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Volume Three

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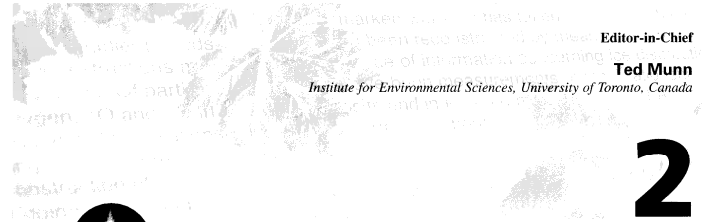
Volume Four

Responding to global environmental change

Volume Five

Social and economic dimensions of global environmental change

Encyclopedia of Global Environmental Change



Editor-in-Chief

Ted Munn

Institute for Environmental Sciences, University of Toronto, Canada



e g e c

**The Earth system:
biological and ecological dimensions of global environmental change**

Volume Editors

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Stanford University, Stanford, USA

and

Josep G Canadell

GCTE/IGBP, CSIRO Sustainable Ecosystems, Australia



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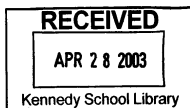
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Terrestrial and Freshwater Ecosystems: Impacts of Global Change

BRUCE A HUNGATE AND JANE C MARKS

Northern Arizona University, Flagstaff, AZ, USA

Humans are altering the environment in many ways. While local environmental damage (landfills, oil spills, urban smog) is still prevalent, we now also realize that human activities are altering the Earth System as a whole, that our environmental crisis has become truly global. For example:

- Our growing use of automobiles, air conditioners, jet planes, and other amenities of modern industrial society has caused the composition and chemistry of the atmosphere to change.
- The increasing concentration of heat-trapping gases in the atmosphere (carbon dioxide (CO₂), nitrous oxide (N₂O), methane (CH₄) and others) is already increasing global temperatures, and the rate of change is likely to increase in the future.
- The increasing concentration of ozone-depleting gases (chlorofluorocarbons and nitrous oxide) in the stratosphere is weakening the ozone shield, allowing more and more damaging ultraviolet (UV-B) radiation to reach the Earth's surface.
- Growing food demand, greater use of irrigation, fertilizer and pesticides in agriculture, and the expansion of food production into previously uncultivated lands has increased the inputs of sediments, nutrients, and other pollutants into watersheds and the inputs of greenhouse and chemically active gases into the atmosphere.
- Of all the available freshwater on the Earth, humans now appropriate 23% for industrial, municipal, and agricultural uses, thereby altering natural hydrologic regimes and threatening freshwater ecosystems and the services those ecosystems provide.
- The spread of exotic species into terrestrial and freshwater ecosystems poses a growing threat to biodiversity conservation and to the services that ecosystems provide to humans.

Such changes in the Earth's environment are collectively referred to as global change. The nature and magnitude of global change has raised the question, how does global change affect the ecosystems upon which we depend? Ecosystems supply humanity's food, clean water, and clean air and also are important sources of recreation and aesthetic value. Global changes threaten the ability of ecosystems to continue to provide these services. Our understanding of these threats will provide a foundation for determining the influence of our activities on the Earth System; and for future decisions we must change our lifestyles and use of resources. This article provides an overview of the effects of global change on terrestrial and freshwater ecosystems in coming decades. Many such effects have been postulated or observed in manipulative experiments, but one of the more serious ecological concerns is the possibility of marked shifts in plant species composition due to differing responses of individual members of ecosystems to major changes in carbon dioxide concentrations, temperature, nitrogen emissions and other elements of the global environment.

ECOSYSTEM PROCESSES AND EFFECTS OF GLOBAL CHANGE: AN OVERVIEW

Considering the effects of global change from an ecosystem perspective warrants an overview of the terms and concepts of ecosystem ecology. An ecosystem comprises

all the organisms in an area and the physical environment with which they interact. *Ecosystem structure* describes the spatial distribution of organisms, elements, and materials in ecosystems, including, for example, above- and below-ground biomass of plant species, soil carbon and nutrient mass, leaf area index in terrestrial ecosystems, or total

biomass of macrophytes and epiphytes and nutrient stores in freshwater ecosystems. By contrast, *ecosystem processes* are the fluxes of materials and energy among ecosystem components and between ecosystems and the surrounding environment. For example, rates of photosynthesis and respiration, predation and herbivory, and nutrient turnover and loss are all ecosystem processes (see **Ecosystem Structure and Function**, Volume 2).

Ecosystems are not static; rather, disturbances, such as fires or insect outbreaks in forests, or scouring floods in rivers, occur in all ecosystems. *Disturbance* in ecology is defined as the catastrophic removal of biomass that creates space available for recolonization. Succession following disturbance and involves species progressively recolonizing the disturbed area and being excluded from it (primarily through competition for resources by other species), resulting in a pattern of species replacements and changing species composition through time. Global change can alter the frequency and intensity of disturbances (increasing flood frequency and intensity, for example), but few global changes (excepting perhaps some land-use changes) constitute ecological disturbances in the strict sense. In ecological parlance, global changes are anthropogenic perturbations to ecosystems, human-caused changes in the conditions (temperature, pH, etc.) or resources (nutrients, carbon dioxide, light, water, etc.) that influence ecosystem structure and processes.

Central to ecosystem ecology is the cycling of biologically essential elements, beginning with carbon. Carbon enters the biosphere through the process of photosynthesis (primary production) by plants and algae, converting atmospheric carbon dioxide to organic forms of carbon. This organic carbon resides in ecosystem compartments, both living (living tissue of plants, animals, and microorganisms) and non-living (as detritus and humus in terrestrial ecosystems and as dissolved or particulate organic matter in aquatic ecosystems). Within ecosystems, carbon is transferred between compartments through trophic interactions (herbivory, predation), senescence, and death. Through respiration by plants, animals, and particularly decomposer microorganisms, organic carbon is returned to the atmosphere as carbon dioxide. *Net primary production* (NPP) is the amount of carbon dioxide taken up by plants through photosynthesis minus respiration by plants, whereas *net ecosystem production* (NEP) is the amount of carbon dioxide taken up by plants through photosynthesis minus the respiration of all organisms in the ecosystem. Ecosystem carbon balance is equivalent to NEP, except when disturbances cause carbon losses by means other than decomposition (fire, for example, which converts organic carbon to carbon dioxide through the process of combustion). As described in detail below, global change can affect all of these important ecosystem processes; carbon gain through photosynthesis, loss through decomposition, and rates of

transfers among ecosystem compartments. Changes in these process rates can alter components of ecosystem structure that depend directly on carbon cycling, such as stores of carbon in organic matter and vegetation.

