

Ecosystem and Plant Response to Environmental Variables and Climate Change

Biotic and Abiotic Interactions in Ecosystems

Plants live in complex environments where many biotic and abiotic factors limit or promote productivity and carbon biosequestration. Temperature and water extremes, nutrient and other resource availabilities, microbe-induced diseases, and insect attacks can limit plant productivity. At the same time, this productivity intimately depends on plant interactions with certain beneficial microorganisms (as described in Chapter 3, Carbon Flows in Ecosystems, p. 27) and access to appropriate temperature, water, and light regimes. Furthermore, these biotic and abiotic factors can influence each other, giving rise to complex environmental conditions to which plants must adapt. This complexity is illustrated by millions of acres of bark-beetle outbreaks triggered by warming climates that in turn increase winter survival of bark-beetle populations. In the coming decades, such ecological complexities will pose increasing challenges in both agricultural and natural ecosystems (see Chapter 5, Ecosystem Dynamics, p. 71, for a discussion on the impacts of climate change on the frequency and severity of such disturbances).

Uncertainty about how abiotic and biotic factors interact at a mechanistic level limits a comprehensive understanding of plant and ecosystem productivity. This knowledge gap reduces our ability to interpret observations, make meaningful projections concerning disturbance and its impacts, and develop the strategies needed for intervening in an ecosystem's response to abiotic and biotic interactions. Thus, determining which abiotic and biotic factors most affect plant productivity, the mechanisms by which these factors act, and whether particular factors influence the quality of biomass accumulation (e.g., transient versus stable biomass) is essential for predicting ecosystem response. Moreover, such knowledge could reveal strategies to either enhance or diminish the extent to which particular interactions affect improved carbon biosequestration.

Consequently, achieving increased plant productivity and carbon biosequestration requires studying and managing abiotic and biotic processes and interactions at multiple levels of organization—from molecular biology to whole-organism phenotypes to ecological communities to global factors that influence Earth's carbon cycle and climate change.

Water Factors in Ecosystem Productivity

Potential alterations in water availability arising from climate change will have significant implications for plant productivity. For example, climatic changes are expected to affect the overall rainfall quantity in many parts of the world, undoubtedly influencing plant growth. More subtle shifts in rainfall patterns throughout the year also might profoundly impact plant and plant-community growth patterns. Additionally, climate warming will alter soil water balance

Key Research Questions

1. **What are the abiotic and biotic factors and interactions that determine nutrient availability?**
2. **How are the carbon, nutrient, and water cycles linked, and how do such linkages determine ecosystem productivity, carbon biosequestration, and response to climate change?**

irrespective of changes in precipitation. The extent of such alterations will depend on soil type. For example, soils unable to absorb and retain moisture may be affected more severely than others able to do so. Moreover, changes in soil water content will have downstream effects on microbial communities and chemical and nutrient mobility in soils. Likewise, climatic changes altering rainfall pH (i.e., acidification of rainwater) could have broad impacts on the chemical composition, bioavailability of inorganic nutrients, and microbial communities in soil. A comprehensive understanding of these complex, climate-induced changes is needed for accurate, predictive modeling of the effects of altered water availability on plant productivity.

Plant Traits and Strategies for Combatting Drought

Plants possess a variety of strategies—some more successful than others—for dealing with water limitation. Such strategies fall into one of three general categories: (1) drought escape, reflecting plants' ability to alter their life cycle to escape periods of water shortages; (2) drought avoidance, in which plants adjust internal processes to maintain their internal water supply; and (3) drought tolerance, which enables plants to continue to grow, though perhaps in an altered manner, despite reduced water (Bray 1997). Limited understanding of the mechanisms directing these strategies impedes our ability to optimize plant traits and productivity amid water deprivation. However, two traits—water use efficiency (WUE) and root systems—have been focuses in research to enhance plant productivity during drought.

Defining Genes and Processes that Determine Water Use Efficiency

Water is central to the distribution and productivity of plants in ecosystems and agriculture. Changing rainfall and temperature patterns give impetus to determining the molecular and developmental mechanisms that influence water use efficiency and plant productivity during drought. Experimental approaches in model plant species and crops have begun to identify causal influences on drought tolerance arising from various plant WUE strategies, including adaptations of traits for stomata, transpiration, root architecture, and other diverse physiological mechanisms. The role of symbiotic fungi in water-deprivation adaptation also must be considered. Combined research approaches using systems biology, omics technologies, spectral analyses of water-stressed plants, and whole-plant phenotypic analyses of natural genetic variation offer great potential for understanding and manipulating drought tolerance in plants. Such an integrated understanding and subsequent optimization strategies would have important implications for plant productivity and carbon biosequestration.

