

# FUNCTIONAL MATRIX: A Conceptual Framework for Predicting Multiple Plant Effects on Ecosystem Processes

---

Valerie T. Eviner

*Institute of Ecosystem Studies, PO Box AB, Millbrook, New York 12545;  
email: evinerv@ecostudies.org*

F. Stuart Chapin III

*Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775;  
email: terry.chapin@uaf.edu*

**Key Words** biogeochemical cycling, climate feedbacks, ecosystem processes, functional group, functional matrix, litter quality, species effects

■ **Abstract** Plant species differ in how they influence many aspects of ecosystem structure and function, including soil characteristics, geomorphology, biogeochemistry, regional climate, and the activity and distribution of other organisms. Attempts to generalize plant species effects on ecosystems have focused on single traits or suites of traits that strongly covary (functional groups). However, plant effects on any ecosystem process are mediated by multiple traits, and many of these traits vary independently from one another. Thus, most species have unique combinations of traits that influence ecosystems, and there is no single trait or functional-group classification that can capture the effects of these multiple traits, or can predict the multiple functions performed by different plant species.

We present a new theoretical framework, the functional matrix, which builds upon the functional group and single trait approaches to account for the ecosystem effects of multiple traits that vary independently among species. The functional matrix describes the relationship between ecosystem processes and multiple traits, treating traits as continuous variables, and determining if the effects of these multiple traits are additive or interactive. The power of this approach is that the ecosystem effects of multiple traits are the underlying mechanisms determining species effects, how the effects of an individual species change across seasons and under varying environmental conditions, the nonadditive effects of plant species mixtures, and the effects of species diversity.

## INTRODUCTION

Plant species can differ in their effects on almost every aspect of ecosystem structure and function. Understanding these effects is critical for predicting the consequences of environmental changes because shifts in vegetation composition can

cause ecosystem changes that are larger in magnitude, or even opposite in direction, than the direct effects of environmental change (Kirkby 1995, Hobbie 1996). An in-depth understanding of the multiple ecosystem functions provided by plant species can also be a critical tool for land management, such as restoration, bioremediation, or sustainable agriculture (Eviner & Chapin 2001, Liste & Alexander 2000).

The ecosystem effects of plant species are usually predicted by focusing on one mechanism that is assumed to dominate a plant's effect on a given ecosystem function. One example is the plant functional type approach, which is based on the assumption that there are suites of related plant traits that can generalize how species affect ecosystem processes or respond to environmental changes (Wilson 1999). For example, plants adapted to low-nutrient environments have high nutrient use efficiency, slow growth and photosynthetic rates, and low litter quality, which, in turn, reinforce low nutrient availability (Chapin 1993). Whereas functional grouping is a powerful framework linking plant characteristics and ecosystem processes, it is most appropriate for categorical differences in species functions (e.g., ability to fix N), rather than functions mediated by traits that vary among species in a continuous manner (e.g., litter chemistry). Functional-type generalizations do not adequately account for multiple plant effects because a given species can be classified into multiple functional groupings depending on the function of interest (Wilson 1999). A second approach to predicting the effects of plant composition is to focus on single traits that vary in a continuous manner. This approach is conceptually similar to functional grouping because single traits (e.g., litter C:N) are indicators of a broader suite of traits with similar ecosystem effects.

Both approaches provide large-scale generalizations of the effects of plant species on processes such as N cycling because at a regional scale, environmental conditions select for certain suites of plant traits (Chapin 1993). Thus, the relationships between litter chemistry and biogeochemical cycling tend to be strong at regional scales (Scott & Binkley 1997, Taylor et al. 1989) because nutrient availability at a given site selects for species that reinforce the site's relative level of nutrients. However, traits that strongly covary over environmental gradients can vary independently at local scales. Within a habitat, differences in traits within a species or among species can be as great as trait differences across the full range of an environmental gradient (Fonseca et al. 2000, Wright & Westoby 1999). Thus, relationships between litter quality and N cycling are often weak within a given site (Eviner 2001, Steltzer & Bowman 1998) because the other mechanisms that determine plant effects on N can vary independently from litter chemistry.

This review examines the multiple traits that determine plant species effects on ecosystem processes, the multiple roles that plant species play in ecosystems, and how these multiple roles influence one another. We then present a generalizable, mechanistic framework to improve predictions of plant species effects based on multiple plant traits.

## MECHANISMS BY WHICH PLANTS INFLUENCE ECOSYSTEMS

### Soil Environment

Plants species can have large effects on the physical structure and chemical properties of soil. These properties strongly influence hydrology, plant growth, biogeochemical cycling, and the activity of soil organisms (reviewed in Angers & Caron 1998, Glinski & Lipiec 1990).

**SOIL STRUCTURE** Plant roots disaggregate compound rock fragments, resulting in more fine soil particles ( $<6.3 \mu\text{m}$ ), and less medium and coarse silt fractions in the rhizosphere relative to bulk soils (Glinski & Lipiec 1990). The aggregation of these soil particles can vary owing to plant species (Eviner & Chapin 2002, Scott 1998). In general, aggregation is determined by species differences in root characteristics (e.g., biomass and length) (Miller & Jastrow 1990), the quantity and quality of carbon inputs, and associated soil biota (Degens 1997). Plant species also alter soil moisture (Gordon & Rice 1993) and freeze-thawing (Hogg & Lieffers 1991), which can initiate aggregate formation. Grass species often foster greater aggregate stability than other vegetation groups owing to their high root and fungal biomass (Jastrow 1987, Rillig et al. 2002). Other species decrease aggregate stability by exuding chelating agents that bind Fe and Al, destroying the links formed by these metals between organic matter and mineral particles (Reid & Goss 1982).

Soil aggregation and plant rooting characteristics determine the size distribution of pores, and pore volume is enhanced by species with high root turnover, organic matter, and animal activity (Challinor 1968). Soil bulk density decreases with increases in pore volume and soil organic inputs (Troeh & Thompson 1993). High densities of roots displace soil and increase its bulk density, whereas species with taproots penetrate and loosen compact soils (Glinski & Lipiec 1990).

**SOIL CHEMISTRY** Soil characteristics such as pH, redox, salinity, cation exchange capacity, and water holding capacity are critical determinants of biogeochemical cycling and plant growth. Plant species play active roles in mediating these soil chemical properties.

**pH and redox** Plants can acidify their rhizosphere soil by as much as two pH units (Glinski & Lipiec 1990). This is largely attributed to release of organic acids in exudates and to higher root uptake of cations than anions, leading to root excretion of  $\text{H}^+$  ions. The balance between cation and anion uptake is primarily determined by the form of N taken up. However, even when species take up the same form of N, species differences in other nutrient requirements lead to substantial changes in soil pH (Marschner 1995). These rhizosphere effects often alter bulk soil pH. For example, N-fixing plants decrease bulk soil pH because of their high cation uptake and promotion of nitrification and base cation loss through enhanced  $\text{NO}_3$  leaching.

Base cations such as Ca and Mg are key players in the soil's capacity to buffer pH (Marschner 1995). Thus, soil pH is increased by species with high litter calcium inputs (Finzi et al. 1998b) and by species that increase cation exchange capacity or base cation weathering rates (Kelly et al. 1998). These species are particularly important in preventing soil acidity as a result of leaching of base cations over long-term soil development (Ovington 1953). In contrast, base cation leaching and soil acidification are enhanced by species with high litter concentrations of organic acids (particularly tannins) (Finzi et al. 1998b, Ovington 1953). Plant species also influence acid deposition. Deposition is higher in conifers than in hardwood stands owing to the high leaf area of conifers (Ranger & Nys 1994).

Soil redox conditions are strongly influenced by the rhizosphere, where oxygen consumption is high owing to root and microbial respiration. Some plant species maintain high redox potentials by transporting oxygen from shoots to roots through aerenchyma (Marschner 1995).

**Salinity** When water arrives at the root faster than it can be absorbed, soil evaporation can lead to accumulations of salt that are toxic to plants, particularly in regions with high rates of evaporation or where low rainfall does not leach salts from the rooting zone. Species effects on soil salinity depend on differences in their salt accumulation and effects on hydrology. Iceplant (*Mesembryanthemum crystallinum*) tolerates large accumulations of salt in its tissue, and when it dies, deposits this salt on the soil surface (Kloot 1983). In arid regions, deep-rooted trees such as *Tamarix* draw up large amounts of salt with water (Zavaleta 2000). The presence of trees in arid areas can further enhance salinity because canopy interception and evaporation reduce the water available to flush salts out of the rooting zone (Munzbergova & Ward 2002). In contrast, in more mesic sites, the removal of deep-rooted trees that use large amounts of water can result in waterlogged conditions and soil salinization as this water evaporates (Bell 1999). High soil calcium decreases sodium on cation exchange sites, and thus salinization is combated by planting species that pump calcium from deep in the soil, dissolve  $\text{CaCO}_3$ , or enhance cation exchange capacity (Qadir et al. 2001).

**Capacity to retain cations and water** Soil cation exchange capacity is critical for the retention of nutrients in soil. Cation exchange sites on organic matter and the edges of clays vary in their capacity to bind cations depending on soil pH, with increases in soil pH by one unit doubling cation exchange capacity in some soils (Camberato 2001). Thus, species effects on soil pH, soil texture, and soil organic matter substantially influence the capacity of soil to retain positively charged nutrients. Organic matter inputs are the primary mechanism by which plants influence cation exchange capacity, and polyphenolic compounds are particularly effective in providing cation exchange sites (Northup et al. 1998). Similarly, water-holding capacity is influenced primarily by organic matter (Troeh & Thompson 1993). Soil porosity can also be important because water is retained more effectively by the large capillary forces of many small pores than in soils with a few large pores.

**SOIL DEVELOPMENT** Plants have long been recognized as key regulators of soil formation (Jenny 1941), and plant species differentially influence soil structure and processes during primary succession (Lawrence et al. 1967, Matson 1990). Plant species affect weathering through the generation of weathering agents (e.g., CO<sub>2</sub>, organic acids, ligands), alteration of hydrology, cycling of cations, and influence on soil pH (Augusto et al. 2000, Kelly et al. 1998). Fulvic and low-molecular-weight humic acids are critical for weathering, and different acids vary in strength and weathering rates of different minerals. Plants also can enhance weathering through the penetration of roots and root-derived acids into the parent material (Viles 1990) explaining why the spread of deeply rooted forests across continental areas resulted in rapid formation of soil (Kelly et al. 1998). Plant species also differentially alter the forms of minerals in the soil. Grass species produce phytoliths, stabilizing soil silica by increasing the fraction of crystalline to noncrystalline soil minerals (Kelly et al. 1998).

In addition to their effects on the weathering of bedrock, plant species alter the accumulation and type of organic matter (Binkley & Giardina 1998). Species differences in the location of organic matter inputs and nutrient redistribution alter the weight, density, and thickness of soil horizons (Boettcher & Kalisz 1990). Podzolic soils typically have a low pH, high C:N and mor-type humus dominated by humic acids. Many conifer and ericaceous species cause acidification and podzolization of the soil largely through inputs of organic acids as a result of the incomplete decomposition of organic matter (Raulund-Rasmussen & Vejre 1995). In contrast, broadleaf trees have a much wider range of effects on pedogenesis, ranging from enhancement to reversal of podzolization (Miles 1985). Herbaceous species often reverse podzolization and acidification of soil through increases in soil base saturation caused by reduced litter acidity and increases in calcium availability (Willis et al. 1997).

