Effects of Global Changes on Above- and Belowground Biodiversity in Terrestrial Ecosystems: Implications for Ecosystem Functioning

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Above- and belowground organisms are critical for the biogeochemical cycles that sustain the Earth, but there is limited knowledge on the extent to which the biota below ground and the functions they perform are dependent on the biota above ground, and vice versa. Hooper et al. (2000) provide a synthesis of the patterns and mechanisms linking above- and belowground biodiversity. The close relationship between vegetation change and soil carbon (C) dynamics (Jobbágy and Jackson 2000) suggests that any disruption of the coupling between plants and soil organisms as a result of global change may have deleterious consequences for functioning of terrestrial ecosystems. However, most of the scientific evidence supporting this hypothesis comes from correlative approaches. The complexity of the numerous interactions between various environmental

WE IDENTIFY THE BASIC TYPES OF INTERACTION BETWEEN VASCULAR PLANTS AND SOIL BIOTA; DESCRIBE THE SENSITIVITY OF EACH TYPE TO CHANGES IN SPECIES COMPOSITION; AND, WITHIN THIS FRAMEWORK, EVALUATE THE POTENTIAL CONSEQUENCES OF GLOBAL CHANGE DRIVERS ON ECOSYSTEM PROCESSES

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factors controlling both plants and soil organisms has hampered formal tests of causation. Moreover, the agents of global change (such as changes in land use, climate, and atmospheric inputs), acting either individually or in combination, may lead to nonlinear changes in above- and belowground relationships, with effects varying in distribution and intensity around the globe (Heal 1997). This places serious constraints on predictions regarding the effects of global change on above- and belowground interactions. Interpretation of future global change scenarios and the consequences to ecosystems globally depends on understanding the primary factors affecting above- and belowground interactions (Ingram and Gregory 1996).

In this article, we synthesize the current knowledge of the potential effects of global change on terrestrial ecosystem processes via changes in above- and belowground biodiversity. We identify the types of interactions between vascular plants and soil biota, describe how each interaction type is sensitive to changes in species composition, apply this framework to evaluate the potential consequences of different global change drivers on ecosystem processes via changes in species composition, and suggest scientific priorities.

Interaction types involving plants and soil organisms

Plants and soil biota influence each other as engineers, as providers of nutritional resources, and as direct interactors (Table 1; see also Hooper et al. 2000). The engineers are organisms that modulate the flux of resources to other organisms through physical modification of the environment, through their physical presence, or through catalytic activities (Jones et al. 1994, Anderson 1995). Providers of nutritional resources modify the availability of mineral nutrients or organic molecules to other organisms by their metabolic activities. Direct interactors are organisms that affect each other in mutualistic or antagonistic relationships.

The three interaction types are not mutually exclusive. Plant transfer of nutrients to symbionts, and vice versa, is a direct interaction occurring through the provision of nutritional resources. Mycorrhizal fungi increase the transfer of phosphorus (P) and other nutrients to plants and may also affect soil aggregation (Douglas 1995). The leaf litter produced within a stand controls the availability of energy and nutrients to the soil biota and also affects the protection of soil from erosion (Swift and Anderson 1993). Similarly, engineers such as earthworms influence not only soil structure, but are linked as well to plant nutrient availability through changes in soil microflora (Edwards and Bohlen 1996).

Biological traits and the system's tolerance to change

Chapin et al. (1996) suggested that a system's tolerance for change is related to the degree of continuity of biological traits among species. Changes in species with traits that are broadly distributed across the community should be minimally recognized at the ecosystem level because more resistant species may compensate for such changes (Schimel 1995). By contrast, changes affecting species with unique traits cannot be compensated for by other species. Invasion or extinction of these species is predicted to be maximized at the level of an ecosystem process if the availability of soil resources to plants is altered, food web interactions are fundamentally changed, or the normal disturbance regime of the ecosystem is strongly modified (Vitousek 1990).

This concept serves as a starting point to examine how linked interactions between above- and belowground biota and accompanying ecosystem processes may be sensitive to environmental change. Invasion or extinction of free-living and mutualistic soil biota with unique traits may alter ecosystem processes by modifying the availability of soil resources to plants (Figure 1). Changes in the composition of the vegetation involving species with unique traits may have large-scale impacts by affecting the utilization of resources by free-living and mutualistic soil biota. This occurs through alterations in the amount, quality and distribution of litter and exudates produced. Finally, changes in engineering activities or in antagonistic effects may alter ecosystem processes by modifying the disturbance regime experienced by those organisms on one side of the above- and belowground interface.