Transfers of carbon dioxide between ecosystems and the atmosphere through photosynthesis and respiration are large enough, for example, that during the Northern Hemisphere summer, the seasonal peak in photosynthesis reduces the temperate zone carbon dioxide concentration by several parts per million, whereas when respiration becomes a relatively larger flux in the winter, atmospheric carbon dioxide concentration increases. These oscillations are mirrored (but more damped because of the smaller land masses) in the Southern Hemisphere, and are much less apparent in tropical regions, where the activities of photosynthesis and respiration are more synchronous throughout the year. These seasonal changes in atmospheric carbon dioxide concentration reflect the breathing of the biosphere and underscore the importance of biological control over atmospheric carbon dioxide concentrations. Because carbon dioxide is a greenhouse gas (increasing in the atmosphere due to fossil fuel burning, cement manufacture, and deforestation, and the major cause of global warming) there has been tremendous interest in understanding how global changes will alter carbon cycling in terrestrial ecosystems and, ultimately, the balance between carbon dioxide release to the atmosphere versus carbon dioxide uptake and storage in ecosystems. Such changes could strongly influence the trajectory of rising carbon dioxide and associated global warming over the next few centuries.

In terrestrial plants, carbon uptake through photosynthesis is coupled to *transpiration*, the evaporation of water from the internal surfaces of leaves to the atmosphere and the major flux in the water cycle directly mediated by biota. Together, transpiration and the evaporation of water from exposed surfaces constitute *evapotranspiration*, the total flux of water from ecosystems to the atmosphere (see also **PET (Potential Evapotranspiration)**, Volume 2). Water not lost through evapotranspiration can be stored in soil and vegetation or lost as surface runoff to aquatic ecosystems and as percolation to groundwater. Precipitation returns water in the atmosphere to the Earth's surface, completing the water cycle. Climate change can alter water cycling through climate-driven shifts in the amount and distribution of precipitation, subsequently affecting ecosystem processes sensitive to water availability, including evapotranspiration, thereby altering surface runoff and percolation. Global changes such as rising carbon dioxide, warming, nitrogen deposition, and increased UV-B radiation can also alter water cycling through their effects on plant transpiration.

Evapotranspiration is regulated by the difference in water vapor pressure between the atmosphere and air above ecosystems and the resistance to water vapor flux between

the ecosystem and the atmosphere. Evapotranspiration occurs when solar radiation striking an ecosystem drives water from liquid to gas, an energy conversion (called latent heat flux, λE) that dissipates solar energy that might otherwise have increased the surface temperature of the ecosystem. Convection (the upward transfer of heat, also called sensible heat flux, C) is also an important way that heat is transferred from ecosystems to the atmosphere. The transfer can also occur in the other direction, if the surface of the ecosystem is colder than the surrounding atmosphere, as is often the case at night. The sum of sensible and latent heat fluxes, along with conduction into the ground (also termed storage, G), balances the net input of radiation (R_n) into terrestrial ecosystems: $R_n = C + \lambda E + G$. Structural and physiological features of ecosystems, including leaf area, stomatal conductance, canopy roughness, and rooting depth, strongly influence the relative importance of these terms, and thus the way in which energy is partitioned in ecosystems. By altering ecosystem structure or physiology through changes in growth or species composition, global change can alter energy partitioning. Such changes have important implications for ecosystem processes sensitive to temperature and moisture availability, as well as for regional climate patterns.

Global change can also alter the cycling of mineral nutrients (such as nitrogen, phosphorus, and others) upon which plant and ecosystem production depend. Indeed, global changes such as nitrogen deposition involve direct changes in the amounts of nutrients added to ecosystems from the atmosphere. Nutrients are made available to primary producers by decomposer organisms in the processes of mineralization (release of mineral nutrients through decomposition of dead organic matter); weathering (release of nutrients from parent material through chemical and physical reactions); biological fixation in the case of nitrogen (conversion of atmospheric N_2 to NH_3 , a form usable by plants and microorganisms), and atmospheric deposition (in which readily available forms of nutrients enter ecosystems through rainfall or dry deposition). Nutrients are removed from this available pool through microbial immobilization or uptake by plants, chemical sorption reactions (formation of covalent bonds with mineral particles or precipitation with other minerals into unavailable forms), leaching and biotic and abiotic transformations to gaseous forms.

Gaseous fluxes of nitrogen from ecosystems to the atmosphere represent not only losses of an essential nutrient but also inputs to the atmosphere of reactive (nitric oxide and nitrogen dioxide) and radiatively active (nitrous oxide) trace gases. Fluxes of other trace gases, such as methane (CH_4), carbon monoxide (CO), and carbonyl sulfide (COS), while relatively small compared to carbon dioxide fluxes in photosynthesis and respiration, for example, are critical in the chemistry and radiation balance of the atmosphere. Through

changes in trace gas fluxes, the responses of ecosystems to global change create feedbacks that can further amplify or mitigate global changes in the atmosphere.

ASSESSING THE EFFECTS OF GLOBAL CHANGE

The scientific community has taken three complementary approaches to assessing the effects of global change on ecosystems: experiments, observations, and models. (1) *Manipulative experiments* compare a set of test plots experiencing current normal conditions to another set where one aspect of the environment is modified to simulate a particular global change factor (e.g., global warming, nitrogen deposition, or the presence of an invading species). The advantage of the experimental approach is that it explicitly identifies the global changes that cause particular ecosystem responses. More complicated experiments involve manipulating two or more global change factors singly and in combination, allowing investigators to test whether knowledge of responses to each factor alone can predict their combined effects, or whether factors interact in surprising ways. Experiments examining full combinations of many factors can address very complex interactions and are extremely valuable in assessing effects of global change. However, such experiments are large and expensive and thus few and far between. Global change experiments are typically long term (1–10 years); they measure responses of ecosystems to a step change, an instantaneous doubling, for example, of atmospheric carbon dioxide concentrations (from 365 to 730 μmol^{-1}). This approach is necessary to be able to discern changes in ecosystem properties against a background of high natural variation. Actual global changes, however, occur more gradually and over longer periods of time (e.g., $3 \mu\text{mol}^{-1} \text{year}^{-1}$, perhaps not reaching 730 μmol^{-1} until the year 2100). Results from experiments must therefore be interpreted within a framework that accounts for these differences in time scale.

(2) *Observations* allow the impact of actual global changes on ecosystems to be observed. This may be carried out by reconstructing global changes that occurred in the past and examining evidence of their effects on ecosystems, through comparing ecosystems that occur along natural climatic or other gradients in space, or by monitoring ecosystems in the present as they are increasingly affected by global change. For example, the concentration and isotopic composition of gases trapped in air bubbles within ice near the poles provide records of atmospheric composition and temperature, and shows how the accumulation of greenhouse gases in the atmosphere in the past has coincided with increases in global temperatures. By combining such records of past temperatures and atmospheric composition with analyses of pollen in lake sediments, one can understand how plant species shifted in distribution

when, or shortly after, the climate changed. This approach has the considerable advantage of revealing how species composition in an area (an important component of ecosystem structure) has changed over hundreds to thousands of years in response to changes in climate. The gradient approach essentially substitutes space for time using, for example, a transect across the landscape along which mean annual temperature changes systematically, such that observations comparing the colder and warmer sites serve as an analog for ecosystem responses to global warming. Another approach is to monitor current ecosystems directly, to observe their responses to year-to-year variations in climate and to ongoing global changes. This type of approach is central to efforts to document global changes *per se* (e.g., rising global temperatures, atmospheric carbon dioxide concentrations, sea levels, rates of nitrogen and acid deposition and glacial retreat, etc.) and is also becoming more important for understanding ecosystem responses to these changes. One of the challenges associated with this observational approach is that, because many kinds of global change are occurring simultaneously, it is difficult to discern which particular change is causing a particular ecosystem response (though this can be overcome with the gradient approach, for example, if only one variable changes along the gradient). Another challenge is that while current rates of global change are unprecedented, they are slow for even a long-term (10–50 years) campaign of observations. This makes it difficult to distinguish the signal caused by global change from the noise associated with natural variation in ecosystem processes in space and time.