**LANDSCAPE FORMATION** In addition to their effects on soil formation, plant species are also the main determinant of geomorphology. In fact, the indirect effects of climate change through shifts in vegetation composition have larger effects on geomorphology than do the direct effects of changes in the climatic regime (Kirky 1995).

**Erosion** The force required to disrupt a mass of soil is soil shear strength. Shear strength is critical for preventing multiple types of erosion, ranging from sediment runoff to landslides. Plant species differentially contribute to shear strength through their root strength and effects on soil cohesion (the capacity of particles to bind together) (Angers & Caron 1998). Species enhance soil cohesion through root-soil bonding (Selby 1993), a function of the length and density of fine roots and root hairs (Waldron & Dakessian 1981). Soil cohesion is also enhanced by plant transpiration that dries the soil thereby reducing the buoyancy of soil particles. Erosion through runoff is low in cohesive soils and is further decreased by soil organic matter, which binds soil particles and enhances water infiltration. Surface erosion is also decreased by canopies that intercept rainfall and wind (Viles 1990).

Species that create variable microtopography or have high aboveground cover enhance water infiltration and thus minimize runoff while recapturing sediments in overland flow (Devine et al. 1998). Plant species effects on faunal burrowing, hydrology, and disturbance regime also play large roles in determining erosion rates (Kirkby 1995, Viles 1990).

Root strength contributes to the shear strength of the overall soil profile and prevents larger erosion events (Terwilliger & Waldron 1991). Landslides and soil slips commonly occur when communities dominated by woody species are converted to grasslands (Jones et al. 1983, Prandini et al. 1977). The soil strength provided by deep interlocking roots of woody plants in the upper soil layers can stabilize the overall soil profile, and deep roots can bind the unstable upper soil layer to rocky substrates. These woody roots often provide this protective role even after aboveground woody vegetation has been harvested, and it is not until these roots begin to decompose that substantial soil slips occur. Whereas tree roots significantly stabilize deep soils, on steep slopes with shallow soils, tree root channels can increase landslides by enhancing water infiltration (de Ploey & Cruz 1979). Erosion as a result of runoff rather than landslides also tends to be lower in forests than grasslands because the forest canopy and litter layer better intercept rain and wind, protecting the soil surface particles from transport. In addition, a thick litter layer decreases runoff by increasing water infiltration and retention. Finally, soil stability is enhanced by low soil moisture levels owing to high evapotranspiration in forests (Prandini et al. 1977).

In contrast, in arid systems, the conversion of grasslands to shrublands often results in substantial increases in erosion owing to bare spaces between shrubs (Schlesinger et al. 1990). In these systems, overland flow of water is the major soil transport mechanism. Erosion is decreased by species traits that minimize the physical impact of rainfall and wind on the soil surface (e.g., high cover) (Abrahams et al. 1994), as well as traits that influence hydrology and infiltration (Wainwright et al. 2000).

**Sedimentation** The architecture of plant shoots and roots determines how well plant species can trap and hold sediments. For example, the dense thickets and extensive root mats formed by *Tamarix* increase sedimentation, resulting in decreases in the width and depth of water channels (Zavaleta 2000). Similarly, invasion of *Spartina alterniflora* into intertidal habitats increases sedimentation, thus increasing the steepness of beaches and decreasing the delivery of sediments to mudflats, converting them to open water habitat (Gleason et al. 1979). Species also produce sediment through the buildup of organic matter. Debris buildup by *Melaleuca quinquenervia* in the Florida everglades leads to the formation of tree islands, converting marshes to swamp forests (Laroche 1994).

## Hydrology

Plant species effects on water dynamics range from altering water availability in their rooting zone to stream flow. A number of different plant traits are responsible for these hydrological effects.

**WATER AVAILABILITY** There are many mechanisms by which plant species alter soil moisture. Species with high litter mass decrease evaporation from the soil (Evans & Young 1970). The amount of water used by species also alters soil water availability, and this effect can be independent of biomass (Gordon & Rice 1993). Root length, water uptake per unit root biomass, and the timing of root development are important influences on the capacity of species to draw down soil water (Gordon & Rice 1993). More extensive water uptake occurs from the fibrous roots of grasses than from the taproots of forbs (Gordon et al. 1989). Deep-rooted species access more water because they tap a larger volume of soil than do shallow-rooted species (Robles & Chapin 1995). Differences in plant phenology can have important effects on ecosystem water fluxes. For example, the invasion of *Andropogon* in Hawaii has led to boggy conditions because its time of maximum evapotranspiration does not coincide with the rainy season (Mueller-Dombois 1973).

Some species can access unique sources of water and, by tapping into these sources, provide water for other plants in the ecosystem. For example, species with canopies that are tall and have high surface area collect water from fog in many coastal and montane ecosystems (Weathers 1999) providing as much as 34% of the annual ecosystem water input (Dawson 1998). Similarly, a substantial amount of water can be provided by hydraulic lifters, deep-rooted species that take up water from deep layers of soil and passively release it into surface soils at night when transpiration ceases (Caldwell et al. 1998).

**WATER MOVEMENT** Plant species influence the pathway and fate of precipitation. Canopies of species with a high leaf area intercept precipitation, increasing the amount that evaporates. Infiltration of the remaining water into the soil increases owing to high plant cover (live + dead) (Devine et al. 1998), burrowing soil fauna (Gijssman & Thomas 1996), or increased pore volume (Angers & Caron 1998). Some plant species decrease infiltration by forming a hydrophobic layer of surface soil through inputs of waxes, fatty acids, resins, aromatic oils, and humic materials (Doerr et al. 2000, Spaccini et al. 2002). Infiltration and the path of water flow, can also be influenced by canopy structure. Stem flow concentrates water flow, leading to local water saturation and runoff (Herwitz 1986).

Changes in plant community composition can affect stream flow, flooding regime, and peak storm discharges due to species differences in transpiration rates (Viles 1990), effects on canopy interception and infiltration (Le Maitre et al. 1999), and alterations of water channels through promotion of sedimentation (Laroche 1994). In a Mediterranean climate, runoff in grasslands is 40% higher than in shrublands, leading to higher stream flow (Pitt et al. 1978). In contrast, in semiarid ecosystems, the conversion of grasslands to shrubs increases the amount and rate of water flow because shrubs decrease water infiltration, which increases overland flow. This overland flow is concentrated into fewer and deeper channels through the effects of shrubs on local surface morphology (Wainwright et al. 2000). Conversion of hardwoods to conifers decreases stream flow if conifers have greater canopy interception and transpiration (Swank & Douglass 1974). The opposite

might be true in places like Alaska, where conifers have lower transpiration than hardwoods and are associated with boggy soils (Chapin et al. 2000).

## Microclimate to Climate

The effects of plant species on soil moisture regimes were discussed above. In this section, we will discuss the effects of plant species on soil temperature, and then extend the local effects of species on soil temperature and moisture to their effects on regional and global climate.

**EFFECTS ON SOIL TEMPERATURE** Plant species influence local soil temperature primarily through the buffering effects of shoot cover, including live plant tissue and litter (Hogg & Leiffers 1991). The color of litter can also influence soil temperature with darker-colored litter increasing warming by increased absorption of sunlight (Hogg & Leiffers 1991). In California annual grasslands, species differences in litter mass determine winter soil temperature. However, in the spring, as this litter mass decomposes and aboveground growth increases, species effects on soil temperature are mediated primarily by live biomass (Eviner 2001). In boreal forests, thick layers of aboveground tissue can delay soil thaw up to one month, and in the summer, can lead to soils that are 4°C cooler (Hogg & Leiffers 1991). Plant species effects on microclimate are likely to be strongest under extreme environmental conditions. For example, in Mediterranean grasslands, species effects on soil temperature are most pronounced during the cold winters when temperature is most limiting to plant and microbial activity, while species effects on soil moisture become stronger in the warm, dry spring (Eviner 2001).

Species influence not only soil microclimate, but also stand humidity, air temperatures, snow accumulation, and wind speed (Baldocchi & Vogel 1996). Dense canopy cover enhances humidity (Binkley & Giardini 1998) and decreases net canopy energy exchange at the forest floor (Baldocchi & Vogel 1996).

**REGIONAL AND GLOBAL CLIMATE** Species differences in energy absorption can greatly affect regional temperature. Vegetation dominated by species with tall, dark, complex canopies absorb more solar radiation (i.e., have a lower albedo) than do short, reflective, simple canopies. For this reason, conversion from graminoid tundra to shrub tundra to forest increases radiation absorption and atmospheric heating, just as does succession from deciduous to coniferous forest (Chapin et al. 2000). The atmospheric heating for each of these vegetation changes is similar to that caused by a doubling of atmospheric CO<sub>2</sub> or increased solar input associated with glacial–non-glacial transitions per unit area and time. This vegetation-induced warming of climate occurs only at the scale of the region in which the vegetation changes occur (Chapin et al. 2000, Foley et al. 1994). These vegetation changes and warming can also influence regional and global climate by influencing fluxes of greenhouse gases such as CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O, and water vapor (Schlesinger 1997).



Energy absorbed by vegetation can be transferred to the atmosphere as sensible heat or as latent heat (evapotranspiration). Species differences in this energy partitioning have strong effects on moisture transfer to the atmosphere and therefore the moisture available for precipitation (Otterman 1989). The proportion of energy transferred to the atmosphere by evapotranspiration is twice as great in deciduous as in conifer boreal forests (Baldocchi et al. 2000). Simulations with general circulation models suggest that widespread replacement of deep-rooted tropical trees by shallow-rooted pasture grasses would reduce evapotranspiration and lead to a warmer, drier climate (Shukla et al. 1990). In semiarid regions of Australia, cloud accumulation occurs over areas of land dominated by native vegetation with high sensible heat flux but not over adjacent agricultural areas dominated by vegetation with high latent heat flux. Despite the higher atmospheric moisture inputs from agricultural areas, the low surface roughness of this system provides insufficient mixing to allow for the condensation necessary for cloud formation. In contrast, the high sensible heat flux and surface roughness of native vegetation promotes atmospheric mixing and thus cloud formation (Lyons et al. 1993).

## General Introduction to Species Effects on Biogeochemical Cycling

Thus far, we have discussed how species influence a number of ecosystem properties that are critical determinants of biogeochemical processes. In the following sections, we discuss how species effects on soil properties and microclimate interact with other species traits (e.g., litter chemistry, exudation rates) to determine rates of biogeochemical cycling.

**CARBON CYCLING** Plant species differ in their effects on almost every aspect of C cycling, from C fixation into biomass, to the extent to which this C is released from the ecosystem. In many cases, species effects on one aspect of C cycling are independent from their effects on other C dynamics.

**Net primary production** The amount of carbon fixed by plants through photosynthesis (NPP) provides the energy that drives most biotic processes, and plant species growing at the same site can greatly differ in their NPP. The unique ability of a sedge species in the tundra to access nutrients from ground water leads to a tenfold increase in productivity compared with other species (Chapin et al. 1988), while replacement of native perennials by the annual *Bromus tectorum* decreases productivity by up to 90% in some years in California rangelands (DiTomaso 2000). Species differences in NPP result from a wide range of plant traits, including growth rate, allocation, phenology, nutrient use efficiency, resource requirements, traits that influence access to resource pools (e.g., root depth, symbioses with mycorrhizae or N fixing microorganisms), and traits that influence conditions that limit growth (e.g., temperature, moisture, nutrient pools) (reviewed in Chapin & Eviner 2003).