Availability of soil resources to plants

Soil organisms appear to have a high level of functional redundancy (Andrén et al. 1995). This suggests that traits involving the transfer of nutrients through the soil food web are broadly distributed across the belowground community. Changes in the taxonomic diversity of the soil food web would thus have little impact on ecosystem processes because there would be little change in the availability of soil resources to plants (Wolters 1998). Functions carried out by species with unique traits, however, are an exception. The most notable example is provided by the few genera of bacteria performing certain transformations within the nitrogen (N) cycle (e.g., nitrification, denitrification; Swift et al. 1998, Hooper 2000). Changes in the species composition of this component of the belowground community may significantly alter the N transfer to plants. Similarly, the ability to degrade recalcitrant organic substrates such as lignin or humic substances is confined to a few microbial genera (Wolters 2000). A greater buildup of litter on the soil surface due to the loss of organisms able to break down recalcitrant materials may drastically alter the availability of nutrients to plants (Schimel and Gulledge 1998).

Mutualistic soil organisms may display traits related to the supply of soil resources to plants that are unique to a few species or conditions. Alternately, other mutualistic soil organisms are broadly distributed among the community and/or expressed under a variety of environmental conditions (Chanaway et al. 1991). For example, associations between plants and N-fixers depend on a few microbial taxa, whereas
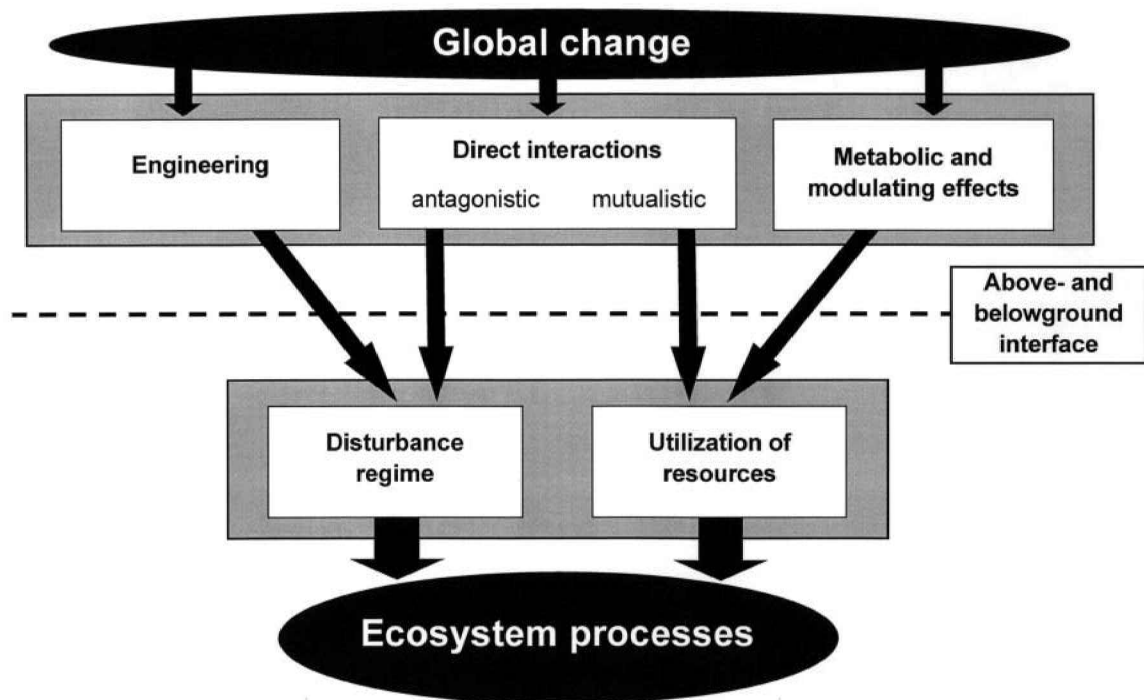
Figure 1: Pathways of global change–induced alterations in ecosystem functioning via changes in above- and belowground interactions.

mycorrhizal fungi have high diversity (Swift et al. 1998). Changes in species composition are thus expected to alter the availability of soil resources to plants in the former but not the latter case. This conclusion contradicts the recent finding that the coexistence of plants can be determined by the diversity of arbuscular mycorrhizae (Van der Heijden et al. 1998). A probable resolution of this paradox is that there may be different effects upon plant performance depending on the number of fungal genotypes that are present; that is, there is no fungal species specificity but there may be functional specificity (Read 1998).