(3) *Mathematical models* are an essential component of efforts to understand the effects of global change on ecosystems. Models provide access to responses of ecosystems to global change that neither manipulative experiments nor observations allow. For example, a manipulative experiment to explore the interactive effects of warming, altered precipitation, increased nitrogen deposition, increased atmospheric carbon dioxide concentrations, and enhanced UV-B radiation on forest ecosystems in the field would be prohibitively expensive, yet models that incorporate information from single-factor manipulative experiments can explore such interactive effects. Similarly, models allow the study of responses over temporal and spatial scales that are impractical with manipulative experiments or observations. Ecosystem models incorporate state-of-the-art scientific understanding of controls over ecosystem processes, and as such, their simulations and predictions are limited by this understanding. Nevertheless, models are one of the more powerful tools available to global change scientists for taking complex and variable processes and translating them to larger spatial and temporal scales.

Efforts to understand ecosystem responses to global change through experiments, observations, or models shed

light on the problem, but limitations are associated with each approach. For this reason, where possible, integrated assessments that take advantage of all three approaches are more powerful than any one approach alone.

ELEVATED ATMOSPHERIC CARBON DIOXIDE

The concentration of CO_2 in the atmosphere has increased by 30% since the mid-1800s and is perhaps the most certain component of atmospheric change. Direct measurements of atmospheric carbon dioxide over the past 50 years show this increase clearly (Keeling and Whorf, 2000), and measurements of the concentrations of carbon dioxide in gas bubbles trapped in ice provide a robust record of carbon dioxide concentrations for the past 420,000 years (Petit *et al.*, 1999). Carbon dioxide is the entry point for carbon into the biosphere because it is the substrate for primary production by plants, algae, and some bacteria. Rising carbon dioxide thus represents an increase in resource availability for primary producers, a change with effects that can cascade through ecosystems.

Effects on Terrestrial Ecosystems (see also Plant Growth at Elevated CO_2 , Volume 2)

Plants usually respond to elevated carbon dioxide by increasing photosynthesis and growth, decreasing transpiration, and by altering patterns of carbon and nutrient use and allocation, patterns that are most clear in short-term laboratory or greenhouse studies. While these physiological changes often lead to responses at the community and ecosystem levels, feedbacks and environmental constraints strongly shape these responses. Indeed, one of the more important conclusions from the past several decades of research on this topic is that, while the short-term physiological responses of plants to elevated carbon dioxide can sometimes guide our predictions of larger-scale responses, in many cases they are misleading about the magnitude (and even the direction) of these responses at the ecosystem scale. For example, in the field, the photosynthetic response to elevated carbon dioxide and the fate of assimilated carbon are sensitive to temperature, water stress, and nutrient availability, and thus the growth responses of plants to elevated carbon dioxide ranges from none to modest to quite large.

Plants grown in elevated carbon dioxide usually have lower nitrogen concentrations, both because the requirement for rubisco and other enzymes (major nitrogen-containing compounds) is reduced in elevated carbon dioxide, and because elevated carbon dioxide often causes accumulation of starch and sugars, diluting the amount of nitrogen they contain. Similarly, plants collected over the past several hundred years and stored in herbaria show a consistent decline in nitrogen concentrations in concert with increasing

atmospheric carbon dioxide since the industrial revolution. Reduced nitrogen concentration in litter usually slows the rate at which that litter decomposes and releases nitrogen in plant-available forms, so the commonly observed reduction in green-leaf nitrogen concentration was expected to reduce decomposition rate and nitrogen availability. This effect is only sometimes observed: litter produced by plants grown in elevated carbon dioxide does not usually decompose more slowly, contrary to previous predictions based on the physiological responses of plants (Norby and Cotrufo, 1998).

However, there are other mechanisms through which elevated carbon dioxide can affect nutrient cycling. By increasing root growth and the flow of labile organic compounds into the soil, elevated carbon dioxide can stimulate microbial nutrient immobilization, thereby exacerbating plant nutrient deficiencies, and decreasing nutrient availability for other microbial processes as well, such as nitrification. By increasing plant growth, elevated carbon dioxide can increase nutrient uptake and nutrient accumulation in biomass and soils, eventually increasing nutrient pools in unavailable, organic forms. On the other hand, elevated carbon dioxide can also increase nutrient availability to plants, both through changes in internal cycling rates and through changes in nutrient inputs and losses. For example, by stimulating microbial turnover, elevated carbon dioxide can increase soil nitrogen mineralization. Elevated carbon dioxide also often favors the growth of plants in association with nitrogen-fixing bacteria, as long as other factors (such as low phosphorus availability) do not limit nitrogen fixation. Nitrogen inputs to ecosystems can therefore increase with enhanced growth of nitrogen-fixing species. Elevated carbon dioxide has been shown to increase plant exudation of phosphatase, enzymes that convert soil phosphorus into a plant available form.

Carbon uptake through photosynthesis ultimately feeds all trophic levels in ecosystems, so it is not surprising that changes in carbon uptake in response to elevated carbon dioxide can alter trophic interactions. For example, the reduction in leaf nitrogen concentrations alters herbivore behavior and survival. Insect herbivores growing on leaves produced by plants grown at high carbon dioxide concentration levels usually consume more leaf tissue, but have slower rates of growth and development because of the lower quality of that tissue. Changes in the performance of herbivores can also alter trophic interactions that amplify the detrimental effects of elevated carbon dioxide on insect herbivores. In one case, elevated carbon dioxide caused a two-fold increase in mortality of insect herbivores because of reduced food quality, but also caused a four-fold increase in mortality because these herbivores are more vulnerable to attack by predators and parasitoids (Stiling *et al.*, 1999). In this case, the indirect effect mediated by predators substantially amplified the direct effect

of reduced forage quality on herbivore mortality. Again, simple extrapolations of responses in the laboratory may differ substantially from responses observed in the field. Elevated carbon dioxide can also affect ruminant herbivores, and studies in tall grass prairie predict that forage produced in elevated carbon dioxide will cause a reduction in ruminant growth rate (Owensby *et al.*, 1996). In contrast to insects, ruminant tissue consumption declines with forage quality, so wild ruminants will likely suffer reduced growth and reproduction as carbon dioxide continues to rise (Owensby, 1996), with possible implications for higher trophic levels. Increased carbon inputs below ground can also alter soil food webs, changing the activity and abundances of bacteria and fungi, their protozoan and nematode predators, and mites and other organisms occupying higher trophic levels as well. Such changes in soil trophic structure could influence nutrient cycling and decomposition rates.