Transpiration and Nutrient Acquisition

Many global climate change variables—including precipitation, temperature, length of growing season, humidity, and radiation intensity—likely will affect water availability and use by plants. The significant and direct impact on primary productivity from climate-induced shifts in plant water status is commonly recognized. Less widely known, however, is that altered soil water availability and transpiration will have important secondary effects on plant acquisition of soluble nutrients, especially nitrate-N, calcium, magnesium, sulfur, and silicon.

Regulation of Root-System Architecture for Water Acquisition

Numerous studies have shown that elevated CO₂ changes root architecture, or the spatial configuration of root systems. Architecture traits significantly correlate with a plant's ability to survive under water stress. For instance, lateral-root density, a key trait in determining productivity, is linked to plant performance when water is limited. Denser lateral roots facilitate more water uptake, thus allowing plants to perform better during drought. Root systems and the mechanisms by which they increase water capture vary widely among drought-tolerant plants. In some plants, roots extending well below the surface obtain water deep into the soil profile. In others, shallow root systems allow rapid capture of rainwater before it is lost to evaporation. Some plants are highly plastic, having root systems that change in response to water availability or shift during development to adjust to seasonal fluctuations in soil water distribution. Moreover, hydrotropism, though poorly understood, is a process allowing roots to sense and grow toward water. These various types of root systems are clearly important to plant productivity and survival during water stress. Thus a thorough understanding of the mechanisms regulating their development and the potential consequences of climate change on root architecture is critical. Also needed is greater insight into how root-system architecture and interactions with rhizobia change in response to shifts in water distribution.

Root Architecture and Nutrient Acquisition

The role of root architecture in mediating plant response to climate change will depend on ecosystem edaphic constraints—the limitations arising from specific soil conditions. Most terrestrial ecosystems have multiple such constraints, including low availability of nitrogen, phosphorus, and often calcium, as well as excessive levels of aluminum, manganese, or salinity. Although root-system response to elevated CO₂ and nitrogen has received some research attention, few studies have investigated how shifts in root architecture affect other nutritional constraints. For example, architectural changes arising from elevated CO₂ may have very different impacts when comparing plant acquisition of phosphorus and calcium, nutrients often limiting in forest soils. Phosphorus is diffusion-mobile, and calcium moves by mass water flow. Thus, architectural changes resulting in finer branching or root proliferation in topsoil may increase phosphorus acquisition, and those resulting in root extensions into deep areas with greater water availability might enhance calcium uptake. Greater analysis is needed of root-system interactions with specific nutrients and edaphic limitations prevalent in most native soils. Without such understanding, making general statements will be difficult when predicting how elevated CO₂ and other climate change variables will alter root architecture and how these alterations will affect nutrient acquisition in future atmospheres.

Rhizodeposition of Root Exudates

About half a plant's belowground carbon allocation is deposited in its rhizosphere or root zone. Most of this carbon material consists of dead root tissue, but a portion contains compounds exuded by living cells. Compounds in these exudates—including mucilage, organic acids, phosphatases, phytosiderophores, and protons—protect growing roots from aluminum stress and, in concert with soil microbial symbionts, mobilize relatively insoluble nutrients such as phosphorus and iron. Interactions of global change variables with root exudates thus

should have important consequences for plant growth in acidic and alkaline soils. However, the few studies examining climate change impacts on root exudates have produced conflicting results. For example, in some studies, elevated CO₂ had no effect on root exudates, while in others it decreased exudates and altered their composition. Further uncertainty surrounds observed increases in rhizosphere respiration amid elevated CO₂, but whether these increases are due to additional exudates per unit root surface area or simply greater root growth is unclear. Adding to the complexity of exudate functioning and composition are interactions with light, temperature, and other variables affecting photosynthesis. Though challenging, the complex interplay of root exudates with root photosynthate supply, root growth and architecture, and the rhizosphere deserves further study because of the importance of these interactions for plant adaptation to acidic and alkaline soils comprising much of Earth's land surface.

New methods must be developed in plant physiology, soil microbiology, biochemistry, and systems biology for improved understanding of these interactions at genomic through organismal scales. Models to support simulations of systems must be written to capture this new level of integrated understanding and thus accurately represent, at organismal to global scales, plant-soil interactions and their link to global carbon cycling.