Resource utilization by free-living and mutualistic soil biota

Litter diversity per se does not seem to have a predictable effect on decomposition processes (Wardle et al. 1997).

Table 1. Types of interaction between plants and soil biota and examples of variables affecting these interactions.

Type of interaction	Variables	
	Plants	**Soil organisms**
Engineering		
Soil structure	Root penetration, water extraction, root exudation	Formation of micro-aggregates by mucilages around hyphae and bacterial colonies, enmeshment of microaggregates by fungi
Microclimate and hydrological fluxes	Vegetation cover, root architecture	Organomineral feces of macroinvertebrates, mounds of termites, burrowing mammals
Provision of nutritional resources	Amount of litter and exudates, quality of litter and exudates, distribution of litter and exudates	Food web interactions, modulating effects on microbiota, transformations within nutrient cycles
Direct interactions		
Mutualistic	Carbon allocation to mycorrhizae	Transfer of nutrients to host plants
Antagonistic	Antibiotic substances, morphological barriers, secondary compounds	Pathogenic effects, rhizovory

Moderate changes in species richness of the vegetation are thus unlikely to have an ecologically important role unless the modifications are associated with distinct changes in litter quality. Strong effects on ecosystem processes are most likely when plant functional types differing in ecological strategies invade or become extinct, because ecological strategies of plants and physicochemical properties of the litter produced are closely related (Hobbie 1992). For example, unpalatable litter produced by the stress-tolerant species *Vaccinium myrtillus* during maturation of spruce forests shifted the humus type from mull to mor by eliminating soil-dwelling organisms from the surface layer (Bernier et al. 1993). The impoverishment of the decomposer community reduced the N availability to the vegetation, which in turn increased the competitive ability of stress-tolerant plant species adapted to acidic infertile soils (Van Breemen and Finzi 1998).

Most plant symbionts have a broad to intermediate host range, especially in natural vegetation (Douglas 1995). Variations in the composition of plant communities thus should rarely affect the utilization of resources by symbiotic soil biota. This conclusion is not valid, however, when plant symbionts do not function equally with all hosts, or on occasions when associations are host specific. For example, coniferous forests in North America and eucalyptus forests in Australia support large guilds of highly specific ectomycorrhizal fungi (Molina et al. 1992). When such close associations exist, traits controlling consumption rates of nutritional resources by mutualistic soil organisms are unique to a few plant species. Shifts in composition, resulting in deletions or additions of new plant species, of the vegetation may have significant effects on ecosystem processes including changes in P or in C:N ratios.

Disturbance regime to plants

Changes in soil structure may dramatically affect plants by altering the physical properties that control plant growth, i.e., resistance to root penetration, water availability, and aeration (Angers and Caron 1998). However, the ability to stabilize soil structure is broadly distributed across the microbial community (see Table 1; Ladd et al. 1996). Changes in the composition of the soil microflora may have little effect on plants because there would be few changes in soil structure stabilization. In sharp contrast, biological formation of soil macrostructure is limited to the physical artifacts created by a comparatively small number of soil-moving macroinvertebrates (earthworms, termites, ants, etc.) and mammals (prairie dogs, gophers, moles, etc.). Invasion or extinction of burrowing macroinvertebrates and mammals is thus expected to have strong effects on plants in systems where soil engineers play a role (Dangerfield et al. 1998, Anderson 2000).

Rhizophagous animals and soil-borne pathogens can strongly modify the disturbance regime to which the vegetation is subjected (Vitousek 1990). Root feeding by invertebrates decreases flowering and seed production, alters patterns of seedling recruitment, reduces plant species richness, and modifies the competitive balance between different plant life-history groupings (Brown 1990). However, alterations in species richness of rhizophages are unlikely to have a strong effect on the disturbance regime encountered by the natural vegetation, because root-feeding animals are comparatively diverse and are usually generalist feeders. By contrast, associations between plant pathogenic nematodes, fungi, and viruses may be highly species specific. For example, Mills and Bever (1998) reported that even co-occurring plant species show differential susceptibilities to the soil pathogens of their neighbors. Because soil pathogens may influence interspecific plant competition, they may also influence plant community dynamics and possibly plant species diversity as well (Van der Putten and Peters 1997). Alteration of the disturbance regime to plants by soil-borne pathogens should therefore have a strong effect on ecosystem processes.