As carbon dioxide diffuses from the atmosphere into leaves through stomata, water vapor diffuses from the leaves to the atmosphere, the process of transpiration. Increasing the concentration of atmospheric carbon dioxide strengthens the air-to-leaf concentration gradient of carbon dioxide, thereby increasing carbon dioxide supply to leaves, allowing stomata to close to save water, and resulting in lower rates of transpiration. While herbaceous species and tree seedlings often show strong reductions in stomatal conductance and transpiration in response to elevated carbon dioxide, responses in mature trees are more variable, and in some species there is no response to elevated carbon dioxide. Differences among species is at least partly related to growth form, as the stomatal response of coniferous trees to elevated carbon dioxide tends to be smaller than the response of herbs, and deciduous trees tend to be intermediate (Saxe *et al.*, 1998). The reduction in plant transpiration in response to elevated carbon dioxide can cause a reduction in evapotranspiration (the flux of water from the ecosystem to the atmosphere). Reduced evapotranspiration (latent heat flux) is usually compensated by increased canopy temperature and thus increased sensible heat flux. The ecosystem level consequences of reduced evapotranspiration include increased soil water storage, leaching, and/or runoff, and these changes, in turn, can alter a number of ecosystem processes sensitive to soil moisture, including plant growth, nutrient mineralization and trace gas fluxes.

Elevated carbon dioxide usually increases photosynthesis at the canopy scale in both managed (e.g., a wheat field) and unmanaged (e.g., an alpine grassland) ecosystems, leading to the suggestion that terrestrial ecosystems could sequester some of the carbon dioxide being added to the atmosphere from fossil fuel burning, cement manufacturing and deforestation. However, observing carbon accumulation in ecosystem components in quantities

that match carbon uptake inferred by measurements of canopy photosynthesis has so far proven elusive. To date, there have been no publications in which these independent measures of carbon uptake can be balanced from a field experiment, but convergence of these approaches will provide greater confidence in our understanding of carbon dioxide effects on carbon uptake. Carbon uptake in elevated carbon dioxide experiments also illustrates the problem of scaling step-change experiments to the more gradual reality of global change. In response to a sudden increase in atmospheric carbon dioxide concentration, plant production can increase immediately, increasing NEP or carbon uptake. However, because the rate of carbon dioxide release from soil through decomposition increases as the amount of carbon in soil increases, carbon dioxide release through decomposition will eventually catch up, though with a lag period as the carbon is transferred from plants to soil pools of varying turnover times. All ecosystem carbon cycling models agree on this point. The ability of ecosystems to hold carbon over long periods requires large carbon reservoirs in pools that cycle slowly, such as wood and soil. Greater distribution to these pools in response to elevated carbon dioxide, and thus increased carbon storage, will be apparent in carbon dioxide doubling experiments if there is a relatively long lag period between increased carbon dioxide uptake and carbon dioxide release. If this lag period is shorter than expected, the extra carbon taken up in elevated carbon dioxide environments is being preferentially distributed to carbon pools with rapid turnover that quickly return carbon dioxide to the atmosphere. Few experiments have tried to determine the patterns of carbon distribution between carbon pools for short vs. long turnover times, but several have shown that elevated carbon dioxide tends to favor carbon distribution to rapidly cycling pools, limiting potential increases in carbon storage.

Effects on Freshwater Ecosystems

Freshwater ecosystems are frequently supersaturated with carbon dioxide, making direct effects of increasing atmospheric carbon dioxide on these ecosystems unlikely. However, freshwater ecosystems receive water, the dissolved nutrients and organic matter contained therein, and dead leaves, stems, and other plant parts from terrestrial ecosystems. Because terrestrial and aquatic ecosystems are linked in this way, effects of elevated carbon dioxide on production, water use, and nutrient cycling in terrestrial systems can have important consequences for freshwater ecosystems. For example, reductions in transpiration due to elevated carbon dioxide could increase streamflow and water yield from watersheds (though increases in evapotranspiration in response to warming will more than compensate for this in many cases). Increased plant production in response

to elevated carbon dioxide could translate into greater inputs of plant litter into aquatic ecosystems, and changes in the chemical composition of that litter (e.g., concentrations of phenolic and other secondary compounds) could affect decomposition rates in aquatic ecosystems. Changes in the balance of microbial mineralization and immobilization of nitrogen in soils, along with changes in nitrification and plant uptake, could alter the export of inorganic nitrogen to streams and lakes. Such effects are only beginning to be documented in global change research.

EUTROPHICATION AND ACIDIFICATION (see also Eutrophication, Volume 2; Nitrogen Cycle, Volume 2; Phosphorus Cycle, Volume 2)

Human production of fertilizer nitrogen, cultivation of nitrogen-fixing crops, livestock husbandry, and fossil fuel burning have dramatically increased the inputs of fixed nitrogen (available for plant and microbial uptake) to terrestrial and aquatic ecosystems. These changes in land-use in watersheds have greatly increased inputs of phosphorus into aquatic ecosystems. These inputs constitute the phenomenon of eutrophication, a global change that alters the balance of nutrients that support ecosystem productivity. Atmospheric deposition of nitric and sulfuric acid is responsible for the acidification of terrestrial and freshwater ecosystems, often with deleterious effects.

Effects on Terrestrial Ecosystems

Current global inputs of anthropogenic nitrogen to terrestrial ecosystems match or exceed, natural pre-industrial inputs through biological nitrogen fixation and lightning. Human-caused changes in the global nitrogen cycle have profound and widespread effects on ecosystems (Vitousek *et al.*, 1997). Of all the resources that plants require, nitrogen most commonly limits plant growth and NPP in terrestrial ecosystems. For this reason, increased inputs of nitrogen often stimulate NPP and carbon uptake by forest, grassland, and tundra ecosystems, as shown by a number of experiments. By stimulating NEP in these ecosystems, nitrogen deposition has likely contributed to the uptake of carbon dioxide derived from fossil fuels.

In ecosystems where nitrogen availability is naturally low, nitrogen deposition can favor the establishment, growth, and reproduction of introduced species adapted to high nitrogen levels over native species adapted to low nitrogen, causing marked shifts in plant transpiration composition, plant species often leading to biodiversity losses and local extinctions. For example, in the Netherlands, where rates of nitrogen deposition are the highest in the world, nitrogen deposition has converted

species-rich heathlands into species-poor grasslands, a complete change in the structure of the ecosystem (Aerts and Berendse, 1988). Nitrogen deposition can also affect an ecosystem's ability to withstand and recover from perturbations. For example, perennial grasslands in the US subjected to nitrogen addition had higher productivity in favorable years, but were affected more severely and recovered more slowly from drought than control plots without nitrogen addition (Tilman *et al.*, 1994).

