elevated atmospheric CO<sub>2</sub> may

Table 3  
Some potential interactions of global change variables with mineral stress

Process	Global change variables	Interaction with mineral stress
Transpiration-driven mass flow	CO <sub>2</sub> , RH, precipitation, light, temperature	NO <sub>3</sub> , SO <sub>4</sub> , Ca, Mg, and Si
Root growth and architecture	CO <sub>2</sub> , precipitation, soil temperature	All nutrients, esp. P and K
Mycorrhizas	CO <sub>2</sub> ?, temperature?	P, Zn (VAM) N (ectomycorrhizas)
Root exudates	CO <sub>2</sub> ?	Al toxicity, metal uptake, and P
Biological N fixation	CO <sub>2</sub>	N
Tissue dilution	CO <sub>2</sub>	Stress responses, nutrient cycling, and nutritive value
Metal photochemistry	Light, UV, temperature, and precipitation	Transition metal deficiency and Mn toxicity
Growth responses	CO <sub>2</sub>	N and P: "no clear pattern"

See text for details.

have specific effects on the architecture of roots (e.g., [Berntson and Bazzaz, 1998](#)) as well as the extent and type of ectomycorrhizal symbioses ([Godbold and Berntson, 1997](#); [Godbold et al., 1997](#); [Runion et al., 1997](#)), and potentially with root lifespan ([Fitter et al., 1996](#); [Eissenstat et al., 2000](#)). Although the large number of possible interactions between climate change variables and edaphic constraints makes generalizations difficult, [Kubiske and colleagues](#) suggested that some of the effect of elevated CO<sub>2</sub> on root activity could be due to enhanced photosynthesis in the lower portion of tree canopies ([Kubiske et al., 1997](#)). [Pritchard and Rogers](#) proposed that direct and indirect signals arising from greater carbohydrate availability in plants grown with elevated CO<sub>2</sub> stimulate lateral root branching, which in turn leads to more shallow, highly branched root architectures ([Pritchard and Rogers, 2000](#)). Whether such changes have a positive or negative impact on plant growth will depend, of course, on many specific features of the system, including the relative importance of nutrients that are enriched in surface horizons, such as phosphorus, versus those that may be found at greater depth, such as nitrogen, and whether greater root densities in a specific soil horizon result in greater soil exploration or merely greater inter-root competition ([Ge et al., 2000](#); [Lynch and Brown, 2001](#); [Rubio et al., 2001](#)). The amount of nutrients obtained by a specific root architecture may be more important than the efficiency with which nutrients are acquired ([Berntson, 1994](#)), especially in a high CO<sub>2</sub> world in which carbon-based currencies are relatively devalued.

In order to predict how elevated CO<sub>2</sub> may affect root architecture, and therefore nutrient acquisition in various ecosystems, we will need a better understanding of the physiological mechanisms linking photosynthesis and root architecture, such as that proposed by [Pritchard and Rogers](#). This is challenging, since we know very little about the physiological mechanisms that regulate root architecture in any circumstance. The dynamic responses of root architecture to the availability of nutrients and water, soil physical conditions and microbes will interact with direct effects of elevated CO<sub>2</sub>, as well as indirect effects of climate change parameters on processes such as soil water status and nutrient release from plant litter. For example, is the shallow root proliferation discussed by

[Pritchard and Rogers](#) the result of plant carbohydrate signals on lateral meristems or rather the result of moister epipedons because of reduced stomatal transpiration ([Arnone et al., 2000](#)). In order to understand how root architecture will respond to a changing climate, we must therefore understand a great deal more about the regulation of root architecture in general. Genotypic variation for root architecture within populations will permit genetic drift towards architectures that are more adaptive to the climate as it changes, so analysis of current genotypes may not permit entirely accurate predictions about the response of future plant populations.

#### 4.3. Mycorrhizal symbioses

Mycorrhizal symbioses are nearly ubiquitous in plants and play important roles in mobilization of nutrients from organic matter (ectomycorrhizas and ericoid mycorrhizas) and acquisition of diffusion limited nutrients, largely P and Zn (arbuscular mycorrhizas). The effects of elevated CO<sub>2</sub> and temperature on arbuscular mycorrhizas appears to be mainly indirect, i.e., mediated by plant growth responses, rather than direct ([Staddon et al., 2002](#)). Numerous studies (see citations above) show increased resource allocation to mycorrhizal roots in plants exposed to elevated CO<sub>2</sub> this may reflect the relative importance of edaphic constraints to plant growth in most ecosystems. Elevated CO<sub>2</sub> appears to have complex effects on ectomycorrhizal communities in forests, with uncertain effects for tree health ([Fransson et al., 2001](#)).

#### 4.4. Root exudates

About half of belowground carbon allocation in plants is deposited in the rhizosphere ([Nguyen, 2003](#)). The majority of this material consists of dead root tissue, but compounds exuded by living cells, including mucilage, organic acids, phosphatases, phytosiderophores, and protons, are important in protecting growing roots from Al stress and mobilizing relatively insoluble nutrients such as P and Fe ([Hinsinger, 2001](#); [Dakora and Phillips, 2002](#)). Interactions of GCVs with root exudates should, therefore, have important consequences for plant growth in acid and alkaline soils. Only a few studies have examined this interaction, with conflicting results. For example, in some studies

elevated CO<sub>2</sub> caused no effect on root exudates (Norby et al., 1987; Hodge, 1996; Uselman et al., 2000), while in others it decreased root exudates but altered exudate composition (Hodge and Millard, 1998; Hodge et al., 1998). Light, temperature, and other variables affecting photosynthesis have complex effects on root exudates, as might be expected (Paterson et al., 1999). Elevated CO<sub>2</sub> increases rhizosphere respiration, but it is not clear whether this is due to increased exudates per unit root surface area or simply increased root growth (Zak et al., 2000; Nguyen, 2003). The complex interplay of root exudates with root photosynthate supply, root growth and architecture, and the rhizosphere environment make this a challenging research topic that nonetheless deserves further study because of its importance for plant adaptation to acid soils.

#### 4.5. Biological nitrogen fixation

Plant taxa capable of symbiotic nitrogen fixation are more responsive to elevated CO<sub>2</sub> than nonfixing taxa because they can directly utilize additional photosynthate to alleviate N limitation. The stimulatory effect of elevated CO<sub>2</sub> on legumes has been observed in mixed stands, such as legume–grass pastures (Hartwig et al., 2002), as well as soybean (*Glycine max* (L.) Merr.) monocultures (Ainsworth et al., 2002). Phosphorus plays a key role in legume response to CO<sub>2</sub>, since legume nodules have a high P requirement (Almeida et al., 2000).