Disturbance regime to soil organisms

Changes in engineering activities of plants can have a dramatic effect on the disturbance regime to soil organisms, i.e., by altering the fire regime, by triggering biological invasions, or by altering structural features of the soil habitat. Here we confine the discussion to the alteration of structural features. Plant engineering of the soil habitat results primarily from individual and plant community attributes such as root architecture and vegetation cover (Table 1). Alterations to the disturbance regime for soil biota through changes in plant engineering should be confined to situations in which plant life forms (trees, shrubs, grasses) differing from the original vegetation become extinct or dramatically change in dominance. For example, when shrubs invade semiarid grasslands, they modify abiotic processes such as the redistribution of soil materials by erosion and the funneling of nutrient-rich stemflow water (Schlesinger and Pilmanis 1998). Consequently, most soil biodiversity (Virginia et al. 1992) and ecosystem functions become localized under shrubs, while the intershrub spaces become increasingly devoid of biotic activity. Invasion by shrubs leads to steep local gradients in the disturbance regime of the soil habitat and changes the spatial distribution of soil resources from a relatively homogeneous pattern in grasslands to a patchy distribution in shrublands. As the area of shrub deserts and barren soils increases, increasing flux of dust and a higher surface albedo may cause considerable feedbacks to global climate (Schlesinger and Pilmanis 1998).

Clearly, changes in plant community structure simultaneously alter both engineering and provision of food resources to soil biota. This is because plant species generally differ in a variety of attributes (e.g., phenologies, growth rates, nutrient- and water-use efficiencies) that differentially alter soil physicochemical properties, accumulation of soil organic matter, and nutrient availability. This is demonstrated by investigations of plant effects on the fluxes of trace gases. Epstein et al. (1998) estimated the fluxes of

trace gases (NO, N_2O, and CH_4) from soils of shortgrass steppe communities dominated by C_3 plants, C_4 plants, or a mixture of the two types. C_3 and C_4 plants differ in timing of growth, water and N-use efficiencies, and tissue N concentrations. The production of NO, N_2O, and CH_4 could affect all of these variables, because microbial processes contributing to the exchange of trace gases are driven by complex interactions between soil moisture and temperature, soil aeration, and the availability of reactive substrates. However, differences in the effects of C_3 and C_4 plants on gas fluxes at a clay site were not apparent, while several differences were found on sandy clay loam. Epstein et al. (1998) concluded that, under certain environmental conditions, particularly when factors such as moisture and temperature are not limiting, plant assemblage composition can regulate belowground processes that modify trace gas exchange. This shows that the mechanisms involved strongly depend on local and regional abiotic conditions.

A framework for global change effects

We suggest that plant relationships to soil biota (above ground to below ground) can be modeled as a nested set of control variables with morphological attributes of dominating life forms determining engineering activities at the ecosystem level, physicochemical properties of plant functional groups modifying the provision of nutritional resources at the community level, and biological properties of individual species controlling direct interactions at the population level (Figure 2). We argue that plant effects on soil biota at the two highest hierarchical levels (ecosystem, community) often depend on continuous traits and are thus likely to be insensitive to moderate changes at the plant species level. Changes in ecosystem functions created by plant-induced alterations in the disturbance regime to, and resource consumption rates by, soil organisms should thus be confined to situations where essential traits of the vegetation are drastically changed. Such a change is most likely when the strength of environmental change overrides all other factors controlling plant assemblage structure, when plants with key attributes/functions invade or become extinct, and when species-poor environments are affected. Under these conditions, even a single species may be the prime initiator of a vegetation switch (Wilson and Agnew 1992).