**Decomposition** Litter C:N ratios reflect the relative amount of energy (C) and N available to microbes and are often negatively associated with rates of decomposition (Melillo et al. 1982, Taylor et al. 1989). Litter C quality can be a more important determinant of decomposition than litter C:N (Hobbie 1996). Lignin generally inhibits decomposition because it is highly resistant to enzymatic attack and can physically interfere with the decay of other chemical fractions (Gloaguen & Touffet 1982), whereas tannins vary substantially in their resistance to decomposition and in the degree to which they decrease decomposition of other compounds (Lewis & Starkey 1968). The ratio of labile C to these recalcitrant compounds is another key determinant of decomposition (Gillon et al. 1994). Plant species also influence decomposition rates through their allocation patterns (Hobbie 1996), because litter chemistry differs among tissue types within the same species, and species effects on root and shoot decomposition are not correlated (Wardle et al. 1998). Whereas litter C:N and lignin:N are frequently used as indicators of decomposition, they do not always correlate with species differences in decomposition rates because the traits that best predict species effects on decomposition can vary across groups of species (Cornelissen & Thompson 1997).

While litter chemistry is a major determinant of decomposition rates, the presence of growing plants significantly alters decomposition dynamics, both decreasing (Dormaar 1990) and increasing (van der Krift et al. 2002) rates of decomposition. Living plants can decrease decomposition rates because (a) microbes preferentially use the labile material provided by living roots rather than more recalcitrant litter, (b) roots release compounds that inhibit microbial activity, (c) plants compete with microbes for uptake of nutrients or organic compounds, and/or (d) exudates stimulate predation on microbes and thus decrease microbial populations. In contrast, growing plants can stimulate decomposition through inputs of labile C that increase the activity and turnover of microbes (Cheng & Coleman 1990, Sallih & Bottner 1988). Plants can also influence decomposition through their effects on soil temperature, moisture (Mack 1998, van der Krift et al. 2002), or O<sub>2</sub> concentrations (Allen et al. 2002). Decomposition of a common substrate can differ substantially in the presence of different plant species, highlighting the importance of plant traits other than litter quality (Eviner 2001, van der Krift et al. 2002).

The relative importance of these different plant effects can vary through the decomposition process. In the early stage of decomposition, microbes degrade primarily labile litter constituents, and rates are determined largely by the stimulating effects of litter nutrients (Berg 2000a, Couteaux et al. 1998), and are often predictable based on litter C:N (Taylor et al. 1989). Once labile compounds are exhausted, decomposition is determined by degradation of more recalcitrant compounds, and, at this stage, litter lignin and phenolic concentrations are the main determinants of decomposition rates (Cortez et al. 1996, Taylor et al. 1989). Microbial degradation of the recalcitrant substrates is often energy limited and thus labile C inputs from growing plants stimulate the later stages of decomposition

(Bottner et al. 1999). The presence of N often inhibits later stages of degradation of high-lignin litter (Heal et al. 1997; but see Melillo et al. 1989) because N and lignin form stable complexes (Couteaux et al. 1998).

**Soil organic matter** In some species, litter decomposition halts at a later stage, leaving as much as 55% of the litter mass in a stable form that directly contributes to the buildup of humic soil organic matter (Berg 2000a). Species effects on soil organic matter can be predicted based on the quantity of litterfall and the fraction of litter that does not decompose ("limit value"). Lignin (Melillo et al. 1982) and polyphenols (Howard et al. 1998) have been particularly linked with the formation of stable soil organic matter. Interestingly, species with high initial litter quality tend to have higher accumulations of recalcitrant, stabilized litter in the later stages of decomposition, and thus higher limit values (Berg 2000b). For example, legumes often are associated with higher soil organic matter contents than other species (Binkley & Giardini 1998, Cole 1995). This may be a result of the rapid decomposition of the more labile fractions of litter, leaving little labile C to fuel decomposition of the more recalcitrant substrates. This can be exacerbated because high-N tissue supports a higher microbial biomass, and, as microbes turnover, there is an accumulation of their recalcitrant residues (Mueller et al. 1998). In some cases, these limit values appear in lab incubations, but, when this same litter is incubated in the field, the litter continues to decompose (Couteaux et al. 1998, Eviner 2001), likely owing to the effects of growing plants, field variations in microclimate, and exposure to soil fauna.

Species can also influence soil organic matter through their tissue allocation. Soil organic matter is often derived primarily from root litter (Balesdent & Balabane 1996, Puget & Drinkwater 2001). This is likely because root litter is more recalcitrant (higher lignin content), is often physically protected within aggregates, and root-derived C forms the most stable aggregates (Gale et al. 2000). Thus the quantity (Christian & Wilson 1999) and quality (Urquiaga et al. 1998) of root litter can determine plant species differences in accumulation of soil C.

Species also affect the vertical distribution of organic matter (Finzi et al. 1998b), %C and %N in soil organic matter (Wardle 2002), composition of soil humic acids (Howard et al. 1998), and the type of organic matter they foster (Northup et al. 1998). Soil organic matter can be physically protected from degradation in soil macro-aggregates (0.25–2 mm), allowing even labile C pools to have long residence times in the soil (van Veen & Kuikman 1990). Species can also increase C sequestration of labile C through inputs of hydrophobic compounds such as humic materials (Spaccini et al. 2002).

Given that plant species differ in the quality of organic matter, it is not surprising that they also differ in the turnover rates of soil organic matter (Scheu 1997, Wedin et al. 1995). Although labile C pools are relatively small, they are one of the main drivers of soil C dynamics (Updegraff et al. 1995). Just as with recalcitrant litter, degradation of organic matter can be influenced by labile C inputs or inorganic

N availability (Bottner et al. 1999, Mueller et al. 1998), with the effects of these differing depending on the pools of C being degraded (Neff et al. 2002).

**Methane dynamics** Plant species influence methane fluxes in water-logged soils through the amount and quality of C substrates provided to methanogens, effects on soil oxygen levels, and methane transport from the soil to the atmosphere through aerenchyma of roots (Verville et al. 1998). The abundance of species with aerenchymous roots is one of the best predictors of ecosystem methane flux (Torn & Chapin 1993). Plant species that enhance soil O<sub>2</sub> decrease CH<sub>4</sub> formation (Grosse et al. 1996), and methane flux is negatively correlated with recalcitrant compounds (Updegraff et al. 1995) and positively correlated with root exudation (Marschner 1995). Plant species can also influence microbial methane consumption owing to inhibition of CH<sub>4</sub> uptake by NH<sub>4</sub> (Epstein et al. 1998).

**N CYCLING** There are many processes involved in terrestrial N cycling, and there are multiple mechanisms by which plant species influence these processes.

**N inputs** N-fixing plants rely on a plant-microbial symbiosis to fix atmospheric N<sub>2</sub> into reduced form. The presence of N-fixing plants can substantially increase soil N supply and recycling rates (Vitousek & Walker 1989). Legume species differ in the amount of N they fix (Franco & de Faria 1997) and the form (exudates versus litter) of N inputs (Ta & Farris 1987). N fixation by legumes can be altered by neighboring species through shading, effects on nutrients, or the presence of secondary compounds such as polyphenolics that inhibit N fixation (Ta & Faris 1987, Wardle et al. 1994). N fixation by free-living heterotrophic bacteria is common in the rhizosphere of a number of plant species (Noskop et al. 1994) and can be decreased through lignin inputs, low soil pH, or high soil N availability (DeLuca et al. 1996, Vitousek et al. 2002). Species with high leaf surface area can foster wet and dry N deposition, which is delivered to the soil in throughfall (Weathers et al. 2001).

**Cycling of N** The net conversion of N from organic to inorganic forms through the processes of mineralization and immobilization can be strongly affected by plant species (Hobbie 1992, Wedin & Tilman 1990). While similar mechanisms determine patterns of decomposition and N cycling, species effects on rates of net N mineralization often do not correlate with rates of decomposition (Hart et al. 1994, Prescott et al. 2000). For example, moss decomposes slowly but promotes rapid rates of net N mineralization (Hobbie 1996) because the recalcitrant carbon leads to C starvation among microbes.

The C:N or lignin:N ratios of litter or soil are often good indicators of plant species patterns of N cycling (Finzi et al. 1998a, Scott & Binkley 1997). When comparing net N mineralization among species, litter C:N has a negative correlation with net N mineralization up to a threshold C:N ratio. Above this threshold, no net mineralization occurs, indicating microbial N immobilization (Prescott et al. 2000). However, the C:N ratio that determines the threshold between net mineralization

versus immobilization is variable and differs among species (Berg & Ekbohm 1993). This is likely because N mineralization is determined both by N concentrations and C quality (decomposability), and there is a linear relationship between N mineralization and C:N only when there is a uniform C recalcitrance among substrates (Jannsen 1996). The presence of secondary compounds can depress N cycling by serving as a C source for microbial immobilization (Schimel et al. 1996), by inhibiting microbial activity (Lodhi & Killingbeck 1980), or by binding labile compounds or mineral N (Hattenschwiler & Vitousek 2000).

Species effects on N cycling are also mediated by litter quantity, with high litter biomass enhancing N fluxes (Aerts et al. 1992, Hobbie 1992). Plant species can supply as much as 87% or as little as 23% of total plant N inputs to soil through root turnover (Aerts et al. 1992), and fine root production positively correlates with rates of net mineralization and nitrification (Aerts et al. 1992). Species differences in labile C inputs can have strong effects on N cycling (Flanagan & Van Cleve 1983), stimulating release of N from litter and soil organic matter (van der Krift et al. 2001) or decreasing rates of net N cycling by fostering microbial immobilization of N (Hobbie 1992). Even though labile C is a relatively small component of the total soil C pool, it is an extremely active pool, and species effects on labile C are responsible for up to tenfold differences in N cycling (Wedin & Pastor 1993). During some seasons, plant labile C inputs have stronger effects on N cycling than does litter chemistry (Eviner 2001).

Because nitrification is often limited by  $\text{NH}_4$  availability, net nitrification rates are often proportional to net mineralization rates (Finzi et al. 1998a, van Vuuren et al. 1993), and species effects on  $\text{NH}_4$  availability can be a key determinant of their effects on nitrification. However, the percent of mineralized N that is nitrified varies with species (Wedin & Tilman 1990). Nitrification can be extremely low or absent in the presence of species with high concentrations of phenolics (Cortez et al. 1996, Eviner 2001). While it is often assumed that these phenolics inhibit nitrifiers, different phenolics can have distinct effects on N cycling (Horner et al. 1988), and decreases in nitrification rates can also be due to decreases in  $\text{NH}_4$  availability imposed by phenolics, or increased microbial immobilization of N through use of phenolics as C substrates (Schimel et al. 1996).

Plant composition can also influence N cycling by altering local conditions such as temperature, pH, soil moisture, and  $\text{O}_2$  concentrations (Mack 1998, van Vuuren et al. 1993). These species effects on microclimate are often more important than litter chemistry or labile C inputs in determining species effects on N dynamics when temperature, moisture, or  $\text{O}_2$  limits microbial activity (Engelaar et al. 1995, Eviner 2001, van Vuuren et al. 1993). Ultimately, multiple traits best explain species effects on N cycling (Eviner 2001, Mack 1998, Steltzer & Bowman 1998, Wedin & Tilman 1990).

**N loss** High levels of N retention are associated with plant species that enhance microbial immobilization and plant uptake, or minimize soil  $\text{NO}_3$  (Epstein et al. 2001). Nitrate loss into streams from forested watersheds can be determined by

plant species effects on soil C:N ratios (Lovett et al. 2002). High rates of DON leaching are associated with species with high concentrations of tannins and phenolics that bind proteins (Hattenschwiler & Vitousek 2000), but these species may decrease overall N leaching by minimizing  $\text{NO}_3$  loss (Northup et al. 1998). Leaching loss can also be influenced by species effects on hydrology (Schlesinger et al. 2000).