#### 4.6. Tissue dilution

Elevated CO<sub>2</sub> can increase carbon gain in C3 plants, which can dilute tissue nutrient concentration. For plants grown at double the current CO<sub>2</sub> concentration, the C:N ratio increases on average about 15% (Gifford et al., 2000). Dilution effects for P are uncertain due to a small number of observations and variable results (Gifford et al., 2000). Elevated CO<sub>2</sub> reduced the content of Ca, S, Mg, and Zn in wheat plants as a result of dilution caused by tissue carbohydrate accumulation, combined with transpiration-driven reductions in Ca uptake (Fangmeier et al., 1997). Reduced nutrient concentration in plant tissue could trigger plant stress responses (Barrett et al., 1998), although this may not be generally true since bulk nutrient concentration may be reduced by starch accumulation and tissue density

effects, which may not directly affect cytoplasmic nutrient availability in chlorenchyma and other metabolically active tissue. Nutrient dilution is more likely to have important consequences at the ecosystem level, such as slower litter decay, although this effect appears to be slight (Canadell et al., 2000) and dietary effects on leaf-feeding insects and other herbivores, including humans (Hesman, 2000). Interestingly, deleterious effects of elevated CO<sub>2</sub> on wheat protein content were pronounced at low N but slight at high N (Kimball et al., 2001).

#### 4.7. Metal photochemistry

Toxic levels of reactive oxygen species can be formed in chloroplasts in certain conditions (Foyer et al., 1994). The role of metals (Mn, Mg, Fe, and Cu) in the light reactions of photosynthesis, as well as in antioxidant enzyme systems (Zn, Cu, and Mn in SOD, Fe in catalase) makes them important in both the generation and the detoxification of reactive oxygen species generated in chloroplasts (Krupa and Bazyński, 1995; Clijsters et al., 1999). A number of GCVs can increase the formation of reactive oxygen species, including ozone, high light, UV radiation, temperature extremes, and drought (Foyer et al., 1994). Plants suffering sub-optimal availability of Mg and transition metals because of high soil pH, base imbalances, Al toxicity, and Mn toxicity may be more sensitive to global change than healthy plants. Manganese toxicity is discussed below as a specific example of the role of metal photochemistry in mediating plant response to light intensity.

#### 4.8. Growth responses

A principal concern in predicting plant response to global change is whether the growth promotive effects of greater atmospheric CO<sub>2</sub> concentration and, in some regions, greater N deposition or precipitation will be nullified by other limitations to plant growth, such as nutrient availability. To this end, a number of studies have addressed the interaction of elevated CO<sub>2</sub> with N availability, and a smaller number of studies have addressed the interaction of elevated CO<sub>2</sub> with P availability. Recent reviews of this literature conclude that although nutrient stress tended to reduce growth stimulation by elevated CO<sub>2</sub> in both herbaceous and

woody species (Poorter and Perez-Soba, 2001), results show “no clear pattern” (BassiriRad et al., 2001): interactions between elevated CO<sub>2</sub> and nutrient stress ranged from antagonist to neutral to synergistic. The complexity of growth responses to resource interactions is consistent with the view that such interactions involve complex biology that varies among organisms, environments, and specific resources, and is not readily predicted from simple conceptual models (Rubio et al., 2003).

### 5. Effects of temperature on plant–nutrient interactions in a changing environment

Relatively little is known about the influence of temperature on plant–nutrient interactions in a changing environment. In an analysis of the available literature in 2001, low-soil nutrition and sub-optimal temperature had the greatest influence on reducing the growth-stimulating effects of elevated CO<sub>2</sub> (Poorter and Perez-Soba, 2001). Soil temperature has marked effects on root characteristics (growth, morphology, longevity, respiration, and membrane fluidity), which influence plant nutrient acquisition efficiency (BassiriRad, 2000). Studies generally suggest that soil warming enhances nutrient uptake (BassiriRad, 2000). However, three studies showed no interactive effect of elevated CO<sub>2</sub> and temperature on P and N acquisition (BassiriRad et al., 1996; Delucia et al., 1997; Veteli et al., 2002) suggesting that higher temperature does not modulate the nutrient dilution effect often observed in plants exposed to elevated CO<sub>2</sub>. Several phenolic compounds in willow leaves were decreased in response to higher temperature (Veteli et al., 2002). Such effects on leaf secondary chemistry could influence nutrient cycling in soils by increasing litter decomposition rates, which are often slowed as C/N ratios increase under elevated CO<sub>2</sub>.

### 6. Effects of light on plant–nutrient interactions in a changing environment

Increases in UV radiation and visible light increase foliar phenolic content (Lavola et al., 2000; Caldwell et al., 2003). Altered secondary chemistry can decrease litter decomposition rates, affecting nutrient cycling

dynamics in the soil. However, the effects of UV radiation on litter decomposition are highly variable in the literature.

High visible light intensity and excessive UV light can trigger photoinhibition leading to photo-oxidative stress, particularly in the presence of other environmental stresses (Foyer et al., 1994; Xu et al., 1998). Foliar nutrient imbalances including nutrient deficiencies and metal toxicity interact strongly with high light to induce photo-oxidative stress (Foyer et al., 1994; Gonzalez et al., 1998), which can have significant negative effects on plant productivity. Because of its influence on primary plant metabolism, elevated CO<sub>2</sub> in theory could have important influences on the redox balance in plant cells (Karnosky, 2003). No clear patterns have emerged with regard to how antioxidant systems respond to elevated CO<sub>2</sub>. Depending on species and environmental conditions, elevated CO<sub>2</sub> has been shown to both induce and repress antioxidant systems in plants (Karnosky, 2003).

### 7. Example of manganese toxicity

Manganese (Mn) toxicity, an important mineral stress in both natural and agricultural systems (Schlichting and Sparrow, 1988), highlights the complexity of the interactions of climate change variables with mineral stress. One mechanism of Mn phytotoxicity is photo-oxidation (Gonzalez et al., 1998). Manganese toxicity could generate photo-oxidative stress through several mechanisms, including (1) direct generation of reactive oxygen from Mn ions in the presence of light through the Fenton reaction, (2) disabling of antioxidant systems reliant on Fe (such as catalase), Cu and Zn (such as forms of SOD) by interference with metal uptake, transport, and metabolism, (3) disruption of normal electron flow from PSII to PSI by antagonism with electron acceptors with metal cofactors, such as plastocyanin, (4) disruption of normal energy dissipation via Rubisco inactivation through interference with Mg uptake, transport, and metabolism (Houtz et al., 1988) and (5) damage to lipids and proteins through reaction of Mn with sulfhydryl groups (Van Assche and Clijsters, 1990) and activation of lipoxygenases (Panda et al., 1986; Somashekaraiah et al., 1992).