Temperature and Light Impacts on Plant Productivity

Shifts in temperature arising from climate change have serious implications for plant productivity and thus carbon biosequestration. Climate warming affects almost all physical, chemical, and biological processes. Several key regulatory mechanisms underlying ecosystem response to such warming include acclimation of photosynthesis and respiration, phenology, nutrient dynamics, and ecohydrological regulation (Luo 2007). Despite the importance of these basic processes, most models still are incapable of representing how they are affected by climate change.

Even small changes in temperature can have profound impacts on chemical reactions determining plant productivity. Understanding how temperature affects these processes is thus critical, particularly when making global-warming projections. For example, shifts in soil temperatures might accompany changes in microbial communities, rates of SOM degradation, and soil chemistry. These in turn may alter nutrient supplies to plants. Furthermore, microbes, plant roots, and degrading litter facilitate the release of a complex array of chemical substances (e.g., proteins, amino acids, and phenolic compounds) whose interactions with each other may be affected by shifting temperatures. Aboveground temperature changes also might influence gas-exchange kinetics in leaves. Moreover, since the plant itself has no buffer against temperature changes, chemical reactions within plant cells may be fundamentally altered.

Equally important to plant productivity is light, and thus understanding how climate change can influence it is critical. A key area requiring further study is climate change effects on cloudiness and aerosols, factors that influence radiation incident on ecosystems. Changes in this primary energy input for plants, therefore, would impact ecosystem growth significantly. Furthermore, the quality, intensity, and spectral distribution of light affect carbon fixation and flux in ways not completely understood. Light quality, for example, triggers signaling cascades in plants that

regulate important aspects of development, including organ morphology, overall shoot and root proliferation, and flowering time. A deeper understanding of such mechanisms and how climate change might affect them is needed to predict future plant productivity and carbon biosequestration.

Change in Growing Season and Resultant Phenology

Changes in the length of growing seasons have been detected over broad areas and are some of the more obvious manifestations of climate change effects on ecosystems. Increased growing-season length will have not only phenological impacts, directly affecting both photosynthesis and respiration fluxes, but also a range of indirect effects (e.g., changes in herbivore-plant interactions, litter quality, and stocks of nonstructural carbohydrate reserves in plants). For many ecosystems, the net effect of growing-season changes on carbon balance is not yet known on decadal time scales. Such changes could influence the effectiveness of forest management for carbon biosequestration in unexpected ways, such as the interactions mentioned above. Shifts in the length of growing seasons present both a modeling challenge and potential test for models of carbon allocation and residence time in ecosystems, especially for examining interactions of changing seasonality with elevated CO₂ and nitrogen deposition.

Experimental Responses of Different Biomes to Atmospheric and Climatic Change

Experimental Results and Extensions to Tropical and Boreal Systems

Manipulative field experiments have been used to quantify the response of net primary productivity (NPP) to elevated CO₂ and simulated climate change in different ecosystems. Synthesizing the results of four Free-Air CO₂ Enrichment (FACE) experiments in forest ecosystems, Norby et al. (2005) concluded that the response of forest NPP to elevated CO₂ concentration is highly conserved across a broad range of productivity, with stimulation at the median of 23% ± 2%. At low leaf-area indices, much of the enhanced productivity was attributed to increased light absorption, but as leaf-area indices expanded, the response to elevated CO₂ concentration was wholly caused by greater light use efficiency. The surprising consistency of response across diverse sites provides a benchmark to evaluate predictions of ecosystem and global models.

For example, in exploring the ramifications of CO₂ fertilization in simulations of future climate change using an intermediate-complexity coupled climate-carbon model, Matthews (2007) simulated the four forest FACE experiments. The model response of NPP to elevated CO₂ concentration was remarkably close to experimental results, lending increased credibility to the model's formulation. Similarly, Hickler et al. (2008) found that the LPJ-GUESS dynamic vegetation model reproduced the magnitude of observed NPP enhancement at the forest FACE sites. However, predicted NPP enhancement in tropical forests is more than twice as high as in boreal forests, suggesting that currently available FACE results are not applicable to tropical ecosystems. This prediction highlights important differences among biomes in their response to elevated CO₂ concentration and sets forth the hypothesis that, relatively, tropical-forest NPP will be more responsive

and boreal-ecosystem NPP less responsive to future CO₂ concentration increases. Testing this hypothesis with manipulative experiments in tropical forests [where gross primary productivity (GPP) is highest] and boreal ecosystems (where more carbon is stored) is a critical research need that likely could clarify important uncertainties about the carbon cycle.