Continuous additions of nitrogen will eventually cause some other resource to become more limiting to photosynthesis and growth, so that these processes will no longer show a positive response to nitrogen additions. At this point, the ecosystem is considered to be nitrogen-saturated. Nitrogen added to a nitrogen-saturated ecosystem is often matched by an equivalent amount of nitrogen leaving the system through leaching and gaseous pathways. In many other cases, though, not all nitrogen added through deposition (experimental or otherwise) to nitrogen-saturated ecosystems can be accounted for in increased biomass production, leaching, or trace gas losses. It appears that a substantial amount remains in the soil, immobilized either biotically or abiotically, and unavailable for plant or microbial uptake. This suggests that not all the nitrogen added through deposition will support extra plant growth, but it also suggests that some soils can absorb more ammonium than previously thought.

Not only will the productivity of nitrogen-saturated ecosystems no longer increase with nitrogen additions, but nitrogen saturation can also actually lead to system decline through several mechanisms. First, acid deposition, either as nitric acid (HNO₃) or sulfuric acid (H₂SO₄), directly leads to soil acidification. Even when nitrogen deposition occurs as ammonium (NH₄⁺), the NH₄⁺ is often quickly converted to nitrate (NO₃⁻) via nitrification, a process releasing hydrogen ions and thus increasing soil acidity. Aluminum is biologically available at low pH, and can build up to toxic levels when soils are acidified. Second, nitrogen-saturated ecosystems lose added nitrogen through nitrate leaching and in gaseous forms through microbial transformations (nitrification and denitrification). Leaching losses of nitrate can substantially reduce soil fertility, because positively charged basic cations (potassium, calcium, and magnesium) are carried away with the negatively charged nitrate as it leaches. Gaseous losses of nitrogen through microbial processes occur as dinitrogen gas (N₂), which is inert in the atmosphere, but also as nitric oxide (NO), nitrogen dioxide (NO₂), and nitrous oxide (N₂O). Nitric oxide and nitrogen dioxide are reactive trace gases that contribute to photochemical smog and acid rain. Nitrous oxide, by contrast, is a very stable radiatively active greenhouse gas, 200 times more effective at trapping heat than carbon dioxide. Through increased nitrous oxide efflux from soils (a major source of nitrous oxide to

the atmosphere), ecosystems effectively translate one facet of global change, nitrogen deposition, to another, global warming.

Effects on Freshwater Ecosystems

Runoff from urban and agricultural areas transports nutrients (nitrogen and phosphorus) from terrestrial to aquatic ecosystems, leading to *eutrophication*, by many accounts the most widespread and severe type of global change affecting lakes (Lodge, 2001) (*see Eutrophication*, Volume 2). Phosphorus is the nutrient most commonly limiting to NPP in freshwaters, particularly in temperate latitudes, so added phosphorus generally increases algal productivity. Nitrogen is often the next most limiting nutrient, so freshwater ecosystems already affected by increased phosphorus inputs are likely to also be very responsive to increased inputs of nitrogen from the atmosphere. Eutrophication, in addition to increasing NPP, can also alter algal species composition, favoring those species better able to take advantage of the higher nutrient levels.

Increased algal productivity in response to moderate eutrophication can stimulate productivity of higher trophic levels in aquatic ecosystems, but more often eutrophication favors particular species of algae that may be inedible and/or toxic, causing noxious *algal blooms*; extremely dense mats of algae that decrease light penetration and alter thermal structure. When these algae die, the input of organic matter fuels decomposition and depletes oxygen concentrations, killing fish and other organisms (Carpenter *et al.*, 1998).

Deposition of sulfuric and nitric acid to lakes causes acidification, particularly in lakes which are low in alkalinity (the chemical capacity to buffer changes in pH in response to acid inputs), such as those in the northeastern part of North America and in Scandinavia (Schindler, 1998). Most organisms are sensitive to changes in pH, so the effects of acidification on species distributions and abundances are often quite direct. For example, crustaceans and mollusks are particularly sensitive to the direct effects of acidification, because it reduces the availability of the calcium and carbonates required to build their exoskeletons. Acidification can reduce algal productivity and alter species composition, indirectly affecting higher trophic levels. Acidification of lakes also increases water clarity and reduces concentrations of dissolved organic carbon (DOC) (Schindler, 1998). Finally, the effects of acidification can be indirect as well. In lakes of the Laurentian Shield, with low-buffering capacity, for example, the increase in hydrogen ion concentration leads to mobilization from the sediments of toxic heavy metals such as mercury. These subsequently accumulate in fish, which then fail to reproduce.

GLOBAL WARMING

Effects on Terrestrial Ecosystems

Global warming will likely alter many ecosystem processes in terrestrial ecosystems, including increasing decomposition, increasing evapotranspiration, altering NPP, and shifting species composition in ways that can substantially modulate the initial direct responses. Potential effects of global warming on terrestrial ecosystems have been investigated in the field by experimentally warming the air around vegetation (using greenhouses or infrared heaters), by warming the soil using heat tape, or by studying natural gradients in temperature across the landscape.

As with elevated carbon dioxide and nitrogen deposition, understanding how global warming will alter the carbon balance of terrestrial ecosystems is a major focus of global change research. In laboratory incubations, microbial respiration responds exponentially to increasing temperature, and litter decomposition in the field shows a similar trend. By contrast, photosynthesis has a saturating relationship with temperature for most plant species, with optimal temperatures close to those typical of the environment in which the plant is found. Warming will likely increase rates of litter decomposition, stimulating a release of carbon dioxide from ecosystems to the atmosphere, and across 30 different ecosystem warming experiments, the flux of carbon dioxide from soil to the atmosphere increased (Rustad *et al.*, 2000). But photosynthesis can increase as well: in tundra, warming did not change the carbon balance; the effects of increased decomposition were counterbalanced by increased photosynthesis (Hobbie and Chapin, 1998). Increased carbon dioxide efflux from arctic and alpine tundra in response to recent warming trends and to experimental manipulations appears to be due to warmer temperatures causing soil drying. In high latitudes, drying of waterlogged peat soils could release large amounts of carbon dioxide to the atmosphere. Increased decomposition should also increase nutrient mineralization and nutrient availability to plants, an effect that could ultimately enhance carbon uptake, as plants sequester nutrients in higher carbon-to-nutrient ratios than those in soils. However, this effect does not seem to have strongly influenced results from warming experiments to date.