Plant species also alter fluxes of  $\text{NO}$  and  $\text{N}_2\text{O}$  (Bronson & Mosier 1993, Woldendorp 1962). Species effects on nitrification are a key determinant of N gas loss because gaseous N forms are released during nitrification (Firestone & Davidson 1989) and because  $\text{NO}_3$  availability often limits denitrification. Species influence denitrification through their C inputs, and effects on soil oxygen,  $\text{NO}_3$ , temperature, and pH (Hume et al. 2002). The relative amount of acid soluble C to  $\text{NO}_3$  is the strongest determinant of species effects on denitrification (Hume et al. 2002), and phenolics are an important C source for denitrifying bacteria (Siqueira et al. 1991). Plant leaves can also directly assimilate and emit N compounds ( $\text{NO}$ ,  $\text{NO}_2$ ,  $\text{HNO}_3$ , organic  $\text{NO}_3$ ), and species differences in leaf  $\text{NO}_2$  flux rates relate to leaf N, nitrate reductase activity, and stomatal conductance (Sparks et al. 2001).

**OTHER NUTRIENTS** The effect of a plant species on any element cycle can be independent of its effects on other elements (Eviner & Chapin 2003). Fluxes of N, Ca, Mg, Mn, and S are mediated by biological mechanisms, while physical processes (e.g., leaching, atmospheric deposition) dominate fluxes of K, Na, Pb, Cd, and Zn, and chemical processes (e.g., interactions of metals with humic substrates) dominate fluxes of P, Fe, Zn, Pb, and Cd (Laskowski et al. 1995). Thus, plant species have different mechanisms by which they influence these cycles.

P availability is largely controlled by chemical interactions with the soil, such as through complexes with other elements (e.g., Ca, Al, Fe). Plant species influence P availability largely by influencing P solubility (Easterwood & Sartain 1990) through exudation of charged organic compounds that compete with  $\text{PO}_4$  for binding surfaces on other elements, alteration of soil pH that influences P-binding with elements, or accumulation of calcium oxalates that enhance P availability by decreasing soil calcium (reviewed in Chapin & Eviner 2003, Eviner & Chapin 2003). Because P is bonded to organic compounds through ester bonds rather than a direct bond to C, mineralization of P does not depend on microbial utilization of C, and plants can release organic P on demand with enzymes (Hinsinger 2001). P inputs from root turnover vary with species, supplying between 21% and 84% of total plant P input to soil (Aerts et al. 1992). Cluster, or proteoid roots are particularly efficient at accessing P because they release large amounts of organic acids that solubilize soil  $\text{PO}_4$  in the rhizosphere (Yan et al. 2002). The main controls over P availability change between systems. The main source of available P is from organic matter in the tundra, litter decomposition in forests, weathering of  $\text{CaPO}_4$  in deserts, and atmospheric deposition in Mediterranean climates (Gressel &

McColl 1997). In waterlogged soils or sediments, plant species that enhance soil O<sub>2</sub> concentrations increase P availability by lowering consumption of SO<sub>4</sub> leading to decreased mobilization of Fe (Christensen 1999).

The control of sulfur dynamics is intermediate between P and N since C-S compounds are mineralized depending on microbial demand for C, and ester-bonded S is released through enzymes. S mineralization rarely occurs in the absence of growing plants (Chowdhury et al. 2000). Mineralization of ester-bonded S compounds is enhanced by plant SO<sub>4</sub> uptake, which decreases soil SO<sub>4</sub>, thus stimulating the production of sulfohydrolases (Maynard et al. 1992). Root turnover is an important source of S and K (Burke & Raynal 1994). K dynamics are primarily determined by plant traits that affect K leaching from leaves (e.g., leaf area, leaf thickness, waxes) and soil (e.g., high fine root biomass in the surface soil) (Challinor 1968).

Species differences in Ca dynamics are primarily related to their rates of calcium release from litter (Dijkstra & Smits 2002), uptake, and allocation to biomass pools with different turnover times (Eriksson & Rosen 1994). In general, species that promote faster mineral weathering and have higher uptake rates enhance accumulations of base cations (Bergkvist & Folkesson 1995) and Ca availability (Challinor 1968, Finzi et al. 1998b) in both plant tissue and soil. Herbaceous dicots have a much higher base content than monocots (Cornelissen & Thompson 1997). Deciduous trees are particularly effective in enhancing Ca cycling (Willis et al. 1997) through cation pumping, where species with high fine root biomass in the lower soil profiles take up calcium from deep in the soil, and deposit it onto the surface soil through litter fall (Dijkstra & Smits 2002).

Species differ in their effects on Mg, Mn, Cu, Fe, Zn, and Al through organic acid input, cation uptake, and effects on soil pH and redox (Finzi et al. 1998b, Chapin & Eviner 2003). In general, plant species influence base cation availability by exuding low-molecular-weight organic acids. These acids act as ligands and, depending on the type exuded, have differential effects on metal solubility and speciation (Jones & Darrah 1994). Species that decrease pH increase Fe and Al solubility, which then out-compete base cations on cation exchange sites (Finzi et al. 1998b) and can lead to leaching of base cations. Organic acids rich in humic acid form water-soluble complexes with Fe, Mn, and P increasing Mn solubility 10- to 50-fold (Marschner 1995). Plant species can also enhance retention of nutrients by binding them with phenolics (Mn, Fe, Cu, Ca, Mg, and K) (Hattenschwiler & Vitousek 2000), or root mucilage (Pb, Cu, Zn, Cd) (Glinski & Lipiec 1990). Plant species differentially influence atmospheric deposition of elements through species differences in canopy structure (Weathers et al. 2001).

## Disturbance

Species effects on disturbance regimes can dominate many plant effects on ecosystem processes (Mack et al. 2001). Species effects on flooding and erosion were discussed earlier in this paper. Species susceptibility to wind throw depends on their morphology, age, size, rooting conditions, and tissue constituents, with taller

trees being more susceptible to wind damage than shorter-statured species with high root allocation. Species with full canopies have increased susceptibility to damage from wind as well as snow and ice accumulation (Boose et al. 1994, Foster 1988). Plant species composition has large impacts on the frequency, intensity, and spatial extent of fires (Billings 1991, D'Antonio & Vitousek 1992). Traits that influence flammability include (from increasing to decreasing importance): litter moisture content, biomass, the fineness of the litter, canopy structure (continuous fuel layer), silica-free ash content, and tissue chemistry (e.g., resins, caloric content). Conifers are more susceptible to high intensity fire than deciduous trees, owing to their lower moisture content, and thinner branches (Johnson 1992). Vegetation can also alter fire regime through its effects on insect outbreaks (Furyaev et al. 1983).

## Plant Species Interactions with Other Organisms

Plant species are frequently associated with a specific suite of other organisms that play key roles in ecosystems. Selective feeding is mediated by plant size (Mittelbach & Gross 1984), energetic content (May 1992), and concentrations of nutrients (Tian et al. 1993) and secondary compounds (Slansky 1997). Secondary compounds not only deter feeding of herbivores, but also can be used selectively by herbivores for protection. For example, crabs utilize unpalatable algae as decoration to deter predatory fish (Stachowicz & Hay 1999).

Plant architecture and litter persistence can alter the microclimate and habitat specificity of organisms. Termite populations increase in the favorable microclimate provided by recalcitrant litter (Tian et al. 1993), while the distribution of grazing animals may focus around sources of shade during warm parts of the day (Sanchez & Febles 1999). Plant architecture can also play a role in the distribution of organisms by altering access of prey to predators (Clark & Messina 1998), the energetics of foraging (Whelan 2001), or pollinator access to flowers (Lortie & Aarssen 1999). Leaf characteristics can deter organisms, with plant cuticles inhibiting microbes and viruses, and spines and leaf hairs irritating herbivores (Gutschick 1999). In many cases, organisms prefer multiple plant species for different reasons (Stachowicz & Hay 1999; V.T. Eviner, F.S. Chapin III, submitted manuscript).

In order to determine the ecosystem impact of a plant species, it is vital to include the impact of plants on these other organisms (Hobbie 1995). For example, gophers selectively build large mounds in association with plant species that increase soil cohesion through their high root surface area. This soil disturbance increases rates of N cycling, and consideration of selective gopher disturbance greatly changes the relative effects of plant species on N cycling (V.T. Eviner, F.S. Chapin III, submitted manuscript). Similarly, plant species differences in C inputs are responsible for distinct microbial communities (Grayston et al. 1998) that vary in their ability to degrade specific substrates (Sharma et al. 1998). Plant species rooting patterns and canopy architecture affect the distribution and activity of earthworms (Zaller & Arnone 1999), which have large effects on nutrient cycling (Cortez et al. 2000, Thompson et al. 1993).



## THE OVERALL IMPACT OF PLANT SPECIES ON ECOSYSTEMS

Several clear messages emerge from this review.

1. Multiple traits determine plant species effects on any ecosystem process.
2. Many plant traits influence a number of ecosystem properties and processes.
3. Plants have multiple, simultaneous effects on ecosystems.
4. Each ecosystem process is influenced by a different suite of traits or, if regulated by the same suite of traits, may be differentially influenced by these traits.

Most plant-effect studies focus on one type of ecosystem process and often on a subset of the key traits involved in that process. It is vital to consider the overall impact of a plant species on its ecosystem. In order to do this, it is crucial to understand how these traits and multiple effects interact. In this section of the review, we explore the relationships between multiple traits and ecosystem effects of plant species, and we propose a mechanistic framework to improve predictions of plant species effects on ecosystem processes.

### Suites of Related Traits or Unique Combinations of Independent Traits?

As discussed in the introduction, there is a solid framework linking a specific plant trait to an ecosystem process. The strength of these correlations results from suites of covarying plant traits that influence plant effects on N cycling (Chapin 1993). However, many ecosystem processes cannot be adequately predicted with a single trait because they are mediated by multiple plant traits that do not covary (Verville et al. 1998, Wardle et al. 1998). For example, species effects on N cycling and decomposition are mediated by litter chemistry, labile C inputs, and effects on soil microclimate (Bottner et al. 1999, Cheng & Coleman 1990, Eviner 2001), and species differences in litter C:N are independent of their differences in labile C inputs and effects on soil moisture (Eviner 2001). Many plant traits vary independently among species (Wardle et al. 1998) and across groups of species (Garnier 1991), and the relative importance of different traits in determining ecosystem processes can change across plant groups (Cornelissen & Thompson 1997). Even plants within the same functional group can have up to a tenfold difference in other traits (Wardle et al. 1998), explaining why the same plant species can be grouped into many different functional groups (Wilson 1999), and why a single plant trait often cannot adequately predict the ecosystem effects of plant species.