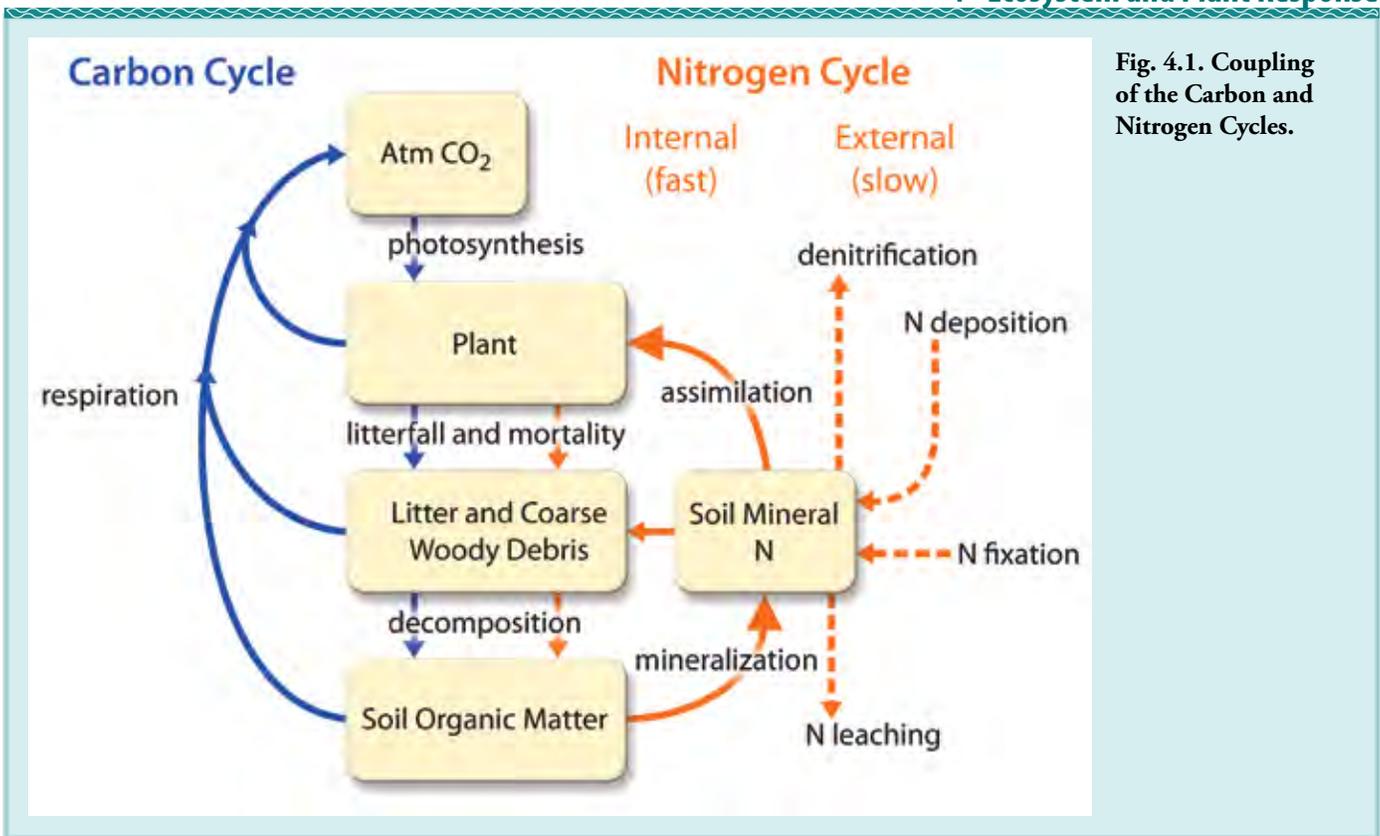
More difficult to address in manipulative field experiments are ecosystem responses to climatic warming. Using meta-analysis, Rustad et al. (2001) reported that aboveground plant productivity increased in response to warming in high-latitude systems but declined as latitude decreased. Unfortunately, no data were available for assessing ecosystems at latitudes lower than 34°. Despite a lack of data on how warming affects GPP and NPP in tropical ecosystems, the most pressing research need is understanding productivity responses in boreal systems. These ecosystems store a large amount of carbon, and climate change, particularly warming, could accelerate decomposition, leading to massive loss of carbon and a positive carbon feedback to the climate system. On the other hand, NPP response to CO₂ fertilization and extended growing seasons caused by warming could produce a negative feedback on atmospheric CO₂. The net effect of warming in boreal systems, including permafrost melting, encroachment of woody shrubs, and altered albedo, is impossible to predict with current data and understanding. Manipulative warming experiments in boreal ecosystems, which thus far have been too small in scale, must be expanded greatly to provide better guidance.