A similar control hierarchy emerges in the soil system, with morphological attributes of burrowing macroinvertebrates and mammals establishing different dynamic equilibria for soil at the ecosystem level, physicochemical properties of trophic groups affecting the vegetation at the community level, and biological properties of individual species regulating direct interactions at the population level (Figure 2). Because plants comprise more than 90% of the living biomass in most land systems, fuel terrestrial food webs, and control many of the variables affecting soil biota, the major impacts of global change on belowground organisms are likely to be indirect (i.e., through aboveground vegetation). Alterations in species composition of the belowground community may significantly amplify environmental changes to ecosystem processes when the disturbance regime is altered by changes in the species composition of macroengineers or
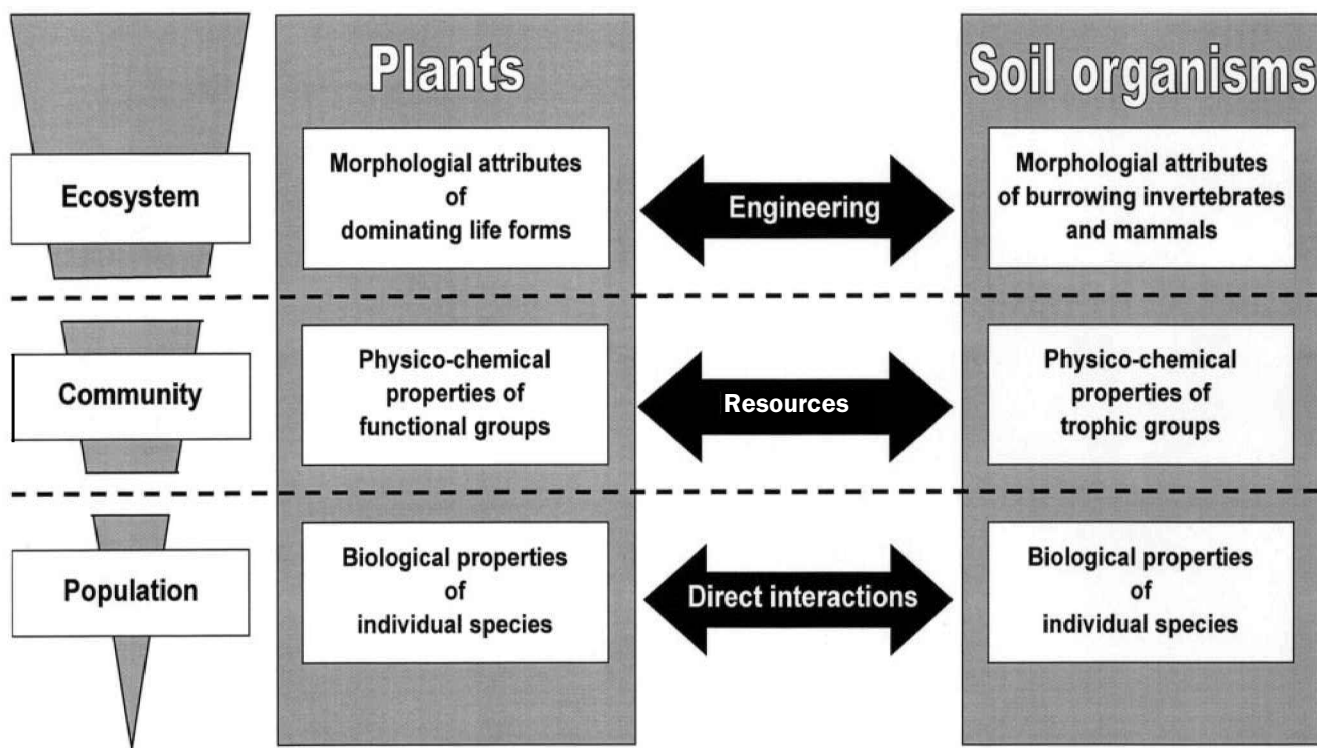

Figure 2. Hierarchy of plant effects on soil biota and vice versa.

specific pathogens, and when the supply of soil resources is modified either by intimate mutualists or by organisms performing specific transformations within decomposition processes and nutrient cycles.

Land-use change

Management practices vary greatly around the globe and range from low-input shifting cultivation to various forms of permanent and high-input intensive agriculture. Conversion of primary habitat and changes in land use and management influence above- and belowground organisms by altering three fundamental sets of factors: physical disturbance, chemical inputs, and biological inputs. Intensive high-yield agricultural practices rapidly override all other factors controlling plant community structure. Intensification of land use is thus considered the major change driver in many regions of the world, particularly in the tropics (Ingram and Gregory 1996, Sala et al. 2000).