### Relationship Between Multiple Ecosystem Effects

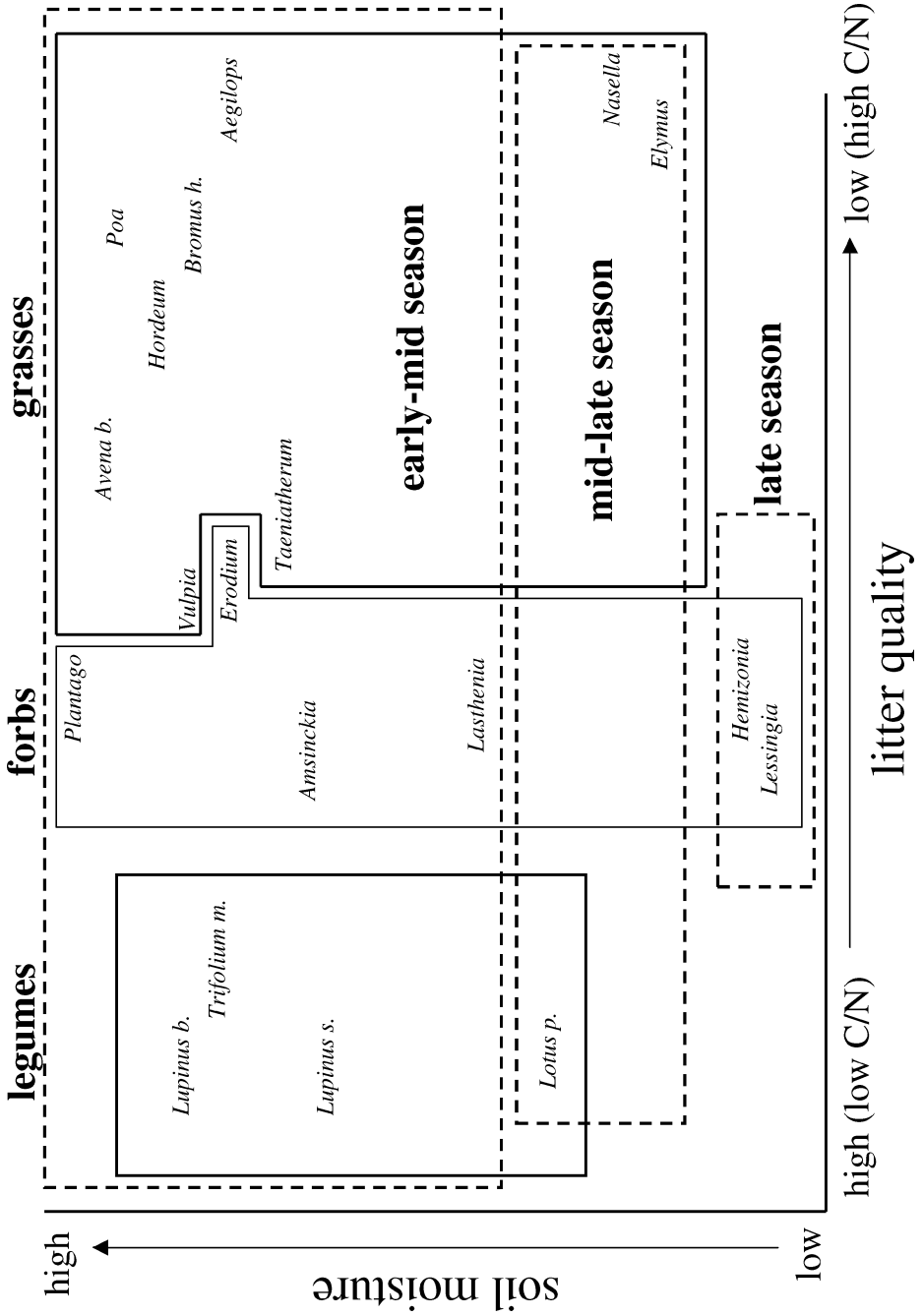
Species play multiple, simultaneous roles in ecosystems, and these functions are often distributed independently among species. For example, plant species effects

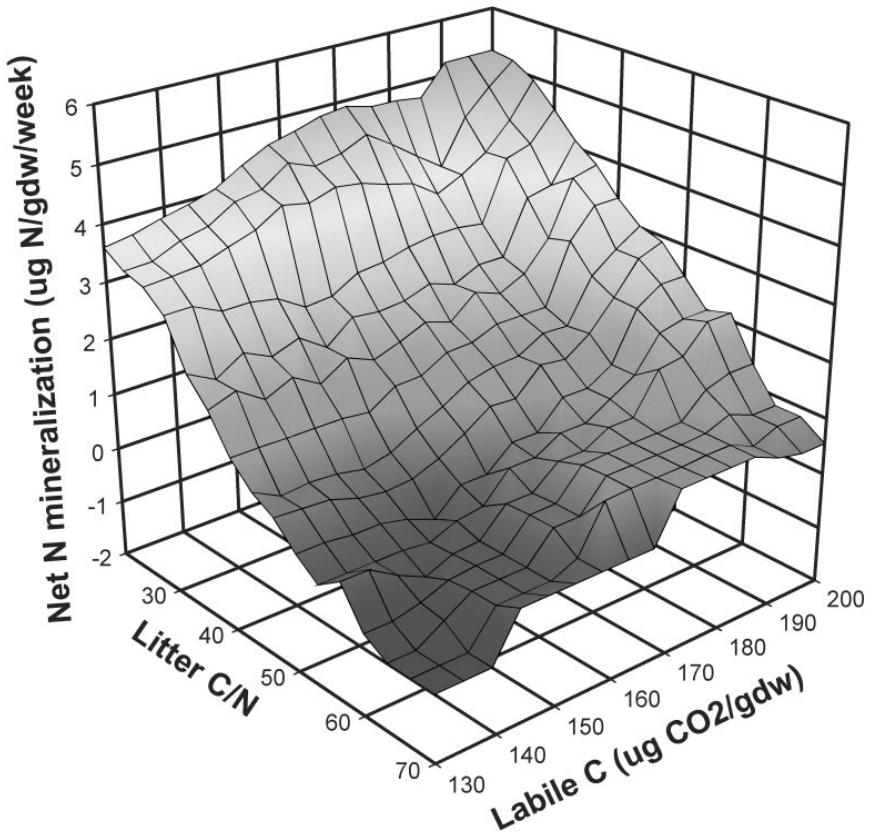
on N cycling are unrelated to their effects on P cycling (Hooper & Vitousek 1998), C cycling (Thomas & Prescott 2000), water fluxes, soil stability, and interactions with pests and beneficial organisms (Eviner & Chapin 2001). This is because many ecosystem processes are mediated by a distinct suite of traits. Just as multiple traits determine a plant species effect on any ecosystem process, the multiple effects of plant species can feedback to alter other ecosystem processes. For example, species effects on water availability can have large impacts on N cycling (Eviner 2001).

## FUNCTIONAL MATRIX: PREDICTING PLANT SPECIES ECOSYSTEM IMPACTS BASED ON MULTIPLE TRAITS

Single traits such as litter chemistry are often inadequate predictors of plant species effects on ecosystem processes because species exhibit unique combinations of traits that influence ecosystems, and multiple traits are responsible for the ecosystem effect of a plant species. The functional matrix approach describes the relationship between ecosystem processes and multiple traits that vary independently from one another. This approach builds upon the functional group and single trait approaches to consider how different traits of functional significance are distributed among species (Figure 1) and the relationship between multiple traits and an ecosystem function (Figure 2). Consideration of multiple plant traits greatly enhances our ability to account for plant species effects, particularly because this approach can account for changes in the relationship between multiple traits and ecosystem processes by highlighting when the effects of multiple traits are additive or interactive (e.g., the strength of N inhibition of lignin degradation increases with higher lignin concentrations). The variables on the axes can be selected based on the ecosystem process and season of interest and by considering attributes

**Figure 1** Existing plant functional type data can be used to form the basis of a functional matrix. Plant species from California annual grasslands are plotted according to their litter quality on the x-axis, and effects on soil moisture on the y-axis. The solid boxes represent functional groups based on litter chemistry, while the dashed boxes represent functional groups based on effects of soil moisture (determined by plant phenology). Both moisture and litter quality are important controllers of species effects on N cycling in California grasslands (Eviner 2001), and these vary independently and continuously among species. Data are from: Brown (1998), Eviner (2001), Franck et al. (1997), Gordon & Rice (1993), Hooper & Vitousek (1998), V.T. Eviner (unpublished manuscript). Species include: *Lupinus bicolor*, *Trifolium microcephalum*, *Lupinus sublanatus*, *Lotus purshianus*, *Plantago erecta*, *Erodium botrys*, *Amsinckia douglasiana*, *Lasthenia californica*, *Hemizonia congesta luzulaefolia*, *Lessingia micradenia*, *Vulpia microstachys*, *Avena barbata*, *Taeniatherum caput-medusae*, *Hordeum brachyantherum*, *Poa secunda*, *Bromus hordeaceus*, *Aegilops triuncialis*, *Nasella pulchra*, and *Elymus glaucus*.





**Figure 2** The functional matrix improves predictions of the ecosystem effects of plant species by considering the effects of multiple traits on ecosystem processes. In California annual grasslands, predictions of species effects on potential rates of net N mineralization are greatly improved by considering both litter C:N and labile C inputs ( $r^2 = 0.7$ ), than when just considering litter C:N ( $r^2 = 0.4$ ) (data from Eviner 2001).

of the species being compared. While our figures highlight the effects of two traits for the sake of simplicity, this approach is not limited to the effects of two traits.

The functional matrix approach is relatively simple and feasible especially because the building blocks for this framework are already well established. Our review clearly demonstrates that for any ecosystem process, there are only a few mechanisms that are critical in determining plant species effects. The traits of importance depend on the characteristics of the ecosystem, and previous studies have already determined the key mechanisms influencing ecosystem function in most ecosystems. In many ecosystems, the species-level information is readily available (Figure 1), and the data we collect to determine species effects on

one ecosystem function can also enhance our ability to predict multiple ecosystem impacts of plant species because the same plant traits are involved in multiple processes. These multiple impacts can influence one another, and the functional matrix approach also accounts for this (e.g., by using soil moisture as a trait axis to determine how it interacts with litter chemistry to influence nutrient cycling).

## Strength of this Approach

The power of this approach is that the ecosystem effects of multiple traits are the underlying mechanisms determining many types of vegetation effects on ecosystem processes. For example, the ranking of species effects on an ecosystem process varies with changing conditions (Cote & Fyles 1994). This approach allows us to consider the context dependence of species effects because it is based on the premise that differences in plant traits have consistent impacts on ecosystems, whether they occur among different plant species, or within a species grown under different conditions (Eviner 2001). Thus, we are able to use this multiple trait approach to account for:

- changes in the relative importance of traits with the stage of the process, season or over environmental gradients
- changes in plant species traits with season, phenology or over environmental gradients
- non-additive effects of plant species mixtures on ecosystem processes.

**CHANGES IN THE RELATIVE IMPORTANCE OF TRAITS** The traits that determine plant species effects on an ecosystem process can change owing to environmental conditions, plant age, growing season, and stage of a process. The functional matrix approach allows us to respond to these changes by selecting different axes or weighting them differently under changing conditions. For example, when environmental factors are the most limiting to ecosystem processes, the effects of plant species on these environmental factors become a key determinant of ecosystem processes (Eviner 2001, Mack 1998). Changes in the functional axes selected can account for changes in the mechanisms influencing species effects at a number of scales, ranging from local environmental gradients to global biomes.

**CHANGES IN PLANT TRAITS** Plant traits can change substantially because of different environmental conditions, seasons, and plant age (Austin & Vitousek 2000, Marschner 1995). Plant traits respond independently to environmental variables (Fonseca et al. 2000, Wright & Westoby 1999), and species differ in the responses of their traits to shifts in the environment (Hobbie & Gough 2002, Shierlaw & Alston 1984). These variations of traits within a species due to environmental change can be larger than interspecific differences (Olf 1992). Because the functional matrix approach determines plant species effects based on traits, it can

account for changes in the ecosystem effects of a given plant species under changing conditions.