Nutrient Availability and Soil Moisture as Determinants of CO₂ Response

The apparently robust conclusion from FACE studies that forest NPP is enhanced by elevated CO₂ masks several significant sources of variation that could be especially important in determining how a specific site will respond to rising CO₂ concentration. At the Duke University FACE site, a wide range of NPP responses to CO₂ enrichment across replicate plots correlated with differences in soil nitrogen availability. Under low nitrogen availability, CO₂ enrichment increased NPP by 19%, whereas under intermediate and high nitrogen availability, NPP rose 27% (Finzi et al. 2002). When soils are poor in nutrients or experience prolonged water limitation (represented by only within-site variation in the Duke dataset), forests may have limited capacity to support any response to CO₂ enrichment (Oren et al. 2001). Furthermore, concurrent increases in tropospheric ozone could negate productivity increases from elevated CO₂ concentration (Karnosky et al. 2001; King et al. 2005). Nitrogen availability is not only a factor in spatial variability (e.g., how specific sites respond to such conditions), it also may influence whether NPP responses observed at the Duke site can be sustained for decades (Hungate et al. 2003; Luo et al. 2004).

The exclusion of nutrient interactions limits confidence in model conclusions simulating the complex feedbacks between carbon cycling and climate change. In fact, although one summary conclusion from the *Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (IPCC 2007) regarded a particular negative climate–carbon cycle feedback as a robust result, the studies on which this conclusion was based used coupled climate–carbon cycle models that excluded nutrient cycles. Several studies have suggested that incorporating nutrient cycles into these coupled models can change not only the magnitude of the feedback, but whether it is positive or negative as well. Current observations and experimentation are not comprehensive enough to constrain this source of modeling uncertainty. IPCC

Fig. 4.1. Coupling of the Carbon and Nitrogen Cycles.



(2007) models included essentially independent responses of photosynthesis and ecosystem respiration to warming. However, introducing nutrient cycling (nitrogen as a first step) into models changes system dynamics by coupling photosynthesis to heterotrophic respiration through mineralization of nitrogen from soil organic matter (see Fig. 4.1. Coupling of the Carbon and Nitrogen Cycles, this page). Central to coupling these cycles in models is also coupling plant and microbial communities in ecosystems through microbial decomposition of detritus and biological nitrogen fixation.

Plant-Soil Interactions (Soil Physicochemistry)

Plants display remarkable plasticity in many processes contributing to GPP, NPP, and the role of terrestrial ecosystems in carbon cycling and biosequestration. This plasticity is driven by various molecular mechanisms and phenotypic traits. Such traits (see discussion in the section, Plant-Trait Variation, NPP, and Carbon Biosequestration, p. 29) are determined by a multitude of genome-by-environment interactions (phenotypic trait = $G \times E$), underscoring environmental and edaphic factors' tremendous potential to modify plant characteristics. Having varying physical and chemical components at local to global scales, soils, in particular, can influence plant traits and thus productivity significantly (see Fig. 4.2. Global Soil Regions, p. 66, and Table 4.1. Soil Types and Their Properties, p. 67).

Furthermore, these chemical and physical factors control processes related to recalcitrance and the fate of carbon in soils around the globe. For example, rhizodeposition, root mortality, and chemical composition of roots are all likely affected by plant-soil interactions. Understanding how soil physicochemistry affects plants is thus critical for assessing carbon biosequestration and the significance of these interactions in regulating GPP and NPP.