The importance of photo-oxidation in Mn phytotoxicity is supported by several lines of evidence. High

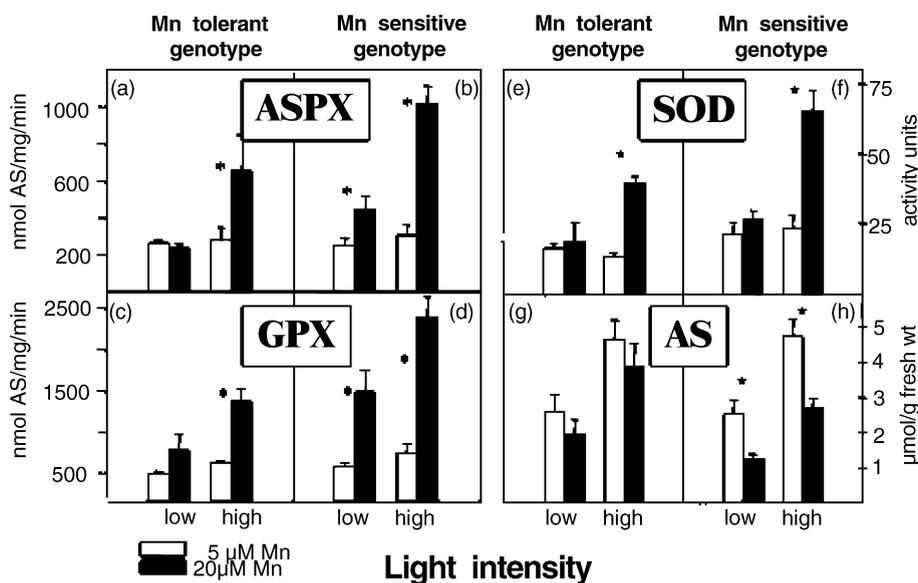


Fig. 2. a–h: Interaction of Mn and light intensity on antioxidant systems in common bean. In leaves with excess Mn, high light intensity upregulates the activity of ascorbate peroxidase (a, b), guaiacol peroxidase (c, d), cytosolic superoxide dismutase (e, f), and decreases leaf ascorbate (g, h), especially in a Mn-sensitive genotype. Asterisks indicate significant differences between Mn-stressed and control plants. These responses, as well as those of other systems not shown here, indicate that excess Mn creates photo-oxidative stress, and that genetic variation in antioxidant metabolism (in this case, maintenance of reduced ascorbate pools), may be related to Mn tolerance (Gonzalez et al., 1998).

light intensity potentiates Mn toxicity in common bean (*Phaseolus vulgaris* L.; Fig. 2) and sugar maple (*Acer saccharum* Marshall; Fig. 3). In common bean, excess Mn induces antioxidant enzyme systems, especially in high light, and a Mn-tolerant genotype is better able to maintain reduced ascorbate pools than a Mn-sensitive genotype under Mn stress (Gonzalez

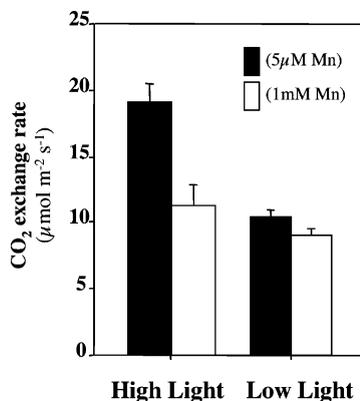


Fig. 3. Interactive effects between excess Mn and light intensity ( $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  vs.  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) on photosynthesis of sugar maple seedlings (St. Clair and Lynch, unpublished data).

et al., 1998). Rice (*Oryza sativa* L.) chloroplasts produce more active oxygen species under Mn stress (Lidon and Teixeira, 2000), and tobacco (*Nicotiana tabacum* L.) cell lines selected for Mn tolerance have elevated guaiacol peroxidase activity (Santandrea et al., 2000). The role of oxidative stress in Mn phytotoxicity explains prior reports of synergism between Mn toxicity and light intensity (McCool, 1935; Horiguchi, 1988; Nable et al., 1988), and Mn toxicity and ozone exposure (Foy et al., 1995).

The role of photo-oxidative stress in Mn toxicity has important implications for the effects of global change on ecosystems prone to Mn stress, such as the Eastern Forest of North America. A number of environmental variables that are changing as a result of human influences interact with oxidative stress, including increased UV radiation, temperature stress, changing light levels, drought stress, and ozone exposure (Foyer et al., 1994). These changes are occurring concurrently with increasing Mn bioavailability in forest soils caused by acid deposition and base leaching (Horsley et al., 2000; Driscoll et al., 2001). Because of the strong interaction of Mn toxicity with the metabolism of other metals, atmospheric factors

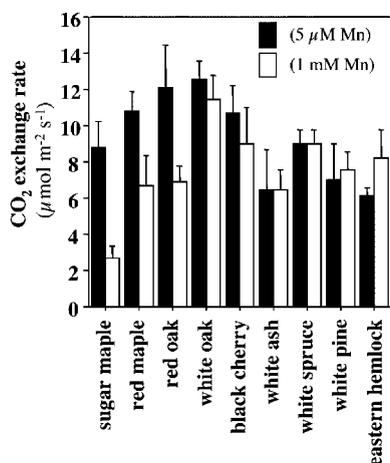


Fig. 4. Effect of toxic levels of manganese on photosynthesis of tree seedlings grown in sand culture. Sugar maple, red maple and red oak—three keystone tree species of the Eastern Forest were the most sensitive (St. Clair, S.B. and Lynch, J.B. Element accumulation patterns of deciduous and evergreen tree seedlings on acid soils and its implications for sensitivity to manganese toxicity. *Tree Physiology*, in press).

that affect the uptake of these nutrients may have important interactions with Mn phytotoxicity. Increasing atmospheric CO<sub>2</sub> should decrease leaf transpiration, and thereby reduce the uptake of Ca and Mg by mass flow to the roots, in addition to changing Ca and Mg allocation to expanding leaves by changing xylem fluxes. These effects may exacerbate Mn inhibition of leaf metabolism of Ca and Mg. Through photo-oxidation, tree responses to Mn toxicity may be greatly magnified in response to other variables such as increasing light intensity. Substantial interspecific differences in tolerance to Mn toxicity (Fig. 4) and other nutrient stresses could lead to changes in species composition, and possibly changes in ecosystem function. Therefore, Mn toxicity and related photo-oxidative processes may play a central role in integrating ecosystem responses to a changing climate (Abrams, 1998) (Fig. 5).

### 8. Genomics as a tool in understanding plant responses to mineral stresses in a changing environment

Plants have evolved multiple mechanisms to maintain nutritional homeostasis in diverse edaphic envi-

ronments. Some of these responses can be genetically simple as only a single or a few gene products contribute to a phenotype. Examples include nutrient transporters or enzymes such as phosphatases where a phenotype is determined by action of a single gene product. However, most traits that confer tolerance to edaphic stress, including products of biosynthetic pathways (e.g., root exudates), morphological changes (e.g., root architecture) and symbiotic associations (mycorrhiza, N fixation) are genetically complex (Marschner, 1995).