**NONADDITIVE EFFECTS OF SPECIES MIXTURES** Although the patterns of species effects in monoculture often can't predict the patterns of mixtures, the same plant traits that determine plant species effects on ecosystem processes also determine the ecosystem effect of plant species mixtures. The multiple trait approach can account for these nonadditive effects because it considers the effects of changes in a species trait due to neighbors (Gordon & Rice 1993, Tremmel & Bazzaz 1995). For example, differences in litter C:N ratios and labile C in species grown in mixtures versus monocultures account for the nonadditive effects of mixtures on N cycling (Eviner 2001). In addition, this approach determines the combined effects of multiple traits, whether these multiple traits occur within a given species, or are associated with different plant species growing together. The stimulating effects of labile C on decomposition of recalcitrant C should occur whether these traits are expressed within one plant, or in neighboring plants.

The functional matrix approach, by focusing on the multiple mechanisms underlying plant species effects on ecosystems, greatly improves our predictions of plant effects over a wide range of conditions. It also encompasses the multiple effects of plant species on ecosystems. The ability to predict the overall effects of plants on ecosystems under a variety of conditions can be a powerful management tool, allowing us to simultaneously provide multiple ecosystem services, or address multiple environmental problems through vegetation manipulations (Eviner & Chapin 2001).

## ACKNOWLEDGMENTS

Thanks to Sarah Hobbie and Gaius Shaver for comments on this manuscript. This is a contribution to the program of the Institute of Ecosystem Studies.

**The *Annual Review of Ecology, Evolution, and Systematics* is online at <http://ecolsys.annualreviews.org>**

## LITERATURE CITED

- Abrahams AD, Parsons AJ, Wainwright J. 1994. Resistance to overland-flow on semi-arid grassland and shrubland hillslopes, Walnut Gulch, southern Arizona. *J. Hydrol.* 156: 431–46
- Aerts R, Bakker C, De Caluwe H. 1992. Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem. *Biogeochemistry* 15:175–90
- Aerts R, De Caluwe H. 1997. Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. *Ecology* 78:244–60
- Allen WC, Hook PB, Biederman JA, Stein OR. 2002. Temperature and wetland plant species effects on wastewater treatment and root zone oxidation. *J. Environ. Qual.* 31:1010–16
- Angers D, Caron J. 1998. Plant-induced changes in soil structure: processes and feedbacks. *Biogeochemistry* 42:55–72

- Augusto L, Turpault MP, Ranger J. 2000. Impact of forest tree species on feldspar weathering rates. *Geoderma*. 96:215–37
- Austin A, Vitousek P. 2000. Precipitation, decomposition and litter decomposability of *Meterosideros polymorpha* in native forests on Hawaii. *J. Ecol.* 88:129–38
- Baldocchi D, Kelliher FM, Black TA, Jarvis P. 2000. Climate and vegetation controls on boreal zone energy exchange. *Glob. Change Biol.* 6:69–83
- Baldocchi D, Vogel C. 1996. Energy and CO<sub>2</sub> flux densities above and below a temperate broad-leaves forest and a boreal pine forest. *Tree Physiol.* 16:5–16
- Balesdent J, Balabane M. 1996. Major contribution of roots to soil carbon storage inferred from maize cultivated soils. *Soil Biol. Biochem.* 28:1261–63
- Bell D. 1999. Australian trees for the rehabilitation of waterlogged and salinity-damaged landscapes. *Aust. J. Bot.* 47:697–716
- Berg B. 2000a. Initial rates and limit values for decomposition of Scots pine and Norway spruce needle litter: a synthesis for N-fertilized forest stands. *Can. J. For. Res.* 30:122–35
- Berg B. 2000b. Litter decomposition and organic matter turnover in northern forest soils. *For. Ecol. Manage.* 133:13–22
- Berg B, Ekbohm G. 1993. Decomposing needle litter in a *Pinus contorta* (Lodgepole pine) and *Pinus sylvestris* (Scots pine) monoculture systems—is there a maximum mass loss. *Scand J. For. Res.* 8:457–65
- Bergkvist B, Folkesson L. 1995. The influence of tree species on acid deposition, proton budgets and element fluxes in south Swedish forest ecosystems. *Ecol. Bull.* 44:90–99
- Billings W. 1991. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. In *The Earth in Transition: Patterns and Processes of Biotic Impoverishment*, ed. G Woodwell, pp. 301–22. New York: Cambridge Univ. Press
- Binkley D, Giardina C. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. *Biogeochemistry* 42:89–106
- Blair J. 1988. Nitrogen, sulfur and phosphorus dynamics in decomposing deciduous leaf litter in the southern Appalachians. *Soil Biol. Biochem.* 20:693–701
- Boettcher S, Kalisz P. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology* 71:1365–72
- Boose E, Foster D, Fluet M. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monogr.* 64:369–400
- Bottner P, Pansu M, Sallih Z. 1999. Modelling the effect of active roots on soil organic matter turnover. *Plant Soil.* 216:15–25
- Bronson K, Mosier A. 1993. Nitrous oxide emissions and methane consumption in wheat and corn-cropped systems in north-eastern Colorado. In *Agricultural Ecosystem Effects on Trace Gases and Global Climate Change*, ed. L Harper, A Mosier, J Duxbury, D Rolston, pp. 133–44. Madison, WI: ASA, CSSA, SSSA
- Brown C. 1998. *Restoration of California central valley grasslands: applied and theoretical approaches to understanding interactions among prairie species*. PhD thesis. Univ. California, Davis. 177 pp.
- Burke M, Raynal D. 1994. Fine root growth phenology, production and turnover in a northern hardwood forest ecosystem. *Plant Soil.* 162:135–46
- Caldwell M, Dawson T, Richards J. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–61
- Camberato J. 2001. Cation exchange capacity—everything you want to know and much more. *S.C. Turfgrass Found. News* Oct–Dec 2001
- Challinor D. 1968. Alteration of surface soil characteristics by four tree species. *Ecology* 49:286–90
- Chapin FS III. 1993. Functional role of growth forms in ecosystem and global processes. In *Scaling Physiological Processes: Leaf to Globe*, ed. J Ehleringer, C Field, pp. 287–312. San Diego: Academic

- Chapin FS III, Eviner VT. 2003. Biogeochemistry of terrestrial net primary production. In *Treatise on Geochemistry. Volume 8: Biogeochemistry*, ed. WH Schlesinger. In press
- Chapin FS III, Fetcher N, Kielland K, Everett KR, Linkins AE. 1988. Productivity and nutrient cycling of Alaskan tundra-enhancement by flowing soil water. *Ecology* 69:693–702
- Chapin FS III, McGuire AD, Randerson J, Pielke R, Baldocchi D, et al. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biol.* 6:211–23
- Cheng W, Coleman D. 1990. Effect of living roots on soil organic matter decomposition. *Soil Biol. Biochem.* 22:781–87
- Chowdhury MAH, Kouno K, Ando T, Nagaoka T. 2000. Microbial biomass, S mineralization and S uptake by African millet from soil amended with various composts. *Soil Biol. Biochem.* 32:845–52
- Christensen KK. 1999. Comparison of iron and phosphorus mobilization from sediments inhabited by *Littorella uniflora* and *Sphagnum* sp. at different sulfate concentrations. *Arch. Hydrobiol.* 145:257–75
- Christian JM, Wilson SD. 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology* 80:2397–407
- Clark T, Messina F. 1998. Foraging behavior of lacewing larvae (Neuroptera: Chrysopidae) on plants with divergent architectures. *J. Insect Behav.* 11:303–17
- Cole D. 1995. Soil nutrient supply in natural and managed forests. *Plant Soil.* 169:43–53
- Cornelissen J, Thompson K. 1997. Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytol.* 135:109–14
- Cortez J, Billes G, Bouche M. 2000. Effect of climate, soil type and earthworm activity on nitrogen transfer from a nitrogen-15-labelled decomposing material under field conditions. *Biol. Fert. Soils.* 30:318–27
- Cortez J, Demard J, Bottner P, Monrozier L. 1996. Decomposition of mediterranean leaf litters: a microcosm experiment investigating relationships between decomposition rates and litter quality. *Soil Biol. Biochem.* 28:443–52
- Cote B, Fyles J. 1994. Leaf litter disappearance of hardwood species of southern Quebec: interaction between litter quality and stand type. *Ecoscience* 1:322–28
- Cooteaux M, NcTiernan K, Berg B, Szuberla D, Dardenne P, Bottner P. 1998. Chemical composition and carbon mineralization potential of scots pine needles at different stages of decomposition. *Soil Biol. Biochem.* 30:583–95
- D'Antonio C, Vitousek P. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23:63–87
- Dawson T. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia.* 117:476–85
- Degens BP. 1997. Macro-aggregation of soils by biological bonding and binding mechanisms and the factors affecting these: a review. *Aust. J. Soil. Res.* 35:431–59
- Deluca TH, Drinkwater LE, Wiefeling BA, DeNicola DM. 1996. Free-living nitrogen-fixing bacteria in temperate cropping systems: Influence of nitrogen source. *Biol. Fert. Soils.* 23:140–44
- De Ploey Y, Cruz O. 1979. Landslides in the serra de Mar, Brazil. *Catena.* 6:111–22
- Devine DL, Wood M, Donart GB. 1998. Runoff and erosion from a mosaic tobosagrass and burrograss community in the northern Chihuahuan Desert grassland. *J. Arid. Environ.* 39:11–19
- Dijkstra F, Smits M. 2002. Tree species effects on calcium cycling: the role of calcium uptake in deep soils. *Ecosystems* 5:385–98
- DiTomaso JM. 2000. Invasive weeds in rangelands: Species, impacts and management. *Weed Sci.* 48:255–65
- Doerr SH, Shakesby RA, Walsh RPD. 2000. Soil water repellency: its causes, characteristics and hydro-geomorphological significance. *Earth Sci. Rev.* 51:33–65
- Dormaar J. 1990. Effect of active roots on