Global circulation models predict that warming will be most pronounced in upper latitudes. In tundra ecosystems, the indirect effects of increased temperature may more strongly determine the responses of tundra ecosystems to climate change than the direct effects. For example, the temperature controls depth of thaw, soil nutrient availability, and growing season length, all of which exert greater control over tundra plant growth than does temperature directly (Chapin, 1983). Growth responses to temperature vary among tundra species, and increased abundance of shrubs and decreases in mosses and other non-vascular species in

response to experimental warming (and that observed over the last decade, a period when mean annual temperatures have also increased) suggest that shifts in species composition in tundra ecosystems will be one of the critical drivers of changes in ecosystem processes in response to global warming (Chapin and Shaver, 1996). In lower latitudes, too, warming could cause shifts in species composition that alter ecosystem processes. For example, warming could favor biological invasions by weedy C4 grasses in hotter climates, because of their higher temperature optimum for photosynthesis and their greater drought tolerance compared to C3 and C4 plants (Dukes and Mooney, 1999; *see C₃ and C₄ Photosynthesis*, Volume 2).

Experimental warming usually results in drying as well, and often the latter is the more critical driver of changes in ecosystem structure and processes, particularly in arid and semi-arid ecosystems. One of the challenges in this research area is to disentangle direct and indirect effects. Climate models predict that changes in precipitation caused by global warming will be regionally specific, increasing in some areas and decreasing in others, and thus are not always well-represented by the drying that occurs with experimental warming.

Effects on Freshwater Ecosystems

Global warming will almost certainly alter the hydrologic cycle, directly altering the amount and distribution of water on the terrestrial surface and thus the extent of freshwater ecosystems. While warming will increase evapotranspiration globally, changes in precipitation will vary from region to region. Thus, regionally-specific climate change scenarios are needed to predict where increases and decreases in the extent of freshwaters are likely to occur. For example, warming is predicted to reduce runoff and lake water levels in the Great Lakes region (Mortsch and Quinn, 1996), but to increase runoff and possibly flood intensity in the Amazon Basin (Neilson and Marks, 1994). Overall, however, evaporation will increase more than precipitation, reducing the extent of freshwater ecosystems globally. In arid and semi-arid regions, as well as in high latitudes, some freshwater habitats could disappear (Schindler *et al.*, 1996).

The paleo record indicates that changes in global temperatures and regional precipitation patterns have strongly affected flood magnitude and frequency (Ely *et al.*, 1993). Global warming is thus likely to alter the *disturbance regime*, an important regulator of ecosystem structure and function in many streams and rivers. Increased temperatures will also likely increase the extent and duration of thermal stratification in lakes (*see also Disturbance*, Volume 2).

Changes in the distribution and abundance of aquatic organisms will likely accompany global warming, leading to increases in the ranges of organisms where corridors between habitats allow migration; and to extinctions where

corridors to habitats with appropriate thermal regimes do not exist. Direct effects of warming on organisms are likely to be greatest in high latitudes, where warming is predicted to be greater and where native biota are more sensitive to increased temperatures. For example, model simulations suggest that warming will increase food requirements of lake trout in arctic lakes, but long-term observations over a recent warming period revealed no changes in primary production to fuel this greater food demand, thus threatening the top trophic level in arctic lakes (McDonald *et al.*, 1996). Such changes are likely to have strong impacts on ecosystem processes, because top predators often are major determinants of nutrient cycling, water clarity, and net ecosystem productivity in freshwater ecosystems (Schindler *et al.*, 1996).

Changes in runoff and in terrestrial ecosystem processes caused by warming could alter the amounts and forms of nutrient and plant litter inputs to freshwaters, affecting production, decomposition, and the food webs these processes fuel in streams, rivers, and lakes. As mentioned above, warming can reduce DOC supply to lakes and streams from terrestrial ecosystems (Schindler *et al.*, 1996), but could cause the opposite effect in northern latitudes, where melting permafrost and increased decomposition of old peat (e.g., Oechel *et al.*, 1993) could enhance DOC transport from tundra to arctic lakes and streams.

ENHANCED UV-B RADIATION

As a direct consequence of human production of ozone-depleting chemicals, such as chlorofluorocarbons and nitrous oxide (N₂O), concentrations of ozone (O₃) in the stratosphere (the ozone shield) are currently at their lowest recorded values. Lower levels of stratospheric ozone allows greater penetration of UV-B radiation (280–315 nm) to the Earth's surface where it can damage deoxyribonucleic acid (DNA), proteins, lipids, and other UV-B absorbing compounds in living tissues, alter tissue composition and growth, and cause photolysis of non-living organic matter, all of which have important consequences for terrestrial and freshwater ecosystems.

Effects on Terrestrial Ecosystems

In terrestrial ecosystems, inhibition of photosynthesis by UV-B reduces leaf area and stem growth in many species, potentially reducing NPP. Water stress can mitigate these effects, because water-stressed plants often produce higher concentrations of UV-B absorbing compounds. The effects of enhanced UV-B radiation on plant growth can also interact with elevated carbon dioxide concentrations.

Some plants tolerate UV-B more than others, such that shifts in species composition are a likely consequence of enhanced UV-B radiation. In some cases, these changes

can buffer reductions in NPP, if UV-B induced reductions in plant growth lead to the acquisition and growth of more tolerant species (Caldwell *et al.*, 1998).

Organisms vary in their natural abilities to cope with enhanced UV-B radiation. Some, particularly microbes and insects in early stages of development (early instars), are not well protected against UV-B, having little ability to adjust concentrations of UV-B absorbing compounds, and are therefore quite sensitive to UV-B damage. This susceptibility is exacerbated when the natural habitats of those organisms, such as the surfaces of leaves, soils or biological crusts in the desert, involve direct exposure to UV-B radiation. Plants often alter their chemical composition in response to enhanced UV-B radiation, producing greater amounts of phenolic compounds (tannins, lignins, and other refractory materials) or antioxidants (e.g., flavonoids) that can absorb some of the damaging radiation and thereby protect the plant. Plants can also alter morphological properties, such as leaf thickness, which offers greater resistance to UV-B damage.

Changes in plant chemistry and morphology can in turn alter rates of herbivory and decomposition processes that are very sensitive to leaf thickness and chemical composition. UV-B can also increase litter decomposition directly, through photolysis, when solar radiation breaks chemical bonds. In these ways, enhanced UV-B radiation can alter the cycling of carbon and nutrients in ecosystems, but the direction of these effects is difficult to predict. For example, in some cases, litter produced under enhanced UV-B decomposes more slowly because the UV-B treatment alters the chemical composition of litter. But in other cases, UV-B increases decomposition, possibly because of the direct effects of photolysis. Enhanced UV-B radiation can also affect nitrogen cycling by inhibiting biological nitrogen fixation.

Effects on Freshwater Ecosystems

In contrast to terrestrial ecosystems, where UV-B radiation is attenuated only by the atmosphere, UV-B penetration into freshwater ecosystems declines with water depth and with increasing concentrations of DOC, particularly DOC high in UV-B absorbing chemical structures (phenols, humins, and other aromatics). Much of this DOC is of terrestrial origin—byproducts of the decomposition of terrestrial plant litter. The water-soluble portion of this material can be transported into freshwater ecosystems and there serve an important role in absorbing UV-B radiation. Through photolysis, UV-B radiation breaks down this DOC into smaller organic compounds that are usually more susceptible to microbial decomposition. Increased photolysis and decomposition in response to enhanced UV-B allow greater penetration of UV-B into the water column and further DOC photolysis, creating a positive feedback cycle. Freshwaters

naturally vary in DOC concentrations, so the penetration of UV-B into the water column, and the potential for detrimental effects of enhanced UV-B on ecosystems, also vary among habitats.