The sequencing and functional analysis of plant genomes is a major scientific initiative aimed at making sense of the genetic complexity of plants. Expression profiling using cDNA and oligonucleotide microarrays is a powerful tool for examining how plant genomes transcriptionally respond to experimental variables, although it is difficult to discriminate primary from secondary responses from such data. Microarray technologies are being used to examine genomic responses to mineral deficiencies and toxicities (Thimm et al., 2001; Milla et al., 2002; Negishi et al., 2002; Tranbarger et al., 2003; Wintz et al., 2003), temperature extremes (Seki et al., 2002), and UV and high light (Rossel et al., 2002; Casati and Walbot, 2003; Kimura et al., 2003). The focus of the majority of these studies was the identification of plant response mechanisms deduced from the upregulation of genes with known function. To begin to make significant progress beyond the verification of these more predictable relationships, future studies will need to focus on linking unknown edaphic stress and GCV-responsive genes with their phenotypic traits using functional genomics tools (Lahner et al., 2003).

Genomic information can be used to identify molecular markers linked to genes of interest for crop adaptation to mineral stress. This 'Marker Aided Selection' (MAS) will be particularly useful when the genes of interest are quantitative traits controlled by many genes, as many stress tolerance genes appear to be. Quantitative Trait Loci (QTL) have been identified for plant–nitrogen dynamics (Agrama et al., 1999; Rauh et al., 2002; Yamaya et al., 2002; Mickelson et al., 2003), aluminum tolerance (Kobayashi and Koyama, 2002; Nguyen et al., 2002; Sledge et al., 2002; Ninamango-Cardenas et al., 2003), iron deficiency (Lin et al., 2000), phosphorus acquisition (Kaeppeler et al., 2000; Hash et al., 2002; Wu and

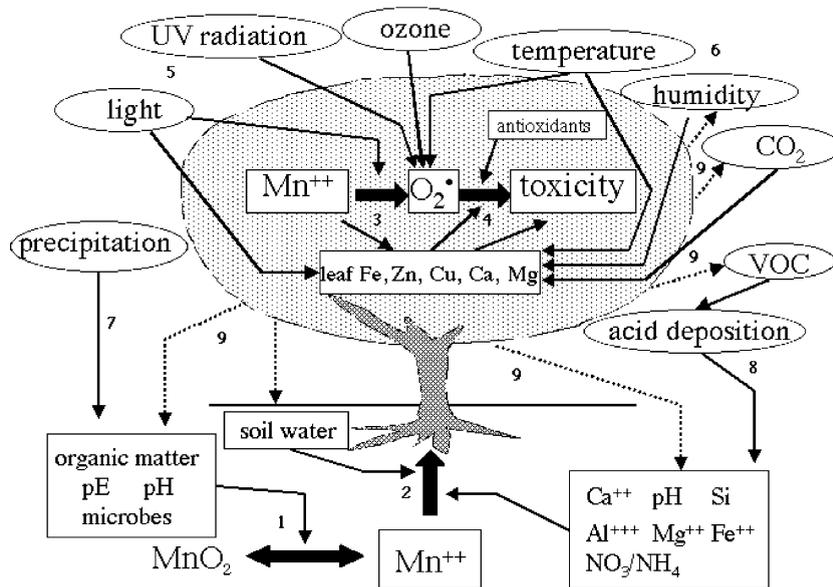


Fig. 5. Conceptual model of Mn biogeochemistry and phytotoxicity. Mn reduction (1) is regulated by soil redox potential, pH, microbial activity, and soil organic matter content and composition. The uptake of reduced Mn by plant roots (2) is influenced by interactions with several plant nutrients, rhizosphere pH (hence the  $\text{NO}_3\text{:NH}_4$  ratio), and soil water status, which regulates mass transport of soluble ions to the root. Mn phytotoxicity occurs in leaves through interference with the metabolism of essential metals and via the production of reactive oxygen species (3). Antioxidant defense chemistry is impeded in Mn-stressed leaves by the diminished activity of transition metals that are components of key antioxidant enzymes (4). Oxidative stress generated by excess Mn is exacerbated by high light intensity, ozone, temperature extremes, and possibly UV radiation (5). Atmospheric factors affecting stomatal transpiration, including light, temperature, ozone, humidity, and  $\text{CO}_2$  will affect leaf metal content, which is partly driven by mass flow of water (6). Precipitation influences soil pE, soil microbial processes, and ion transport to roots (7). Acid deposition influences soil pH and the concentration of Al and other cations that interact with Mn uptake (8). Feedbacks from Mn phytotoxicity in the forest canopy (9) include altered production and composition of organic debris, altered microbial activity in the rhizosphere, reduced soil water use, reduced cycling of plant nutrients, altered production of volatile organic compounds and thus acid deposition, altered ambient humidity, and at the global scale, altered interaction with atmospheric  $\text{CO}_2$ . Human effects on many of the atmospheric and soil factors shown here could increase the severity of Mn phytotoxicity in the Eastern Forest.

Ni, 2000; Liao et al., 2004; Yan et al., 2004), and UV tolerance (Sato et al., 2003).

Progress in the understanding of plant responses to edaphic stress and GCVs at the genomic level would be valuable in two general ways. First, it would provide basic knowledge of plant–environment interactions leading to the discovery of unknown mechanisms of tolerance to edaphic stresses. For example, antioxidant gene arrays could be designed to test whether interactions between metal toxicity and UV interact to induce oxidative stress. Where robust and consistent relationships are identified, the regulation of selected genes could then be used to monitor environmental change over time relative to an established baseline. This could employ sentinel organisms amenable to genetic analysis, or as progress with molecular methods proceeds, could focus on genetic

signals conserved across species. A second general benefit from this effort will be the availability of more genetic targets of known function for transgenic and MAS approaches to enhanced stress tolerance in crops.