- the decomposition of soil organic materials. *Biol. Fert. Soils*. 10:121–26
- Easterwood G, Sartain J. 1990. Clover residue effectiveness in reducing orthophosphate sorption on ferric hydroxide coated soil. *Soil Sci. Soc. Am. J.* 54:1345–50
- Engelaar W, Symens J, Laanbroek H, Blom C. 1995. Preservation of nitrifying capacity and nitrate availability in waterlogged soils by radial oxygen loss from roots of wetland plants. *Biol. Fert. Soils*. 20:243–48
- Epstein HE, Burke IC, Mosier AR. 2001. Plant effects on nitrogen retention in shortgrass steppe 2 years after N-15 addition. *Oecologia*. 128:422–30
- Epstein H, Burkey I, Mosier A. 1998. Plant effects on spatial and temporal patterns of nitrogen cycling in shortgrass steppe. *Ecosystems*. 1:374–85
- Eriksson H, Rosen K. 1994. Nutrient distribution in a Swedish tree species experiment. *Plant Soil*. 164:51–59
- Evans R, Young J. 1970. Plant litter and establishment of alien annual species in rangeland communities. *Weed Sci*. 18:697–702
- Eviner VT. 2001. *Linking plant community composition and ecosystem dynamics: interactions of plant traits determine the ecosystem effects of plant species and plant species mixtures*. PhD thesis. Univ. California, Berkeley. 404 pp.
- Eviner VT, Chapin FI. 2001. The effects of California grassland species on their ecosystems: implications for sustainable agriculture and rangeland management. *Calif. Agr.* 55:254–59
- Eviner VT, Chapin FS III. 2002. The influence of plant species, fertilization and elevated CO<sub>2</sub> on soil aggregate stability. *Plant Soil*. 246:211–19
- Eviner VT, Chapin FS III. 2003. Selective gopher disturbance influences plant species effects on nitrogen cycling. *Oikos*. Submitted
- Eviner VT, Chapin FS III. 2003. Biogeochemical interactions and biodiversity. In *Element Interactions: Rapid Assessment Project of SCOPE*, ed. J Melillo, C Field, M Moldan. Washington, DC: Island. In press
- Finzi A, Canham C, Van Breemen N. 1998b. Canopy tree-soil interactions within temperate forests: species effects on pH and cations. *Ecol. Appl.* 8:447–54
- Finzi A, Van Breeman N, Canham C. 1998a. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecol. Appl.* 8:440–46
- Firestone MK, Davidson E. 1989. Microbiological basis of NO and N<sub>2</sub>O production and consumption in soils. In *Exchanges of Trace Gases Between Terrestrial Ecosystems and the Atmosphere*, ed. M Andreae, D Schimel, pp. 7–21. New York: Wiley
- Flanagan P, Van Cleve K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Can. J. For. Res.* 13:795–817
- Foley J, Kutzbach J, Coe M, Lewis S. 1994. Feedbacks between climate and boreal forests during the Holocene epoch. *Nature*. 371:52–54
- Fonseca C, Overton J, Collins B, Westoby M. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *J. Ecol.* 88:964–77
- Foster D. 1988. Species and stand response to catastrophic wind in central New England. *J. Ecol.* 76:135–51
- Franck VM, Hungate BA, Chapin FS III, Field CB. 1997. Decomposition of litter produced under elevated CO<sub>2</sub>: Dependence on plant species and nutrient supply. *Biogeochemistry*. 36:223–37
- Franco A, De Faria S. 1997. The contribution of N<sub>2</sub>-fixing tree legumes to land reclamation and sustainability in the tropics. *Soil Biol. Biochem.* 29:897–903
- Furyaev V, Wein R, McLean D. 1983. Fire influences in Abies-dominated forests. In *The role of fire in northern circumpolar ecosystems*, ed. R Wein, D McLean, pp. 221–34. New York: Wiley
- Gale WJ, Cambardella CA, Bailey TB. 2000. Surface residue- and root-derived carbon in stable and unstable aggregates. *Soil Sci. Soc. Am. J.* 64:196–201
- Garnier E. 1991. Resource capture biomass

- allocation and growth in herbaceous plants. *Trends Ecol. Evol.* 6:126–31
- Gijsman A, Thomas R. 1996. Evaluation of some physical properties of an oxisol after conversion of native savanna into legume-based or pure grass pastures. *Tropical Grasslands.* 30:237–48
- Gillon D, Joffre R, Ibrahima A. 1994. Initial litter properties and decay rate: a microcosm experiment on Mediterranean species. *Can. J. Bot.* 72:946–54
- Gleason M, Elmer D, Pien N, Fisher J. 1979. Effects of stem density upon sediment retention by salt marsh cord grass, *Spartina alterniflora* Loisel. *Estuaries.* 2:271–73
- Glinksi J, Lipiec J. 1990. *Soil Physical Conditions and Plant Roots.* Boca Raton, FL.: CRC. 250 pp.
- Gloaguen J, Touffet J. 1982. C-N evolution in the leaves and during litter decomposition under Atlantic climate—the beech and some conifers. *Ann. Sci. Forest.* 39:219–30
- Gordon D, Rice K. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology* 74:68–82
- Gordon D, Welker J, Menke J, Rice K. 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia.* 79:533–41
- Grayston S, Wang S, Campbell C, Edwards A. 1998. Selective influence of plant species on microbial diversity in the rhizosphere. *Soil Biol. Biochem.* 30:369–78
- Gressel N, McColl J. 1997. Phosphorus mineralization and organic matter: a critical review. In *Driven by Nature: Plant Litter Quality and Decomposition*, ed. G Cadish, K Giller, pp. 297–309. Wallington, UK: CAB
- Grosse W, Jovy K, Tiebel H. 1996. Influence of plants on redox potential and methane production in water-saturated soil. *Hydrobiologia.* 340:93–99
- Gutschick V. 1999. Biotic and abiotic consequences of differences in leaf structure. *New Phytol.* 143:3–18
- Hart S, Nason G, Myrold D, Perry D. 1994. Dynamics of gross nitrogen transformations in an old-growth forest—the carbon connection. *Ecology* 75:880–91
- Hattenschwiler S, Vitousek PM. 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol. Evol.* 15:238–43
- Heal O, Anderson J, Swift M. 1997. Plant litter quality and decomposition: an historical overview. In *Driven by nature: plant litter quality and decomposition*, ed. G Cadish, K Giller, 3–30. Wallington, UK: CAB
- Herwitz S. 1986. Infiltration-excess caused by stemflow in a cyclone-prone tropical rainforest. *Earth Surf. Process.* 11:401–12
- Hinsinger P. 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant Soil.* 237:173–95
- Hobbie SE. 1992. Effects of plant-species on nutrient cycling. *Trends Ecol. Evol.* 7:336–39
- Hobbie SE. 1995. Direct and indirect effects of plant species on biogeochemical processes in arctic ecosystems. In *Arctic and Alpine Biodiversity*, ed. FS Chapin III, C Korner, pp. 213–24. Berlin: Springer-Verlag
- Hobbie SE. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* 66:503–22
- Hobbie SE, Gough L. 2002. Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in northern Alaska. *Oecologia.* 131:453–62
- Hogg E, Lieffers V. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. *Can. J. For. Res.* 21:
- Hooper D, Vitousek P. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.* 68:121–49
- Horner J, Gosz J, Cates R. 1988. The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems. *Am. Nat.* 132:869–83
- Howard P, Howard D, Lowe L. 1998. Effects of tree species and soil physiochemical conditions on the nature of soil organic matter. *Soil Biol. Biochem.* 30:285–97

- Hume N, Fleming M, Horne A. 2002. Denitrification potential and carbon quality of four aquatic plants in wetland microcosms. *Soil Sci. Soc. Am. J.* 66:1706–12
- Janssen B. 1996. Nitrogen mineralization in relation to C:N ratio and decomposability of organic materials. *Plant Soil.* 181:39–45
- Jastrow J. 1987. Changes in soil aggregation associated with tallgrass prairie restoration. *Am. J. Bot.* 74:1656–64
- Jenny H. 1941. *Factors of Soil Formation*. New York: McGraw-Hill
- Johnson D. 1992. Effects of forest management on soil carbon storage. *Water Air Soil Poll.* 64:83–0
- Jones DL, Darrah PR. 1994. Role of root derived organic-acids in the mobilization of nutrients from the rhizosphere. *Plant Soil.* 166:247–57
- Jones M, Koenigs R, Vaughn C, Murphy A. 1983. Converting chaparral to grassland increases soil fertility. *Calif. Agr.* 37:23–24
- Kelly E, Chadwick O, Hilinski T. 1998. The effect of plants on mineral weathering. *Biogeochemistry* 42:21–53
- Kirkby M. 1995. Modeling the links between vegetation and landforms. *Geomorphology* 13:319–35
- Kloot PM. 1983. The role of common ice-plant (*Mesembryanthemum-crystallinum*) in the deterioration of medic pastures. *Aust. J. Ecol.* 8:301–6
- Laroche F. 1994. *Melaleuca management plan for Florida*. Florida: Exotic Pest Plant Council. 88 pp.
- Laskowski R, Niklinska M, Maryanski M. 1995. The dynamics of chemical elements in forest litter. *Ecology* 76:1393–406
- Lawrence D, Schoenike R, Quispel A, Bond G. 1967. The role of *Dryas drummondii* in vegetation development following ice regression at Glacier Bay, Alaska, with special reference to nitrogen fixation by root nodules. *J. Ecol.* 55:793–813
- Le Maitre DC, Scott DF, Colvin C. 1999. A review of information on interactions between vegetation and groundwater. *Water SA.* 25:137–52
- Lewis J, Starkey R. 1968. Vegetable tannins, their decomposition and effects of decomposition of some organic compounds. *Soil Sci.* 106:241–47
- Liste HH, Alexander M. 2000. Plant-promoted pyrene degradation in soil. *Chemosphere.* 40:7–10
- Lodhi M, Killingbeck K. 1980. Allelopathic inhibition of nitrification and nitrifying bacteria in ponderosa pine (*Pinus ponderosa* Dougl.) community. *Am. J. Bot.* 67:1423–29
- Lortie CJ, Aarssen LW. 1999. The advantage of being tall: Higher flowers receive more pollen in *Verbascum thapsus* L.-(Scrophulariaceae). *Ecoscience* 6:68–71
- Lovett GM, Weathers KC, Arthur MA. 2002. Control of nitrogen loss from forested watersheds by soil carbon: Nitrogen ratio and tree species composition. *Ecosystems* 5:712–18
- Lyons T, Schwerdtfeger P, Hacker J, Foster I, Smith R, Huang X. 1993. Land atmosphere interaction in a semiarid region—the bunny fence experiment. *Bull. Am. Meteorol. Soc.* 74:1327–34
- Mack M. 1998. *Effects of exotic grass invasion on ecosystem nitrogen dynamics in a Hawaiian woodland*. PhD thesis. Univ. California, Berkeley. 209 pp.
- Mack M, D'Antonio C, Ley R. 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C4 grasses in Hawaii. *Ecol. Appl.* 11:1323–35
- Marschner H. 1995. *Mineral Nutrition of Higher Plants*. London: Academic
- Matson P. 1990. Plant-soil interactions during primary succession at Hawaii Volcanoes National Park. *Oecologia.* 85:241–46
- May P. 1992. Flower selection and the dynamics of lipid reserves in two nectarivorous butterflies. *Ecology* 73:2181–91
- Maynard DG, Stadt JJ, Mallett KI, Volney WJA. 1992. A comparison of sulfur impacted and non-impacted lodgepole pine stands in west central Alberta. *Can. J. Soil Sci.* 72:327–
- McClougherty C, Pastor J, Aber J, Melillo J. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology* 66:266–75