Increased processing of DOC and altered rates of microbial metabolism can in turn affect nutrient cycling and primary production in freshwater ecosystems. For example, photolysis can release nitrogen compounds (ammonium and amino acids) that stimulate microbial activity and turnover, and thus the rates of nitrogen cycling. Many of the enzymes involved in nitrogen transformations, however, such as nitrogenase (nitrogen fixation) and glutamine synthetase (ammonium uptake) are inhibited by UV-B radiation, such that the overall effects of UV-B on rates of nitrogen cycling are difficult to predict. Changes in algal production in response to enhanced UV-B radiation, likewise, will reflect the direct negative impacts of enhanced UV-B on photosynthesis and growth, as well as any indirect effects on the availability of nutrients limiting to production. UV-B also affects zooplankton, both directly, by damaging tissues, and indirectly, by affecting the amount and quality of primary production upon which these grazers depend.

For both phytoplankton and zooplankton, enhanced UV-B often results in a shift in community composition, because species differ in sensitivity to UV-B damage. In some ecosystems, entire trophic levels vary in sensitivity to UV-B damage. For example, algal production increased in response to enhanced UV-B in a stream habitat (Häder *et al.*, 1998). Although the algae in isolation were negatively affected by UV-B, the dominant grazers (larval chironomids) were even more sensitive, and largely eliminated by the UV-B treatment, releasing the algae from grazing pressure. These observations highlight the danger in predicting ecosystem responses to global change by examining any part of the system in isolation.

Because of the central role of DOC in attenuating UV-B penetration into aquatic ecosystems, any global change factor that influences DOC concentrations will interact with enhanced UV-B radiation. A number of such interactions have been identified and observed through both experiments and observations in the Experimental Lakes Area in Canada. Here, observations over two decades, along with a number of long-term experiments showed that increases in lake temperatures and lake acidification occurred in concert with reductions in DOC concentrations, allowing greater penetration of UV-B into the water column. The reductions in DOC were caused by reduced inputs of DOC through runoff (particularly during drought years), increased microbial processing of DOC, decreased primary productivity, and greater lake stratification, which reduced the transfer of UV-B absorbing compounds from deeper water into the upper layers.

LAND-USE CHANGE

More and more land is used for livestock grazing, agriculture, forestry, and settlement, and these changes in land use and land cover are projected to increase. Land-use change is currently the most severe global change affecting terrestrial ecosystems, and it is likely to remain the dominant one in tropical regions over the next several decades.

Land-use change alters both ecosystem structure and ecosystem processes. For example, land-clearing removes vegetation, and such clearing is often accomplished by burning, so the carbon stored in the plants is thereby released to the atmosphere as carbon dioxide. Similarly, tillage in agriculture disrupts soil associations that stabilize soil organic matter, stimulating decomposition and releasing carbon dioxide to the atmosphere. Largely due to these processes, past land-use changes have already substantially increased carbon losses from ecosystems to the atmosphere, accounting for nearly half of the observed increase in atmospheric carbon dioxide concentrations between 1750 and the present (Houghton, 1994).

Greater rates of nutrient losses often occur after land clearing or conversion to agriculture, due to both higher microbial activity and lower plant nutrient uptake. When land is cleared for agriculture, higher rates of nutrient losses are usually compensated by application of fertilizers and lime, allowing such ecosystems to maintain equal or even higher rates of NPP (particularly where agricultural fields are also irrigated). Nutrient cycling in agricultural ecosystems is thus fundamentally different from that in the natural terrestrial ecosystems they replaced. Typical rates of fertilizer application in intensive agriculture far exceed natural rates of nutrient importation (e.g., through natural nitrogen fixation), and losses of fertilizer also greatly exceed natural rates of nutrient loss (e.g., through leaching and gaseous pathways). For these reasons, managed ecosystems (particularly agricultural ones) are said to save *open nutrient cycles*, where inputs to and losses from the ecosystem are the dominant transfers. By contrast, nutrient cycles in natural terrestrial ecosystems are *closed*, in the sense that inputs and losses are far smaller than exchanges within ecosystems (e.g., mineralization of organic to inorganic forms). Nutrient losses from agricultural ecosystems contribute to a number of global changes: 1) losses of gaseous nitrous oxide contribute to global warming, as nitrous oxide has nearly 200 times more warming potential than carbon dioxide, molecule for molecule; 2) losses of gaseous nitric oxide and nitrogen dioxide contribute to photochemical smog and acidic nitrogen deposition; and 3) leaching losses of nutrients (e.g., NO₃⁻ and PO₄³⁻) from agriculture contribute substantially to eutrophication of aquatic ecosystems.

Other changes in ecosystem structure and processes accompany land-use changes. For example, converting a native forest to a pasture reduces canopy height and rooting depth, thereby altering water and energy exchange with

the atmosphere (reducing latent heat flux and increasing sensible heat flux, for example). Over large enough scales, such changes in energy partitioning can change regional and potentially even global climate (Shukla *et al.*, 1990). Land-use changes also alter connections between habitats, converting, for example, a large homogenous forest stand to a patchwork mosaic of managed ecosystems and remnant forest. Such changes in ecosystem structure can threaten animal species that require large ranges and can facilitate species invasions.

Rates of soil erosion driven by both wind and water are also typically much higher as a result of land-use change. Losses of soil are not easily replaced, so increasing soil erosion caused by land-use change remains a serious global problem, affecting the long-term fertility of agricultural ecosystems, as well as the integrity of ecosystems downstream and downwind.

HYDROLOGIC ALTERATIONS

Direct human changes in the global water cycle (through impoundments (dams), surface water diversions, and groundwater extraction) have dramatically altered freshwater ecosystems. Globally, nearly a million dams interrupt natural river flows, appropriating more than half of the available global runoff for human use (Postel *et al.*, 1996).

Water impoundment through dam building converts upstream rivers to reservoirs, and dampens the natural variation in flow regimes downstream, both of which constitute fundamental changes in the structure of river ecosystems. Upstream, converting a river to a reservoir introduces thermal stratification, drastically reduces water flow, and changes the light environment, leading to a complete change in the structure of the producer community with associated changes in food web structure. Additionally, buried terrestrial vegetation and soil organic matter decomposes in reservoirs, releasing carbon dioxide to the atmosphere, and also methane (CH₄), a greenhouse gas produced when decomposition proceeds in the absence of oxygen (St. Louis *et al.*, 2000). Downstream, dams largely eliminate natural flooding regimes, seasonal fluctuations in water temperature, and sediment loads, often endangering or causing the extinction of the native species that were adapted to such fundamental characteristics of the river, including species important to fisheries (Postel, 1998). Such changes in water flow regimes can detrimentally affect important habitat, including floodplains, riparian zones, wetlands, and estuaries, all of which are particularly sensitive to changes in water flow. Reduced water flow can also impair water quality, as pollutants become less and less dilute. The dam itself also constitutes a formidable barrier to species migration, leading to genetic isolation and potentially to extinction (Pringle, 1997). Nutrient delivery (particularly of silicates) is interrupted by impoundments, with detrimental

effects on marine algae and associated food webs. For a larger-scale example, see Humborg *et al.* (1997), who reported on the impacts of a recently constructed dam on the Danube River between Hungary and Slovakia, on ecosystem structure in the Black Sea.