While genomic techniques have much to offer, they also face serious challenges. Studying plant responses to multiple and interacting edaphic and GCV variables at the organismic and physiological levels has proven to be extremely complicated, as evidenced by the lack of consensus in the literature reviewed in this paper. Attempts to unravel the complex gene networks that underlie these higher order responses adds yet another level of complexity. Phenotypic responses are the sum of multiple and interacting gene products passing through several levels of regulation (transcription, translation, and post-translation modifications) and even within the same plant, genetic responses are

highly variable from one tissue type to another. The microarray studies cited above generally examined a single variable in a single species (*Arabidopsis thaliana* (L.) Heynh.) grown in artificial environments. Even under these optimal circumstances, obtaining reproducible results can be challenging, and the information tells us little about other plant species, or how responses will differ in real world environments. At the genetic level, quantitative traits are of paramount importance, and substantial genotypic variation is apparent, meaning that diversity among haplotypes could be more important than the population mean for a species. While this argues for genomic rather than physiological approaches, where typically only a small number of genotypes are observed, it also poses a challenge since the functional complexity of numerous haplotypes of numerous interacting genes is immense. At the cellular level, we are finding a bewildering array of interacting signaling responses associated with environmental stress. At the tissue, organ, and organismic levels, we have achieved much in understanding photosynthesis and water relations, but much remains unknown, especially concerning roots and the rhizosphere, where many of the key processes appear to be occurring. Our understanding of mineral metabolism, apart from nitrogen, lags substantially behind our understanding of photosynthesis and leaf responses to light, temperature, and carbon dioxide. We do not understand plant responses to mineral stresses very well, and we lack general models of how stresses are likely to interact. It is also not clear to what extent stress interactions and responses may be generalized across species and ecosystems, and to what extent the functional importance of genetic changes may be specific to a unique organismic and ecological context. These challenges are not trivial and are unlikely to be resolved simply by more comprehensive sequencing efforts. We need a true integration of functional disciplines with genomics to understand these processes. Given the pace of global change, it remains to be seen whether such understanding will be predictive or retrospective.

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### References

- Abrams, M.D., 1998. The red maple paradox. *Bioscience* 48, 355–364.
- Adams, F. (Ed.), 1984. *Soil Acidity and Liming*. ASA, CSSA, SSSA, Madison, WI.
- Aerts, R., Chapin, F.S., 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30, 1–67.
- Agrama, H.A.S., Zakaria, A.G., Said, F.B., Tuinstra, M., 1999. Identification of quantitative trait loci for nitrogen use efficiency in maize. *Molecular Breeding* 5, 187–195.
- Ainsworth, E.A., Davey, P.A., Bernacchi, C.J., Dermody, O.C., Heaton, E.A., Moore, D.J., Morgan, P.B., Naidu, S.L., Ra, H.S.Y., Zhu, X.G., Curtis, P.S., Long, S.P., 2002. A meta-analysis of elevated CO<sub>2</sub> effects on soybean (*Glycine max*) physiology, growth and yield. *Global Change Biol.* 8, 695–709.
- Almeida, J.P.F., Hartwig, U.A., Frehner, M., Nosberger, J., Luscher, A., 2000. Evidence that P deficiency induces N feedback regulation of symbiotic N<sub>2</sub> fixation in white clover (*Trifolium repens* L.). *J. Exp. Bot.* 51, 1289–1297.
- Arnone, J.A.I., Zaller, J.G., Spehn, E., Niklaus, P.A., Wells, C.E., Körner, C., 2000. Dynamics of root systems in native grasslands: effects of elevated atmospheric CO<sub>2</sub>. *New Phytol.* 147, 73–85.
- Baligar, V.C., Duncan, R.R. (Eds.), 1990. *Crops as Enhancers of Nutrient Use*. Academic Press Inc., San Diego.
- Bank, W., 2002. *World Development Indicators*, The World Bank, New York.
- Barber, S.A., 1995. *Soil Nutrient Bioavailability: a Mechanistic Approach*, second ed. John Wiley & Sons Inc., New York, USA.
- Barrett, D., Richardson, A., Gifford, R., 1998. Elevated atmospheric CO<sub>2</sub> concentrations increase wheat root phosphatase activity when growth is limited by phosphorus. *Aust. J. Plant Physiol.* 25, 87–93.
- BassiriRad, H., 2000. Kinetics of nutrient uptake by roots: responses to global change. *New Phytol.* 147, 155–169.
- BassiriRad, H., Gutschick, V.P., Lussenhop, J., 2001. Root system adjustments: regulation of plant nutrient uptake and growth responses to elevated CO<sub>2</sub>. *Oecologia* 126, 305–320.
- BassiriRad, H., Tissue, D.T., Reynolds, J.F., Chapin, F.S., 1996. Response of *Eriophorum vaginatum* to CO<sub>2</sub> enrichment at different soil temperatures: effects on growth, root respiration and PO<sub>4</sub><sup>3-</sup> uptake kinetics. *New Phytol.* 133, 423–430.
- Berntson, G.M., 1994. Modelling root architecture: are there trade-offs between efficiency and potential of resource acquisition? *New Phytol.* 127, 483–493.
- Berntson, G.M., Bazzaz, F.A., 1996. Belowground positive and negative feedbacks on CO<sub>2</sub> growth enhancement. *Plant Soil* 187, 119–131.
- Berntson, G.M., Bazzaz, F.A., 1998. Regenerating temperate forest mesocosms in elevated CO<sub>2</sub>: belowground growth and nitrogen cycling. *Oecologia* 113, 115–125.