Change to a few crop plants immediately alters the morphological attributes determining plant engineering activities. Subsequent alterations in microclimate and soil conditions strongly affect the structure and function of the belowground community (Freckman and Ettema 1993). Moreover, the decomposer habitat is changed through alterations in the quantity and placement of plant residues, expanded use of agrochemicals, and mechanized tillage. Agriculture also dramatically alters provision of food resources to soil biota because the amount and the quality of litter and exudates produced by cultivated plants generally differ from those produced by the native vegetation. As a consequence, key functional groups of the soil macrofauna are eliminated and early colonizers and species adapted to perturbation are favored (Swift and Anderson 1993). The elimination of soil macroengineers through cultivation could amplify the results of land-use change on ecosystem processes by altering the disturbance regime to plants. The same holds for changes in the supply of soil resources to plants arising from alterations in the metabolic and modulating effects of soil organisms.

After deforestation of an Amazon forest and subsequent replacement by pastures, for example, the compacting earthworm species *Pontoscolex corethrurus* became dominant and represented 90% of the invertebrate biomass. The accumulation of compact casts near the soil surface in a very moist environment led to the formation of a 5-cm-thick surface crust with low permeability. Large areas of bare soil several meters in diameter appeared as grass disappeared and anoxic conditions developed in the soil beneath the crust. The fact that 18 tons of carbon per hectare (18t C /ha^{-4}) was released in three years as earthworm-respired CO_2 and through methane emission points to the potential feedback of land-use intensification to atmospheric change via alterations of above- and belowground relationships (Chauvel et al. 1999). Agricultural practices also disrupt direct interactions. Breeding crop plants for higher productivity, for instance, normally reduces the effectiveness of plants'

chemical defense against rhizovores (Van Noordwijk et al. 1998). This effect is amplified by the elimination of natural enemies and competitors. As a result, the disturbance regime and the provision of nutritional resources are additionally altered. The need for pest control and fertilizer application increases, and functional relationships between plants and soil biota are further disrupted. Thus, land-use change rapidly and persistently alters all levels of above- and belowground interactions and acts on a large scale.

Climate change

An average global temperature increase of 2.5°C over the next century is predicted as a consequence of increasing atmospheric concentrations of greenhouse gases (IPCC 1996). Dramatic changes, not only in temperature but also in precipitation patterns, seasonality, and the occurrence of catastrophic events, are expected. The close association of vegetation types with particular climate zones indicates that global climate change will lead to a major shift in the boundaries of ecological systems (Smith et al. 1992). Some evidence suggests that climate-induced alterations in the composition and structure of plant communities will drastically change disturbance regimes and resource availability to the soil biota. The predicted replacement of southern boreal mixed spruce–hardwood forest by hardwood forest due to global warming (Pastor et al. 1988) is one example of potential feedback of alterations in plant physicochemical traits to the vegetation through changes in the provision of resources to soil biota. Hardwood forests produce a higher quality litter and have a higher primary production than the original mixed spruce–hardwood forests. Increased availability of organic resources is expected to increase the biomass of the soil microflora and of the food web groups influenced by both bottom-up control and litter quality (Wardle et al. 1998). Enhanced activity of soil organisms and associated changes in decomposition rates could significantly alter the availability of soil resources to the vegetation.

Soil biota are also directly affected by climatic conditions. In tundra soils, for example, different temperature optima of enzymes produced by different fungal strains may significantly affect fungal competition for organic resources and thus nutrient provision to plants under fluctuating summer temperatures (Flanagan and Scarborough 1974, Linkins et al. 1984). The potential impact of sudden climatic changes on soil organisms has been experimentally tested by various approaches (e.g., tents, buried heating cables, and translocation of soil cores). Changes in water supply and ambient humidity are particularly important. Alterations in ecosystem functions should be great when the soil communities that are affected by climate change include organisms that carry out functions performed by few other organisms. Schimel and Gulledge (1998) hypothesized that in areas where episodic drying and rewetting of soil associated with climate change becomes more severe, populations of cellulytic and lignolytic fungi may be reduced, resulting in a decrease in litter decomposition greater than

would be predicted by considering only the changes in soil and litter moisture. In areas without a distinct wet season, litter accumulation could ultimately result in greater C sequestration and lower plant productivity, as nutrients accumulate in slowly degrading litter. In addition, a greater fuel load might increase the frequency or intensity of fires, with impacts on the fluxes of a range of trace gases (Schimel and Gulledge 1998).

Another important aspect of climatic change is that direct species interactions will be disrupted because of different migratory rates of plants, mycorrhizae, N-fixing symbionts, and slow-moving invertebrates (Melillo et al. 1993). For instance, plant species may be introduced into soils with root-feeding invertebrates against which they have no defense (Van Noordwijk et al. 1998). Moreover, desynchronization of population cycles may alter patterns of both pest and parasite infestation (in timing and hosts) as well as mutualistic interactions between plants and soil biota. Thus, as with land-use change, alterations in climate will act on a large scale and all levels of above- and belowground interactions are likely to be affected. In contrast to land-use change, however, climate change occurs more slowly and is strongly dependent upon regional conditions.