INVASIVE SPECIES

Through intentional introductions and through accidental hitchhikers in our global transportation systems, humans have dramatically redistributed the species on earth. Some of these species introductions are relatively benign, but other invasive species detrimentally affect native species and ecosystems. Invasive species are first transported to a new geographic area, they survive and persist in this new area, and eventually they thrive, reproducing successfully, spreading in areal extent, and outcompeting native species, not infrequently driving some native species to extinction. The species that make up an ecosystem strongly influence that ecosystem's structure and processes, so the changes in species composition caused by invasions can have ecosystem-scale effects. In general, invasive species can alter ecosystem processes by changing trophic structure, resource availability, or disturbance frequency or intensity (Vitousek, 1989).

Nile perch, introduced into Africa's Lake Victoria, severely altered the trophic structure of the lake by literally eating the species beneath it on the food chain, leading to the elimination of many of the lake's 500 endemic species of cichlid fishes. Other invasions alter the nutrient or water cycles, such as the nitrogen-fixing tree, *Myrica faya*, which invaded the Hawaiian islands and caused a 90-fold increase in nitrogen inputs. A number of tree species that have invaded the South African Cape Province fynbos ecosystem whose high rates of water extraction have strongly reduced, and in some cases even eliminated, river flow. Australian paperbark has invaded south Florida, covering nearly 200,000 acres, and promotes more intense fires, altering the natural disturbance cycle. Many other invasive species have similar effects, particularly grasses which can cause a buildup of dead flammable material, leading to fires that favor the expansion of the invading grass (D'Antonio and Vitousek, 1992). Given their global extent and strong effects on ecosystems, biological invasions are a critical component of human caused global change (Mack *et al.*, 2000).

See also: *Biological Invasions*, Volume 2; *Plant Dispersal and Migration*, Volume 2.

INTEGRATION

Most global change research addresses how one particular type of global change (rising carbon dioxide, nitrogen deposition, or invasion of a particular species) will affect

one (or a few) characteristics of a particular ecosystem. Yet, in reality, global changes are occurring together and they affect many (if not all) aspects of ecosystems, not just those of a particular researcher's specialty. It is thus critical to attempt more integrative assessments of responses to global change. For example, warming or nitrogen deposition can favor the success of an invasive plant that alters the fire cycle. Similarly, global warming or rising carbon dioxide can alter the export of DOC from terrestrial to freshwater ecosystems, fundamentally changing how these aquatic systems respond to enhanced UV-B radiation. Land-use changes can alter albedo and sensible heat flux, causing changes in climate. Elevated carbon dioxide, through a number of indirect pathways, can affect microbial processes in soil that produce other trace gases, including the greenhouse gases nitrous oxide and methane and the reactive gases nitric oxide and nitrogen dioxide. Global changes can thus interact in surprising ways: the response of a given ecosystem to one component of global change can affect its response to another, a neighboring ecosystem's responses, and even the extent of other global changes. Understanding these interactions is a formidable challenge.

CONCLUSIONS

Human activities are clearly changing Earth's terrestrial and freshwater ecosystems, changing both their structure and the processes they perform. No longer can one find pristine habitats free from human influence (Vitousek *et al.*, 1997): rising atmospheric carbon dioxide concentration is a global phenomenon, and pollutants are evident everywhere that researchers have looked, in the high arctic and in remote tropical islands, a clear example of humanity's global shadow.

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Acidification, Lakes and Soils see Nitrogen Cycle (Volume 2)

Angiosperm/Gymnosperm

Higher plants, called *Spermatophytes* (seed bearing) are vascular plants characterized by the production of seeds. More primitive non-vascular plants such as fungi and mosses and vascular plants such as ferns reproduce by spores. Spermatophytes are divided into two classes: the *gymnosperms* (bearing naked seeds) and *angiosperms* (bearing enclosed seeds). The gymnosperms (*Pinophyta*), the more primitive group, are woody or perennial plants that are commonly evergreen; that is, they retain leaves (frequently needles) for two to several years so that the plant is leafy throughout the year. The angiosperms (*Magnoliophyta*) constitute the largest and most diverse group of plants, which has invaded and adapted to some of the world's most inhospitable habitats. Their habit of growth ranges from annual to perennial; many of the woody perennials are deciduous, losing all their leaves in winter or drought seasons.

Gymnosperms normally produce gametes in the axes of nodes clustered densely on a shoot with shortened internodes called a *strobilus* or *cone*. The gametes may be protected by bracts or scales, but the seeds (the female gametes or ovules) are not enclosed by the structure that bears them, nor in an ovary, and are therefore said to be naked even though they may be protected by the bracts of a cone. Angiosperms produce seeds that are normally born in structures called fruits, and the ovule is enclosed in an ovary; angiosperm seeds are therefore longer lasting after they have been shed. This evolutionary development appears to be largely responsible for the rapid and effective spread of angiosperms throughout the accessible habitats in the world. However, among woody plants, particularly trees, gymnosperms may better survive periods of extreme drought and cold (the most important consequence of intense cold is drought caused by freezing of available water) because of modifications that control water loss from their leaves.

Allometric

Allometric is a term most commonly used with reference to growth, usually of plants. *Allometric growth* describes a situation in which the rate of growth of one part of an organism is in a constant ratio with the rate of growth of another part. It may be expressed as the *allometric coefficient* (k), which is the ratio of relative growth rates: $k = (d \ln x/dt)/(d \ln y/dt)$. When $k = 1$ the growth of the two parts is said to be *isometric*; when $k > 1$ or $k < 1$ the situations are described as positive or negative allometry, respectively.

Allometric growth of plant organs or parts strongly suggests that correlative effects control one or the other part of the plant, or both. The nature of such effects is often unclear, but is usually internal (e.g., genetic or hormonal). However, environmental effects may affect or disrupt allometric growth. For example, under ideal growing conditions the root/shoot ratio of some plants is essentially constant over considerable periods of the plant's life. This is almost certainly an internal correlative effect that maintains the balance between root and shoot. Environmental factors that may disrupt this allometry include excess soil humidity, which tends to slow root growth, or reduced soil water content, which tends to stimulate it. An understanding of allometric growth may assist agricultural efforts to achieve maximum yield consistent with optimal growth of, for example, fruit or root crops.

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