- Melillo J, Aber J, Linkins A, Ricca A, Perry B, Nadelhoffer K. 1989. Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. *Plant Soil*. 115: 189–98
- Melillo J, Aber J, Muratore J. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–26
- Miles J. 1985. The pedogenic effects of different species and vegetation types and the implications of succession. *J. Soil Sci.* 36:571–84
- Miller R, Jastrow J. 1990. Hierarchy of root and mycorrhizal fungal interactions with soil aggregation. *Soil Biol. Biochem.* 22:579–84
- Mittelbach G, Gross K. 1984. Experimental studies of seed predation in old-fields. *Oecologia*. 65:7–13
- Mueller-Dombois D. 1973. A non-adapted vegetation interferes with water removal in a tropical rainforest area in Hawaii. *Tropical Ecol.* 14:1–18
- Mueller T, Jensen L, Nielsen E, Magid J. 1998. Turnover of carbon and nitrogen in a sandy loam soil following incorporation of chopped maize plants, barley straw and blue grass in the field. *Soil Biol. Biochem.* 30:561–71
- Munzbergova Z, Ward D. 2002. Acacia trees as keystone species in Negev desert ecosystems. *J. Veg. Sci.* 13:227–36
- Neff JC, Townsend AR, Gleixner G, Lehman SJ, Turnbull J, Bowman WD. 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature* 419:915–17
- Northup R, Dahlgren R, McColl J. 1998. Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: a positive feedback? *Biogeochemistry* 42:189–20
- Noskopliss LC, Cook FD. 1994. The association of free-living nitrogen-fixing bacteria with the roots of high arctic graminoids. *Arctic Alpine Research* 26:180–86
- Olf H. 1992. Effects of light and nutrient availability on dry-matter and N-allocation in 6 successional grassland species testing for resource ratio effects. *Oecologia*. 89:412–21
- Otterman J. 1989. Enhancement of surface-atmosphere fluxes by desert fringe vegetation through reduction of surface albedo and of soil heat flux. *Theor. Appl. Climatol.* 40:67–79
- Ovington J. 1953. Studies of the development of woodland conditions under different trees. I. Soils pH. *J. Ecol.* 41:13–34
- Pitt M, Burgy R, Heady H. 1978. Influences of brush conversion and weather patterns on runoff from a northern California watershed. *J. Range Manage.* 31:23–27
- Prandini L, Guidicini G, Bottura J, Poncano W, Santos A. 1977. Behavior of the vegetation in slope stability: a critical review. *B. Int. Assoc. Eng. Geol.* 16:51–55
- Prescott C, Chappell H, Vesterdal L. 2000. Nitrogen turnover in forest floors of coastal Douglas-fir at sites differing in soil nitrogen capital. *Ecology* 81:1878–86
- Puget P, Drinkwater LE. 2001. Short-term dynamics of root- and shoot-derived carbon from a leguminous green manure. *Soil Sci. Soc. Am. J.* 65:771–79
- Qadir M, Schubert S, Ghafoor A, Murtaza G. 2001. Amelioration strategies for sodic soils: A review. *Land Degrad. Dev.* 12:357–86
- Ranger J, Nys C. 1994. The effect of spruce (*Picea-abies karst*) on soil development—an analytical and experimental approach. *Europ. J. Soil Sci.* 45:193–204
- Raulund-Rasmussen K, Vejre H. 1995. Effect of tree species and soil properties on nutrient immobilization in the forest floor. *Plant Soil*. 168–169:345–52
- Reid J, Goss M. 1982. Interactions between soil drying due to plant water use and decreases in aggregate stability caused by maize roots. *J. Soil Sci.* 33:47–53
- Rillig M, Wright S, Eviner VT. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. *Plant Soil*. 238:325–33
- Robles M, Chapin FS III. 1995. Comparison of the influence of two exotic species on ecosystem processes in the Berkeley hills. *Madrono*. 42:349–57

- Sallih Z, Bottner P. 1988. Effect of wheat (*Triticum aestivum*) roots on mineralization rates of soil organic matter. *Biol. Fert. Soils*. 7:67–70
- Sanchez R, Febles I. 1999. Behaviour of grazing Holstein cows in natural shade. *Cuban J. Agric. Sci.* 33:241–46
- Scheu S. 1997. Effects of litter (beech and stinging nettle) and earthworms (*Octolasion lac-teum*) on carbon and nutrient cycling in beech forests on a basalt-limestone gradient: A laboratory experiment. *Biol. Fert. Soils*. 24:384–93
- Schimel J, Van Cleve K, Cates R, Clausen T, Reichardt P. 1996. Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: implications for changes in N cycling during succession. *Can. J. Bot.* 74:84–90
- Schlesinger W, Ward T, Anderson J. 2000. Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: II. Field plots. *Biogeochemistry* 49:69–86
- Schlesinger WH. 1997. *Biogeochemistry*. San Diego: Academic
- Schlesinger WH, Reynolds J, Cunningham G, Huenneke L, Jarrel W, et al. 1990. Biological Feedbacks in Global Desertification. *Science*. 247:1043–48
- Scott N. 1998. Soil aggregation and organic matter mineralization in forests and grasslands: plant species effects. *Soil Sci. Soc. Am. J.* 62:1081–89
- Scott N, Binkley D. 1997. Foliage litter quality and annual net N mineralization: Comparison across North American forest sites. *Oecologia* 111:151–59
- Selby MJ. 1993. *Hillslope Materials and Processes*. Oxford: Oxford Univ. Press
- Sharma S, Rangger A, von Lutzow M, Insam H. 1998. Functional diversity of soil bacterial community increases after maize litter amendment. *Eur. J. Soil Biol.* 34:53–60
- Shierlaw J, Alston A. 1984. Effect of soil compaction on root growth and uptake of phosphorus. *Plant Soil*. 77:15–28
- Shukla J, Nobre C, Sellers P. 1990. Amazon deforestation and climate change. *Science* 247:1322–25
- Siqueira J, Muraleedharan G, Hammerschmidt R, Safir G. 1991. Significance of phenolic compounds in plant soil-microbial systems. *CRC Crit. Rev. Plant Sci.* 10:63–121
- Slansky F Jr. 1997. Allelochemical-nutrient interactions in herbivore nutritional ecology. In *Herbivores: Their interactions with secondary plant metabolites*, ed. G Rosenthal, M Berenbaum, pp. 135–75. San Diego: Academic
- Spaccini R, Piccolo A, Conte P, Haberhauer G, Gerzabek M. 2002. Increased soil organic carbon sequestration through hydrophobic protection by humic substances. *Soil Biol. Biochem.* 34:1839–51
- Sparks J, Monson R, Sparks K, Lerdau M. 2001. Leaf uptake of nitrogen dioxide (NO<sub>2</sub>) in a tropical wet forest: implications for tropospheric chemistry. *Oecologia* 127:214–21
- Stachowicz J, Hay M. 1999. Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores. *Ecology* 80:495–509
- Steltzer H, Bowman W. 1998. Differential influence of plant species on soil nitrogen transformations with moist meadow alpine tundra. *Ecosystems* 1:464–74
- Swank W, Douglass J. 1974. Streamflow greatly reduced by converting deciduous hardwood stands to pine. *Science* 185:857–59
- Ta T, Faris M. 1987. Species variation in the fixation and transfer of nitrogen from legumes to associated grasses. *Plant Soil*. 98:265–74
- Taylor B, Parkinson D, Parsons W. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70:97–104
- Terwilliger V, Waldron L. 1991. Effects of root reinforcement on soil-slip patterns in the Transverse Ranges of southern California. *Geol. Soc. Am. Bull.* 103:775–85
- Thomas K, Prescott C. 2000. Nitrogen availability in forest floors of three tree species on the same site: the role of litter quality. *Can. J. For. Res.* 30:1698–706

- Thompson L, Thomas C, Radley J, Williamson S, Lawton J. 1993. The effect of earthworms and snails in a simple plant community. *Oecologia* 95:171–78
- Tian G, Brussaard L, Kang B. 1993. Biological effects of plant residues with contrasting chemical composition under humid tropical conditions: effects on soil fauna. *Soil Biol. Biochem.* 25:731–37
- Torn MS, Chapin FS III. 1993. Environmental and biotic controls over methane flux from arctic tundra. *Nato Advanced Research Workshop On Atmospheric Methane: Sources, Sinks And Role In Global Change, Mount Hood, Oregon, Usa, October 7–11, 1991. Chemosphere.* 26:357–68
- Tremmel D, Bazzaz F. 1995. Plant architecture and allocation in different neighborhoods: implications for competitive success. *Ecology* 76:262–71
- Troeh F, Thompson L. 1993. *Soil and soil fertility*. New York: Oxford Univ. Press
- Updegraff K, Pastor J, Bridgman S, Johnston C. 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. *Ecol. Appl.* 5:151–63
- Urquiaga S, Cadisch G, Alves BJR, Boddey RM, Giller KE. 1998. Influence of decomposition of roots of tropical forage species on the availability of soil nitrogen. *Soil Biol. Biochem.* 30:2099–106
- Van der Krift TAJ, Gioacchini P, Kuikman PJ, Berendse F. 2001. Effects of high and low fertility plant species on dead root decomposition and nitrogen mineralisation. *Soil Biol. Biochem.* 33:2115–24
- Van der Krift TAJ, Kuikman PJ, Berendse F. 2002. The effect of living plants on root decomposition of four grass species. *Oikos* 96:36–45
- Van Veen JA, Kuikman PJ. 1990. Soil structural aspects of decomposition of organic matter by microorganisms. *Biogeochemistry* 11:213–34
- Van Vuuren MMI, Berendse F, de Visser W. 1993. Species and site differences in the decomposition of litters and roots from wet heathlands. *Can. J. Bot.* 71:167–73
- Verville J, Hobbie S, Chapin FI, Hooper D. 1998. Response of tundra CH<sub>4</sub> and CO<sub>2</sub> flux to manipulation of temperature and vegetation. *Biogeochemistry* 41:215–35
- Viles H. 1990. The agency of organic beings: a selective review of recent work in biogeomorphology. In *Vegetation and Erosion*, ed. J Thornes, pp. 5–24. New York: Wiley
- Vitousek PM, Cassman K, Cleveland C, Crews T, Field CB, et al. 2002. Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry* 57:1–45
- Vitousek PM, Walker L. 1989. Biological invasion by *Myrica fayan* Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecol. Monogr.* 59:247–65
- Wainwright J, Parsons AJ, Abrahams AD. 2000. Plot-scale studies of vegetation, overland flow and erosion interactions: case studies from Arizona and New Mexico. *Hydrol. Process.* 14:2921–43
- Waldron L, Dakessian S. 1981. Soil reinforcement by roots: calculation of increased soil shear resistance from root properties. *Soil Sci.* 132:427–35
- Wardle D. 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton, NJ: Princeton Univ. Press. 392 pp.
- Wardle D, Barker G, Bonner K, Nicholson K. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species in ecosystems? *J. Ecol.* 86:405–20
- Wardle D, Nicholson K, Ahmed M, Rahman A. 1994. Interference effects of the invasive plant *Carduus nutans* L. against the nitrogen fixation ability of *Trifolium repens* L. *Plant Soil.* 163:287–97
- Weathers KC. 1999. The importance of cloud and fog in the maintenance of ecosystems. *Trends Ecol. Evol.* 14:214–15
- Weathers KC, Cadenasso ML, Pickett STA. 2001. Forest edges as nutrient and pollutant concentrators: Potential synergisms between fragmentation, forest canopies, and

- the atmosphere. *Conserv. Biol.* 15:1506–14
- Wedin D, Pastor J. 1993. Nitrogen mineralization dynamics in grass monocultures. *Oecologia* 96:186–92
- Wedin D, Tieszen L, Dewey B, Pastor J. 1995. Carbon isotope dynamics during grass decomposition and soil organic matter formation. *Ecology* 76:1383–92
- Wedin D, Tilman D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84:433–41
- Whelan C. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology* 82:219–31
- Willis K, Braun M, Sumegi P, Toth A. 1997. Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. *Ecology* 78:740–50
- Wilson J. 1999. Guilds, functional types and ecological groups. *Oikos*. 86:507–22
- Woldendorp J. 1962. The quantitative influence of the rhizosphere on denitrification. *Plant Soil*. 17:267–70
- Wright I, Westoby M. 1999. Differences in seedling growth behavior among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *J. Ecol.* 87:85–97
- Yan F, Zhu YY, Muller C, Zorb C, Schubert S. 2002. Adaptation of H<sup>+</sup>-pumping and plasma membrane H<sup>+</sup> ATPase activity in proteoid roots of white lupin under phosphate deficiency. *Plant Physiol.* 129:50–63
- Zaller J, Arnone JJ. 1999. Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO<sub>2</sub>. *Ecology* 80:873–81
- Zavaleta E. 2000. Valuing ecosystem services lost to *Tamarix* invasion in the United States. In *Invasive Species in a Changing World*, ed. H Mooney, R Hobbs, pp. 261–302. Washington, DC: Island