- Bloom, A.J., Chapin, F.S.I., Mooney, H.A., 1985. Resource limitation in plants—an economic analogy. *Ann. Rev. Ecol. Syst.* 16, 363–392.
- Caldwell, M.M., Ballare, C.L., Bornman, J.F., Flint, S.D., Bjorn, L.O., Teramura, A.H., Kulandaivelu, G., Tevini, M., 2003. Terrestrial ecosystems increased solar ultraviolet radiation and interactions with other climatic change factors. *Photochem. Photobiol. Sci.* 2, 29–38.
- Canadell, J., Norby, R., Cotrufo, M.F., Nosberger, J. (Eds.) 2000. Litter quality and decomposition under elevated atmospheric CO<sub>2</sub>. *Plant Soil* (special issue) 224.
- Casati, P., Walbot, V., 2003. Gene expression profiling in response to ultraviolet radiation in maize genotypes with varying flavonoid content. *Plant Physiol.* 132, 1739–1754.
- Chazdon, R.L., 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* 6, 51–71.
- Clijsters, H., Cuypers, A., Vangronsveld, J., 1999. Physiological responses to heavy metals in higher plants; defence against oxidative stress. *Z. Naturforsch. C: Biosci.* 54, 730–734.
- Conway, G., 1997. *The Doubly Green Revolution: Food for All in the 21st Century*, Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Dakora, F.D., Phillips, D.A., 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant Soil* 245, 35–47.
- Delucia, E.H., Callaway, R.M., Thomas, E.M., Schlesinger, W.H., 1997. Mechanisms of phosphorus acquisition for ponderosa pine seedlings under high CO<sub>2</sub> and temperature. *Ann. Botany* 79, 111–120.
- Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., Weathers, K.C., 2001. Acidic deposition in the Northeastern United States: sources and inputs, ecosystem effects, management strategies. *Bioscience* 51, 180–198.
- Eissenstat, D., 1997. Trade-offs in Root Form and Function. In: Jackson, L. (Ed.), *Ecology in Agriculture*. Academic Press, San Diego, pp. 173–199.
- Eissenstat, D.M., Wells, C.E., Yanai, R.D., Whitbeck, J.L., 2000. Building roots in a changing environment: implications for root longevity. *New Phytol.* 147, 33–42.
- Epstein, E., 1999. Silicon. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 50, 641–664.
- Fangmeier, A., Gruters, U., Hogy, P., Vermehren, B., Jager, H.J., 1997. Effects of elevated CO<sub>2</sub> nitrogen supply and tropospheric ozone on spring wheat .2. Nutrients (N, P, K, S, Ca, Mg, Fe, Mn, Zn). *Environ. Pollut.* 96, 43–59.
- Fitter, A.H., Self, G.K., Wolfenden, J., Vuuren, M.M.I.V., Brown, T.K., Williamson, L., Graves, J.D., Robinson, D., 1996. Root production and mortality under elevated atmospheric carbon dioxide. *Plant Soil* 187, 299–306.
- Flowers, T., Garcia, A., Koyama, M., Yeo, A., 1997. Breeding for salt tolerance in crop plants—the role of molecular biology. *Acta Physiol. Plant.* 19, 427–433.
- Foy, C.D., Lee, E.H., Rowland, R., Devine, T.E., Buzzell, R.I., 1995. Ozone tolerance related to flavonol glycoside genes in soybean. *J. Plant Nutr.* 18, 637–647.
- Foyer, C., Lelandais, M., Kunert, K.J., 1994. Photooxidative stress in plants. *Physiol. Plant.* 92, 696–717.
- Fransson, P.M.A., Taylor, A.F.S., Finlay, R.D., 2001. Elevated atmospheric CO<sub>2</sub> alters root symbiont community structure in forest trees. *New Phytol.* 152, 431–442.
- Ge, Z., Rubio, G., Lynch, J.P., 2000. The importance of root gravitropism for inter-root competition and phosphorus acquisition efficiency: results from a geometric simulation model. *Plant Soil* 218, 159–171.
- Gifford, R.M., Barrett, D.J., Lutze, J.L., 2000. The effects of elevated CO<sub>2</sub> on the C:N and C:P mass ratios of plant tissues. *Plant Soil* 224, 1–14.
- Godbold, D.L., Berntson, G.M., 1997. Elevated atmospheric CO<sub>2</sub> concentration changes ectomycorrhizal morphotype assemblages in *Betula papyrifera*. *Tree Physiol.* 17, 347–350.
- Godbold, D.L., Berntson, G.M., Bazzaz, F.A., 1997. Growth and mycorrhizal colonization of three north american tree species under elevated atmospheric CO<sub>2</sub>. *New Phytol.* 137, 433–440.
- Gonzalez, A., Steffen, K.L., Lynch, J.P., 1998. Light and excess manganese - implications for oxidative stress in common bean. *Plant Physiol.* 118, 493–504.
- Gorissen, A., 1996. Elevated CO<sub>2</sub> evokes quantitative and qualitative changes in carbon dynamics in a plant/soil system: mechanisms and implications. *Plant Soil* 187, 289–298.
- Gregory, P.J., Palta, J.A., Batts, G.R., 1996. Root systems and root:mass ratio - carbon allocation under current and projected atmospheric conditions in arable crops. *Plant Soil* 187, 221–228.
- Hartwig, U.A., Luscher, A., Nosberger, J., Van Kessel, C., 2002. Nitrogen-15 budget in model ecosystems of white clover and perennial ryegrass exposed for four years at elevated atmospheric pCO<sub>2</sub>. *Global Change Biol.* 8, 194–202.
- Hash, C.T., Schaffert, R.E., Peacock, J.M., 2002. Prospects for using conventional techniques and molecular biological tools to enhance performance of ‘orphan’ crop plants on soils low in available phosphorus. *Plant Soil* 245, 135–146.
- Hesman, T., 2000. Greenhouse gassed: carbon dioxide spells indigestion for food chains. *Sci. News* 157, 200–202.
- Hinsinger, P., 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant Soil* 237, 173–195.
- Ho, M.D., McCannon, B.C., Lynch, J.P., 2004. Optimization modeling of plant root architecture for water and phosphorus acquisition. *J. Theoret. Biol.* 226 (3), 331–340.
- Hodge, A., 1996. Impact of elevated CO<sub>2</sub> on mycorrhizal associations and implications for plant growth. *Biol. Fertil. Soils* 23, 388–398.
- Hodge, A., Millard, P., 1998. Effect of elevated CO<sub>2</sub> on carbon partitioning and exudate release from *Plantago lanceolata* seedlings. *Physiol. Plant.* 103, 280–286.
- Hodge, A., Paterson, E., Grayston, S.J., Campbell, C.D., Ord, B.G., Killham, K., 1998. Characterisation and microbial utilisation of exudate material from the rhizosphere of *Lolium perenne* grown under CO<sub>2</sub> enrichment. *Soil Biol. Biochem.* 30, 1033–1043.
- Horiguchi, T., 1988. Mechanism of manganese toxicity and tolerance of plants vii. Effect of light intensity on manganese-induced chlorosis. *J. Plant Nutr.* 11, 235–245.

- Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A., Hall, T.J., 2000. Factors associated with the decline disease of sugar maple on the Allegheny Plateau. *Can. J. Forest Res.* 30, 1365–1378.
- Houtz, R., Nable, R., Cheniae, G., 1988. Evidence for effects on the in vivo activity of ribulose-bisphosphate carboxylase/oxygenase during development of Mn toxicity in tobacco. *Plant Physiol.* 86, 1143–1149.
- Kaeppler, S.M., Parke, J.L., Mueller, S.M., Senior, L., Stuber, C., Tracy, W.F., 2000. Variation among maize inbred lines and detection of quantitative trait loci for growth at low phosphorus and responsiveness to arbuscular mycorrhizal fungi. *Crop Sci.* 40, 358–364.
- Karnosky, D.F., 2003. Impacts of elevated atmospheric CO<sub>2</sub> on forest trees and forest ecosystems: knowledge gaps. *Environ. Int.* 29, 161–169.
- Kimball, B., Morris, C., Pinter, P., Wall, G., Hunsaker, D., Adamsen, F., LaMorte, R., Leavitt, S., Thompson, T., Matthias, A., Brooks, T., 2001. Elevated CO<sub>2</sub>, drought and soil nitrogen effects on wheat grain quality. *New Phytol.* 150, 295–303.
- Kimura, M., Yamamoto, Y.Y., Seki, M., Sakurai, T., Sato, M., Abe, T., Yoshida, S., Manabe, K., Shinozaki, K., Matsui, M., 2003. Identification of Arabidopsis genes regulated by high light-stress using cDNA microarray. *Photochem. Photobiol. Sci.* 77, 226–233.
- Kobayashi, Y., Koyama, H., 2002. QTL analysis of Al tolerance in recombinant inbred lines of *Arabidopsis thaliana*. *Plant Cell Physiol.* 43, 1526–1533.
- Kochian, L.V., 1995. Cellular mechanisms of aluminum toxicity and resistance in plants. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 46, 237–260.
- Krupa, Z., Baszynski, T., 1995. Some aspects of heavy metals toxicity towards photosynthetic apparatus—direct and indirect effects on light and dark reactions. *Acta Physiol. Plant.* 17, 177–190.
- Kubiske, M.E., Pregitzer, K.S., Mikan, C.J., Zak, D.R., Maziasz, J.L., Teeri, J.A., 1997. *Populus tremuloides* photosynthesis and crown architecture in response to elevated CO<sub>2</sub> and soil N availability. *Oecologia* 110, 328–336.
- Lahner, B., Gong, J., Mahmoudian, M., Smith, E.L., Abid, K.B., Rogers, E.E., Guerinot, M.L., Harper, J.F., Ward, J.M., McIntyre, L., Schroeder, J.I., Salt, D.E., 2003. Genomic scale profiling of nutrient and trace elements in *Arabidopsis thaliana*. *Nature Biotechnol.* 21, 1215–1221.
- Lavola, A., Julkunen-Tiitto, R., de la Rosa, T.M., Lehto, T., Aphalo, P.J., 2000. Allocation of carbon to growth and secondary metabolites in birch seedlings under UV-B radiation and CO<sub>2</sub> exposure. *Physiol. Plant.* 109, 260–267.
- Liao, H., Yan, X., Rubio, G., Beebe, S.E., Blair, M.W., Lynch, J.P., 2004. Genetic mapping of basal root gravitropism and phosphorus acquisition efficiency in common bean. *Funct. Plant Biol.*, in press.
- Lidon, F.C., Teixeira, M.G., 2000. Oxy radicals production and control in the chloroplast of Mn-treated rice. *Plant Sci.* 152, 7–15.
- Lin, S.F., Grant, D., Cianzio, S., Shoemaker, R., 2000. Molecular characterization of iron deficiency chlorosis in soybean. *J. Plant Nutr.* 23, 1929–1939.
- Lynch, J., 1998. The role of nutrient efficient crops in modern agriculture. *J. Crop Prod.* 1, 241–264.
- Lynch, J.P., Brown, K.M., 2001. Topsoil foraging—an architectural adaptation of plants to low phosphorus availability. *Plant Soil* 237, 225–237.
- Marschner, H., 1995. *Mineral Nutrition of Higher Plants*, second ed. Academic Press, London, San Diego.
- Marschner, H., Romheld, V., 1994. Strategies of plants for acquisition of Iron. *Plant Soil* 165, 261–274.
- McCool, M.M., 1935. Effect of light intensity on the manganese content of plants, Contribution, Boyce Thompson Institute.
- Mickelson, S., See, D., Meyer, F.D., Garner, J.P., Foster, C.R., Blake, T.K., Fischer, A.M., 2003. Mapping of QTL associated with nitrogen storage and remobilization in barley (*Hordeum vulgare* L.) leaves. *J. Exp. Bot.* 54, 801–812.
- Milla, M.A., Butler, E., Huete, A.R., Wilson, C.F., Wilson, O., Gustafson, J.P., 2002. Expressed sequence tag-based gene expression analysis under aluminum stress in rye. *Plant Physiol.* 130, 1706–1716.
- Nable, R.O., Houtz, R.L., Cheniae, G.M., 1988. Early inhibition of photosynthesis during development of Mn toxicity in tobacco. *Plant Physiol.* 86, 1136–1142.
- Negishi, T., Nakanishi, H., Yazaki, J., Kishimoto, N., Fujii, F., Shimbo, K., Yamamoto, K., Sakata, K., Sasaki, T., Kikuchi, S., Mori, S., Nishizawa, N.K., 2002. cDNA microarray analysis of gene expression during Fe-deficiency stress in barley suggests that polar transport of vesicles is implicated in phytosiderophore secretion in Fe-deficient barley roots. *Plant J.* 30, 83–94.
- Nguyen, C., 2003. Rhizodeposition of organic C by plants: mechanisms and controls. *Agronomie* 23, 375–396.
- Nguyen, V.T., Nguyen, B.D., Sarkarung, S., Martinez, C., Paterson, A.H., Nguyen, H.T., 2002. Mapping of genes controlling aluminum tolerance in rice: comparison of different genetic backgrounds. *Mol. Genet. Genomics* 267, 772–780.
- Ninamango-Cardenas, F.E., Guimaraes, C.T., Martins, P.R., Parentoni, S.N., Carneiro, N.P., Lopes, M.A., Moro, J.R., Paiva, E., 2003. Mapping QTLs for aluminum tolerance in maize. *Euphytica* 130, 223–232.
- Norby, R.J., O'Neill, E.G., Hood, W.G., Luxmoore, R.J., 1987. Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO<sub>2</sub> enrichment. *Tree Physiol.* 3, 203–210.
- Panda, S., Mishra, A.K., Biswal, U.C., 1986. Manganese-induced modification of membrane lipid peroxidation during aging of isolated wheat chloroplasts. *Photobiol. Photobiophys.* 13, 53–61.
- Paterson, E., Hodge, A., Thornton, B., Millard, P., Killham, K., 1999. Carbon partitioning and rhizosphere C-flow in *Lolium perenne* as affected by CO<sub>2</sub> concentration, irradiance and below-ground conditions. *Global Change Biol.* 5, 669–678.
- Poorter, H., Perez-Soba, M., 2001. The growth response of plants to elevated CO<sub>2</sub> under non-optimal environmental conditions. *Oecologia* 129, 1–20.
- Poorter, H., Remkes, C., Lambers, H., 1990. Carbon and nitrogen economy of 24 wild-species differing in relative growth-rate. *Plant Physiol.* 94, 621–627.