Many results are thus expected to be transient and differ between systems, especially in the next few decades. The influence of climate change on above- and belowground interactions will be delayed by the buffering mechanisms associated with moderate changes in species composition related to plant control of both disturbance regime of and provision of food resources to soil biota. Changes in ecosystem function should be particularly strong in systems hosting impoverished communities because traits controlling above- and belowground relationships are discontinuously distributed at each level of the ecological hierarchy, and boundary shifts cause strong alterations of the disturbance regime, soil resources and rates, and consumption rates of resources. This is the case, for example, in high latitudes and mountain regions, where harsh environmental conditions lead to communities with a low internal diversity and favor slow-growing species with long generation times and infrequent reproduction (Callaghan et al. 1992). These species are generally vulnerable to change and more responsive to increasing temperature. Considerable feedback to climate is to be expected from changes in species composition. Northward expansion of trees into current tundra, for instance, could accelerate global warming, mainly through changes in albedo and annual energy exchange (Foley et al. 1994).

Atmospheric inputs

The regional and global atmospheric dispersal and deposition of pollutants impact terrestrial ecosystems. Airborne pollutants include a wide array of organic compounds, heavy metals, radionuclides, gases, and nutrients. Pollution is not restricted to local areas and some changes occur on a large scale. Alterations in the atmospheric composition of trace gases in the tropics, for example, are identical to those in high latitudes, despite differences in source and sink strength (Scholes and Van Breemen 1997). Here we confine the discussion to the impact of increased CO_2 levels.

Given current trends, atmospheric CO_2 concentration is predicted to be, by the middle of the next century, twice that of the preindustrial concentration. A survey of controlled CO_2 exposure studies revealed a mean increase of 32% in the growth response of a large number of plant species with exposures to high CO_2 (Wullschleger et al. 1995). Enhanced primary production, diminished litter quality, and shifts in plant assemblage structure resulting from CO_2 enrichment may all have large effects on global vegetation patterns (Melillo et al. 1993).

A major shortcoming of past research is that it focused almost exclusively on system responses to doubled CO_2 concentrations, while the actual increase in CO_2 is gradual, with presumably different response curves for different species and genotypes. Moreover, the response will depend on the demography and ecological strategy of the organisms involved. For instance, ruderal species are particularly responsive to CO_2 enrichment (Hunt et al. 1993). It is doubtful that soil biota will respond directly to increased levels of atmospheric CO_2 because of existing high concentrations in soil, although indirect changes are very likely. Interception by a larger canopy may lower soil temperature and moisture, and altered root architecture may change hydrological fluxes. The provision of food resources to soil biota is affected by increases in the amount of energy available as a result of more productive plant communities, by alterations in the chemical composition of litter, and by alterations in mycorrhizal symbioses.

According to a scenario of the effects of increasing CO_2 concentration on temperate grasslands suggested by Swift et al. (1998), a disproportionate increase of primary production relative to decomposition rate is to be expected. Soil organic matter is likely to accumulate, rendering grasslands net sinks of carbon under elevated CO_2. Changes in the provision of organic resources by plants may promote significant functional shifts within the soil community. Alterations in resource acquisition rates by plants due to sensitive responses of mutualistic symbionts (e.g., mycorrhiza, rhizobia) to high CO_2 may lead to considerable feedback effects between global change and nutrient cycling. An important role for biodiversity is indicated by the fact that alterations of ecosystem functions seem to be strongly modulated by changes in competition between plants, changes in plant species composition, and changes in amounts and qualities of litter (Swift et al. 1998).

The direction and magnitude of CO_2 effects are highly species specific and depend on other environmental factors, such as soil nutrient status and plant growth conditions (Lavelle et al. 1997). For example, the increased C:N ratio in plant litter may reduce decomposition rates and thus the supply of plant-available soil nutrients. On the other hand, increased C input could also increase N availability by stimulating the microbiota in soil or by altering plant engineer-

ing of soil moisture as a result of decreased stomatal conductance. Moreover, nutrient feedbacks through changes in the performance of the belowground community under elevated CO_2 are likely to be more important in N-poor systems or in systems with low levels of N deposition. Hungate et al. (1996) suggested that grasses invading nutrient-poor serpentine grasslands may gain a competitive advantage under increased levels of CO_2 by mediating N provision by belowground organisms. Thus, whether elevated CO_2 increases or decreases N availability depends on the ecosystem of interest and on the organisms involved.