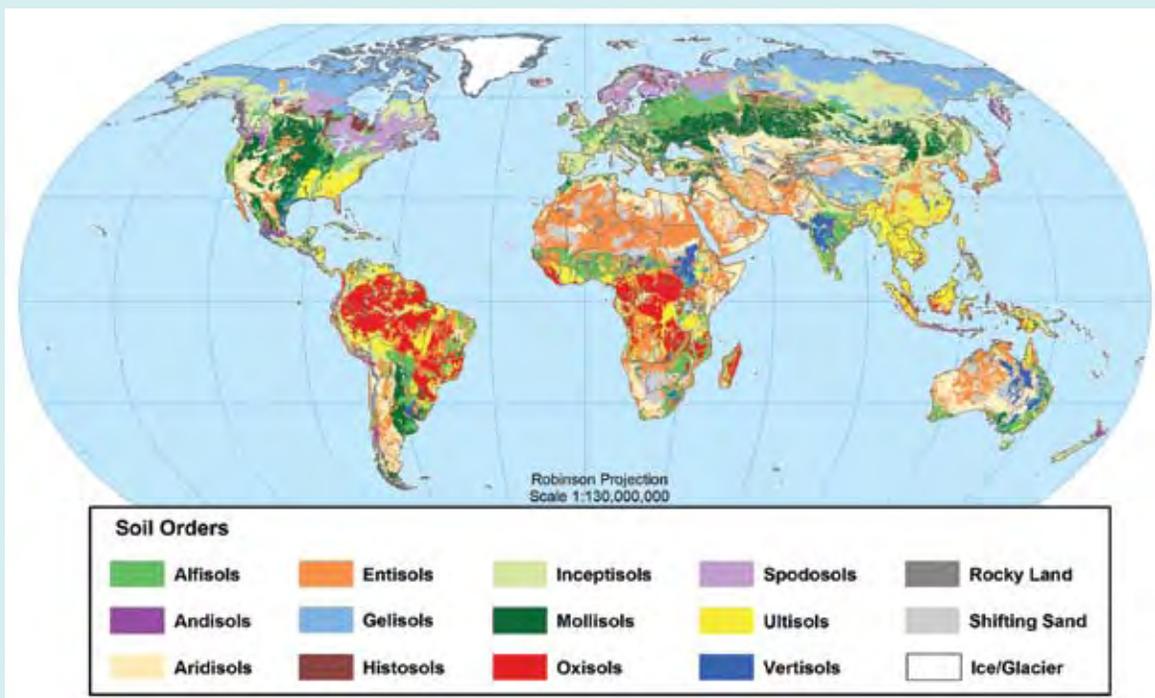


Fig. 4.2. Global Soil Regions. [Source: U.S. Department of Agriculture, Natural Resources Conservation Service. <http://soils.usda.gov/use/worldsoils/>]

Plant Responses to Multiple Nutrient Limitations in Soils

Little is known about the fundamental mechanisms by which limitations in nutrients—especially those other than nitrogen and phosphorus—affect processes related to plant primary production. Advancing our understanding of these mechanisms requires research and accompanying mechanistic models investigating plant response to multiple stress factors, including availabilities of 16 essential nutrients and exposure to 6 common ion toxicities (see Box 4.1, Metal Roles in Photochemistry: Global Limitations to Photosynthetic Carbon Assimilation, p. 68).

Mineral Stress Limitations on Primary Productivity

Mineral stress is prevalent in native soils. In fact, many natural and agricultural ecosystems are characterized by ion toxicities and suboptimal availability of mineral nutrients. Much terrestrial vegetation, for example, is supported by highly weathered tropical soils with low availability of phosphorus, calcium, and magnesium as well as aluminum and manganese toxicities. On the other hand, dense plant communities in more fertile soils face intense competition for nutrients. Predominant global soils having various toxicities and nutrient constraints represent complexes of mineral stresses. As major limitations to global primary productivity, such stresses warrant vigorous research to quantify the extent and severity of their effects on terrestrial ecosystems (see Table 4.1, p. 67).

Scientific understanding of plant response to stress from individual minerals is limited. However, only just beginning to be revealed is how plants and their associated microbial symbionts respond to concurrent multiple stresses—and in the context of climate change. Today's conceptual models of plant response to multiple resource limitations are inadequate for accurately representing the combination of mineral

Table 4.1. Soil Types and Their Properties*

Soil Name	Characteristics	Environmental Properties
Alfisols	Slightly acidic fertile surface layer over mineral- and clay-rich subsoil	Semiarid to humid climates; forests and mixed vegetation
Andisols	Rich mineral content with little orderly crystalline structure; volcanic origins	Cool, moderate- to high-precipitation environments near volcanoes
Aridisols	Dry with low organic material content; possible high salt content or mineral formation	Deserts and arid regions; hot and cold; low-population rangelands
Entisols	Recently formed, lack of soil horizon development; possible high rates of erosion or deposition	Diverse environments: dunes, steep slopes, river valleys, exposed bedrock, floodplains
Gelisols	Permafrost near surface; accumulated organic matter; reduced microbial activity	Freezing temperatures at high latitudes or elevations
Histosols	Anoxic and mostly saturated; accumulated organic matter	Wetlands at all latitudes
Inceptisols	Moderate soil horizon development; diverse characteristics	Various semiarid to humid climates; crops, timberlands, mountains, rangelands
Mollisols	Dark-colored surface horizon; high base and organic matter content	Grasslands, prairies, steppes; moderate to marked seasonal moisture loss
Oxisols	Highly weathered; rich in low-activity minerals such as metal oxides	Subtropical and tropical forests, crops; slash and burn often applied
Spodosols	Acidic with sandy texture; high organic matter, iron and aluminum oxides in subsoil	Cool humid or temperate; mostly coniferous forests
Ultisols	Acidic and highly weathered; reddish to orange, clay-rich subsoil with minerals	Humid climates; forests
Vertisols	Expanding clay when moist and shrinking when dry to form cracks	Subhumid and semiarid; long dry seasons; rangelands, crops