- Pritchard, S.G., Rogers, H.H., 2000. Spatial and temporal deployment of crop roots in CO<sub>2</sub>-enriched environments. *New Phytol.* 147, 55–71.
- Rauh, B.L., Basten, C., Buckler, E.S., 2002. Quantitative Trait Loci analysis of growth response to varying nitrogen sources in *Arabidopsis thaliana*. *Theor. Appl. Gen.* 104, 743–750.
- Rogers, H.H., Prior, S.A., Runion, G.B., Mitchell, R.J., 1996. Root to shoot ratio of crops as influenced by CO<sub>2</sub>. *Plant Soil* 187, 229–248.
- Rossel, J.B., Wilson, I.W., Pogson, B.J., 2002. Global changes in gene expression in response to high light in *Arabidopsis*. *Plant Physiol.* 130, 1109–1120.
- Rubio, G., Walk, T., Ge, Z., Yan, X., Liao, H., Lynch, J.P., 2001. Root gravitropism and belowground competition among neighboring plants: a modeling approach. *Ann. Bot.* 88, 929–940.
- Rubio, G., Zhu, J., Lynch, J.P., 2003. A critical test of the two prevailing theories of plant response to nutrient availability. *Am. J. Bot.* 90, 143–152.
- Runion, G.B., Mitchell, R.J., Rogers, H.H., Prior, S.A., Counts, T.K., 1997. Effects of nitrogen and water limitation and elevated atmospheric CO<sub>2</sub> on ectomycorrhiza of longleaf pine. *New Phytol.* 137, 681–689.
- Santandrea, G., Pandolfini, T., Bennici, A., 2000. A physiological characterization of Mn-tolerant tobacco plants selected by in vitro culture. *Plant Sci.* 150, 163–170.
- Sato, T., Ueda, T., Fukuta, Y., Kumagai, T., Yano, M., 2003. Mapping of quantitative trait loci associated with ultraviolet-B resistance in rice (*Oryza sativa* L.). *Theor. Appl. Gen.* 107, 1003–1008.
- Schlichting, E., Sparrow, L., et al., 1988. Distribution and amelioration of manganese toxic soils. In: Graham, R. (Ed.), *Manganese in Soils and Plants*. Kluwer Academic Publishers, Dordrecht, pp. 277–288.
- Seki, M., Narusaka, M., Ishida, J., Nanjo, T., Fujita, M., Oono, Y., Kamiya, A., Nakajima, M., Enju, A., Sakurai, T., Satou, M., Akiyama, K., Taji, T., Yamaguchi-Shinozaki, K., Carninci, P., Kawai, J., Hayashizaki, Y., Shinozaki, K., 2002. Monitoring the expression profiles of 7000 *Arabidopsis* genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. *Plant J.* 31, 279–292.
- Sledge, M.K., Bouton, J.H., Dall'Agnoli, M., Parrott, W.A., Kochert, G., 2002. Identification and confirmation of aluminum tolerance QTL in diploid *Medicago sativa* subsp. *coerulea*. *Crop Sci.* 42, 1121–1128.
- Somashekaraiah, B., Padmaja, K., Prasad, A., 1992. Phytotoxicity of cadmium ions on germinating seedlings of mungbean (*Phaseolus vulgaris*): involvement of lipid peroxides in chlorophyll degradation. *Physiol. Plant.* 85, 85–89.
- Staddon, P.L., Heinemeyer, A., Fitter, A.H., 2002. Mycorrhizas and global environmental change: research at different scales. *Plant Soil* 244, 253–261.
- Thimm, O., Essigmann, B., Kloska, S., Altmann, T., Buckhout, T.J., 2001. Response of *Arabidopsis* to iron deficiency stress as revealed by microarray analysis. *Plant Physiol.* 127, 1030–1043.
- Tomlinson, G.H., 2003. Acidic deposition, nutrient leaching and forest growth. *Biogeochemistry* 65, 51–81.
- Tranbarger, T.J., Al-Ghazi, Y., Muller, B., de la Serve, B.T., Dumas, P., Touraine, B., 2003. A macro-array-based screening approach to identify transcriptional factors involved in the nitrogen-related root plasticity response of *Arabidopsis thaliana*. *Agronomie* 23, 519–528.
- Uselman, S.M., Qualls, R.G., Thomas, R.B., 2000. Effects of increased atmospheric CO<sub>2</sub>, temperature, soil N availability on root exudation of dissolved organic carbon by a N-fixing tree (*Robinia pseudoacacia* L.). *Plant Soil* 222, 191–202.
- Van Assche, F., Clijsters, H., 1990. Effects of metals on enzyme activities in plants. *Plant Cell Environ.* 13, 195–206.
- van der Ploeg, R., Bohm, W., Kirkham, M., 1999. On the origin of the theory of plant nutrition of plants and the law of minimum. *Soil Sci. Soc. Am. J.* 63, 1055–1062.
- Veteli, T.O., Kuokkanen, K., Julkunen-Tiitto, R., Roininen, H., Tahvanainen, J., 2002. Effects of elevated CO<sub>2</sub> and temperature on plant growth and herbivore defensive chemistry. *Global Change Biol.* 8, 1240–1252.
- Wintz, H., Fox, T.C., Wu, Y.Y., Feng, V., Chen, W., Chang, H.S., Zhu, T., Vulpe, C.D., 2003. Expression profiles of *Arabidopsis thaliana* in mineral deficiencies reveal novel transporters involved in metal homeostasis. *J. Biol. Chem.* 278, 47644–47653.
- Wu, P., Ni, J.J., 2000. Detection of the quantitative trait loci with AFLP and RFLP markers for phosphorus uptake and use efficiency in rice. *Acta Botanica Sinica* 42, 229–233.
- Wullschlegel, S.D., Tschaplinski, T.J., Norby, R.J., 2002a. Plant water relations at elevated CO<sub>2</sub>-implications for water-limited environments. *Plant Cell Environ.* 25, 319–331.
- Wullschlegel, S.D., Gunderson, C.A., Hanson, P.J., Wilson, K.B., Norby, R.J., 2002b. Sensitivity of stomatal and canopy conductance to elevated CO<sub>2</sub> concentration—interacting variables and perspectives of scale. *New Phytol.* 153, 485–496.
- Xu, Z., Luo, G., Wang, A., Cheng, Y., 1998. Effects of strong light and exogenous active oxygen species on chlorophyll fluorescence in lettuce. *Acta Phytophysiologica Sinica* 24, 279–284.
- Yamaya, T., Obara, M., Nakajima, H., Sasaki, S., Hayakawa, T., Sato, T., 2002. Genetic manipulation and quantitative-trait loci mapping for nitrogen recycling in rice. *J. Exp. Bot.* 53, 917–925.
- Yan, X., Liao, H., Beebe, S.E., Blair, M.W., Lynch, J.P., 2004. QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant and Soil*, in press.
- Zak, D.R., Pregitzer, K.S., King, J.S., Holmes, W.E., 2000. Elevated atmospheric CO<sub>2</sub>, fine roots and the response of soil microorganisms: a review and hypothesis. *New Phytol.* 147, 201–222.
- Zak, D.R., Pregitzer, K.S., Curtis, P.S., Teeri, J.A., Fogel, R., Randlett, D.L., 1993. Elevated atmospheric CO<sub>2</sub> and feedback between carbon and nitrogen cycles. *Plant Soil* 151, 105–117.