In principle, the conclusions drawn for the functional implications of climate-induced changes in above- and belowground interactions also apply to alterations in atmospheric inputs, that is, changes will be dose dependent and local. Effects of atmospheric inputs are quite variable and show strong temporal and spatial variations (Wolters and Schaefer 1994). Present knowledge suggests that supplementation of resources (e.g., CO_2, N) leads to changes (probably decreases) in above- and belowground diversity. The response curves can vary for different resources and resource combinations. As a general trend, effects of increased nutrient levels on species richness tend to be hump-shaped (Heal 1997): Changes are positive with low inputs and in nutrient-poor soils, but are negative at high inputs and in nutrient-rich soils (nutrient saturation). Changes in atmospheric inputs are thus not expected to cause strong and large-scale alterations in above- and belowground interactions in the short term. Nevertheless, the ecological significance of atmospheric inputs may increase considerably through interactions with other drivers of global change. For example, Eggerton-Warburton and Allen (2000) reported that increased N deposition converts a species-rich arbuscular– mycorrhizal community into one that is dominated by small-spored mutualists. This may increase the susceptibility of the vegetation to environmental change, because small-spored species exert a net negative C balance on the host that is reminiscent of parasitic, rather than mutualistic, associations (Eggerton-Warburton and Allen 2000).

Conclusions

Ecosystem-level responses to changes in above- and belowground interactions are difficult to assess because interactions are complex and include simultaneous direct and indirect effects of ecosystem engineers, food web processes, and mutualistic, symbiotic, and antagonistic relationships among the soil biota and plants. These factors feed back on above- and belowground organisms to alter their sensitivity to, and the buffering capacity of, environmental change. However, several conditions have been identified in this article under which alterations of above- and belowground interactions are expected to drastically alter ecosystem functioning, because traits affecting the supply of soil resources, consumption rates of resources, and disturbance regime are unique to a few species or taxa. These traits include changes favoring plants strongly differing in life form

and ecological strategy, alteration of the performance of soil macroengineers, modifications to communities with a high degree of functional specialization, and interruption of highly specific associations. Moreover, different life spans and turnover times for plants and soil organisms could lead to the decoupling of the above- and belowground subsystems resulting from perturbations or disturbance events.

Most of the vegetation change occurring today is very likely to cause a major shift in plant life form and ecological strategy because it alters the proportion of woody and herbaceous plants (Jackson et al. 2000). This happens in tropical and subtropical regions experiencing deforestation, in temperate and tropical regions with reforestation and afforestation, and in arid and semiarid systems where there is expansion of woody vegetation. The sensitivity of above- and belowground relationships to changes in species composition has important implications for prioritizing future research and management (Hooper et al. 2000).

Two areas are particularly important: intensification of land use and catastrophic events caused by changes in both climate and atmospheric inputs affecting the boundaries of communities at their ecological limits. In both cases, all levels of the ecological hierarchy governing the interactions among species at both sides of the above-belowground interface are either strongly affected or particularly sensitive to environmental change. Research in these areas not only provides the basis for detecting the most severe alterations in ecosystem functions but also holds a great capacity for developing new strategies of management under a variety of environmental conditions.

Detecting alterations in ecosystem functions caused by environmentally induced changes in above- and belowground relationships requires detailed analysis of specific interactions in field and laboratory experiments, and monitoring over large areas and long periods (Huber-Sannwald and Wolters 1998). There is a need for research networks and for setting up new experiments in poorly known but important habitats (e.g., tropical forests; high latitudes). Monitoring should include system mosaics along environmental gradients to provide insights into compositional changes and potential losses of biodiversity and ecological complexity of these systems. In systems most vulnerable to global change, the demography and phenology of dominant and keystone species both above ground and below ground governing engineering, provision of food resources, and direct interactions should be monitored in long-term efforts.

A proper understanding of both changing interactions between above- and belowground organisms and feedbacks between atmosphere and biosphere that may occur through shifts in vegetation types will allow us to develop more reliable global change scenarios of ecosystem functioning that include soil biota and soil processes (Schimel and Gulledge 1998).

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