*Information from U.S. Department of Agriculture, Natural Resources Conservation Service. http://soils.usda.gov/technical/soil_orders/ and The Missouri Cooperative Soil Survey. <http://www.soilsurvey.org/tutorial/page4.asp>.

stresses typical of most terrestrial ecosystems. To create robust models, greater insight is needed into how mineral stresses structure communities, underpin competition and fitness, and are integrated through adaptive and maladaptive responses at organismal and cellular scales to determine carbon assimilation and use.

Mineral Stress Interactions with Climate Change

Mineral stresses likely have important, complex, yet poorly understood interactions with global climate change variables. Each of these stresses has complex yet distinct interactions with global change variables, complicating predictions of how plants in these environments will respond to possible future climates. Though sources of great uncertainty, important interactions between mineral stress and climate variables include the effects of transpiration on root acquisition of soluble nutrients, particularly calcium and silicon; impacts of altered root architecture on the acquisition of immobile nutrients, especially phosphorus; consequences of altered root-exudate production on aluminum toxicity and transition-metal acquisition; and the interaction of photochemical processes with transition-metal availability.

Metal Roles in Photochemistry: Global Limitations to Photosynthetic Carbon Assimilation

Metals are required for biological redox reactions and thus are integral to light harvesting in chloroplast membranes. For example, metals contribute to this process through the magnesium ion in the center of chlorophyll through hydrolysis in Photosystem II (PSII). Metals also are needed as cofactors for antioxidant enzyme systems that detoxify reactive oxygen species (ROS) generated in chloroplasts by the combination of excited electrons and molecular oxygen. Particularly important in ROS detoxification are iron in catalase and ascorbate peroxidase and the various transition metals in superoxide dismutase (SOD) isoforms. Imbalances in metal supply to chloroplasts generate dysfunctions in electron transport during photosynthesis that lead to increased ROS formation and persistence, damaging photosynthetic tissues in what is known as photo-oxidative stress. This damage is exacerbated by environmental conditions such as temperature extremes, intense visible or ultraviolet (uv) radiation, and ozone. Metal imbalance is common in many terrestrial ecosystems. For example, in acidic soils supporting most terrestrial vegetation (e.g., those in tropical and subtropical forests as well as many humid temperate systems), low calcium and magnesium availabilities as well as aluminum, manganese, and iron toxicities are widespread. In alkaline soils typical of drier systems, iron, manganese, copper, and zinc availabilities often are suboptimal. These various limitations and toxicities may disturb leaf photochemistry, thereby limiting photosynthetic carbon assimilation.

Substantial genetic variation controlling tolerance of metal imbalances exists within and among species. However, with the exception of aluminum tolerance in crops and New England tree response to calcium, the genetic controls for coping with these imbalances are little researched and poorly understood. Genetic differences among plants are manifest in variations in metal acquisition, metabolism, and compartmentation as well as in tolerance to photo-oxidative stress via altered antioxidant metabolism. Such variations provide interesting opportunities for new research into the genetic influences on plant response to stress. For example, a research area deserving further investigation is the role of manganese toxicity as a key constraint to light utilization, photosynthetic carbon assimilation, and species composition in the eastern forests of North America where acid deposition, logging, and soil erosion are increasing metal imbalances. Molecular aspects of this research might relate to antioxidant systems, ion channels, or rhizosphere exudates that account for genetic variation in tolerance. Understanding this variation likely will become increasingly important in light of future climate change that could include more temperature extremes and altered ozone and radiation intensity.

Key Research Question

1. **How do transition-metal toxicities and deficiencies interact with plant photochemistry to limit carbon assimilation, especially in the presence of other photo-oxidative stresses such as ozone, uv and visible light, and temperature extremes?**

Example-specific hypotheses to be tested using the example of manganese toxicity include:

- a. **Genetic taxa with greater antioxidant capacity are more tolerant of manganese toxicity. (This may be useful as a molecular marker of manganese tolerance across species or for selection and transgenesis of manganese-tolerant plants.)**
- b. **High temperature, ozone, and uv radiation are synergistic with manganese toxicity in susceptible taxa. (Synergy of light intensity and manganese toxicity already has been demonstrated.)**
- c. **Genetic taxa with greater uptake capacity for magnesium, zinc, copper, and iron are more tolerant of manganese toxicity.**

Photochemical Processes

Toxic levels of reactive oxygen species (ROS) can form in chloroplasts under certain conditions. Important to both the generation and detoxification of these species are metals involved in the light reactions of photosynthesis (e.g., manganese, magnesium, iron, and copper) and in antioxidant enzyme systems [e.g., zinc, copper, and manganese in superoxide dismutase (SOD) and iron in catalase]. Several global change variables, including ozone, high light, ultraviolet (uv) radiation, temperature extremes, and drought, can increase ROS formation. Thus plants suffering suboptimal availability of magnesium and transition metals because of high soil pH, base imbalances, and aluminum and manganese toxicity may be more sensitive to global change than healthy plants (see Box 4.1, p. 68).

Genomic Approaches to Understanding Plant-Soil Interactions and Edaphic Stress

Plants have evolved multiple mechanisms to maintain nutritional homeostasis in diverse edaphic environments. Some of these responses can be genetically simple, with only a single or a few gene products contributing to a phenotype. For example, nutrient transporters or enzymes such as phosphatases are phenotypic traits determined by the action of a single gene product. However, most traits facilitating tolerance to edaphic stress are genetically complex, including products of biosynthetic pathways (e.g., root exudates), morphological changes (e.g., shifts in root architecture), and symbiotic associations (e.g., mycorrhizae and nitrogen fixation).

Advancing genomic-level understanding of plant responses to edaphic stress would be valuable in two general ways. First, such insight would provide basic knowledge of plant-environment interactions, leading to discovery of tolerance mechanisms for edaphic stresses. For example, antioxidant gene arrays could be designed to test whether interactions between metal toxicity and uv light induce oxidative stress. Where robust and consistent plant-environment relationships are identified, regulation of selected genes could then be used to monitor environmental change over time relative to an established baseline. This monitoring approach could employ sentinel organisms amenable to genetic analysis or, as molecular methods advance, could focus on genetic signals conserved across species. A second benefit of progress in genomics-based understanding of plant tolerance will be the increased availability and use of more genetic targets of known function to enhance crop response to edaphic stress.

The sequencing and functional analysis of plant genomes are major scientific efforts aimed at understanding plant genetic complexity. Expression profiling using microarrays is a powerful tool for examining how genes respond to experimental variables, although distinguishing primary and secondary responses from such data is exceedingly difficult. Microarrays also are being used to examine genomic responses to mineral deficiencies and toxicities deduced from the up-regulated expression of genes with known function. Significant progress in understanding genetic response requires using functional genomic tools in future studies to focus on linking known edaphic stress factors—either alone or in combination with climate change variables—to resulting phenotypic traits. Resulting genomic information can be used to identify molecular markers linked to genes of interest for crop and natural-ecosystem adaptation to mineral stress.

Key Research Questions

1. How do abiotic edaphic factors influence the nature, development, productivity, and response of ecosystems to climate variables?
2. How do plant-microbe associations facilitate adaptation to local climate and edaphic conditions to balance the carbon, nutrient, and water cycles?

Analyzing plant responses to multiple and interacting edaphic variables at the organismal and physiological levels has proven to be extremely complicated. Attempts to understand these complex systems at the levels of gene metabolic and gene regulatory networks underlying these higher-order plant responses add yet another dimension to the challenge. Moreover, phenotypic responses are the sum of multiple and interacting gene products passing through several levels of regulation (e.g., transcription, translation, and post-translation modifications); even within the same plant, genetic responses vary widely from one tissue type to another.

At the genetic level, quantitative traits are of paramount importance, and substantial genotypic variation is apparent. Thus diversity among haplotypes (a segment of DNA containing closely linked gene variations inherited as a unit) could be more important than the population mean for a species' ability to tolerate stress. While this argues for using genomic rather than physiological approaches, in which typically only a few genotypes are observed, it also poses a challenge considering the immense functional complexity of numerous haplotypes of a multitude of interacting genes. At the cellular level, researchers are discovering a complex system of interacting signaling responses associated with environmental stress. At the tissue, organ, and organismal levels, greater insight into photosynthesis and water relations has been gained, but much remains unknown concerning, in particular, roots and the rhizosphere, where many key processes appear to occur.

Finally, scientific understanding of mineral metabolism, apart from nitrogen, is substantially less than that of photosynthesis and leaf responses to light, temperature, and CO₂. Genomic and molecular biology investigations must be coordinated with classical ecosystem research to determine to what extent stress interactions and responses may be generalized across species and ecosystems. Such research also will reveal whether the functional importance of genetic changes applies only to a unique organismal and ecological context.