# FEEDBACK IN THE PLANT-SOIL SYSTEM

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■ **Abstract**  Feedback between plants and the soil is frequently invoked on the ba-
sis of evidence of mutual effects. Feedback can operate through pathways involving
soil physical properties, chemical and biogeochemical properties and processes, and
biological properties, including the community composition of the microbiota and soil
fauna. For each pathway, we review the mechanistic basis and assess the evidence that
feedback occurs. We suggest that several properties of feedback systems (for example,
their complexity, specificity, and strength relative to other ecological factors, as well
as the temporal and spatial scales over which they operate) be considered. We find that
the evidence of feedback is strongest for plants growing in extreme environments and
for plant-mutualist or plant-enemy interactions. We conclude with recommendations
for a more critical appraisal of feedback and for new directions of research.

*Let us not make arbitrary conjectures about the greatest matters.*

*Heraclitus* (1)

CONTENTS

**75**

# INTRODUCTION

The interactions of plants with the soil in which they grow are a topic central to the understanding of both soils and plant ecology. Early civilizations, including the Mayans, the Chinese, and the Romans, appreciated these interactions, recognizing that inherent differences among soils affected agricultural productivity (2). The role of soil conditions was explicitly recognized in determining both the plant species found in a locale and the productivity of agricultural lands. Plant-soil interactions are now enshrined as a primary factor in the genesis of soils (3, 4) and implicated in the evolution of the terrestrial flora (5). In the past several decades, scientific analysis of the multiple pathways of plant-soil interaction has flourished, as appreciation for both the complexity and importance of these interactions has grown (6). As a simple indicator, no papers linking the words plant and soil in the title or abstract appeared in the BIOSIS database until 1985, but since 1995, such papers have appeared at a rate of about 3500 per year (6a).

Plant-soil feedback processes are not only integral to many ecological processes, but they are also a prominent component of the ecological responses to global environmental changes. Climate change, the ever-increasing concentration of carbon dioxide ($CO_2$) in the atmosphere, and the large-scale changes in the global cycles of nitrogen (N), phosphorus (P), and water ($H_2O$) (7) all directly affect the mechanisms at the core of plant-soil interactions. Feedbacks in the plant-soil system will not only affect the biosphere's response to anthropogenic environmental change but can themselves create large-scale feedbacks that affect the magnitude of the anthropogenic perturbation. This is well illustrated by the role of plant-soil feedbacks as a component of regional and global climate systems (8–11). Other global-scale changes resulting from human activities affect plant-soil feedbacks, and in turn, these feedbacks may alter the magnitude and ecological impact of such changes. For example, plant-soil feedbacks are implicated as a potential causative mechanism promoting the invasion of nonnative plant species (12–14). The eutrophication of terrestrial ecosystems due to atmospheric and water-borne excess nutrients similarly causes ecological changes through mechanisms of plant-soil feedback (15, 16). Finally, because plant-soil feedbacks may stabilize alternative ecosystem states (17–23), it is crucial to understand the role of such feedbacks in underpinning ecosystem responses to the multiple anthropogenic environmental changes currently under way.

Research on plant-soil interactions has been wide-ranging, resulting in several disparate lines of inquiry. Ecologists have focused on plant traits, particularly those that affect ecosystem-level processes (6, 24–32) and have looked to soil properties

to explain community composition and community dynamics (33–35). Microbiologists have focused on the size, composition, and activity of the microbiota associated with plant roots as well as the role of plants in driving these variables. Plant scientists have focused on the mechanisms and functions of plant-microbe symbioses, particularly N fixation and mycorrhizae (e.g., References 36–38), parasitic and pathogenic organisms, microorganisms that mitigate or prevent disease (39, 40), and microorganisms, particularly *Agrobacterium tumefaciens*, which can alter the genome of plants. At a very different scale, climate modelers are concerned with large-scale effects of plant communities on soil characteristics that affect heat transfer (10, 11), whereas geomorphologists examine how plant communities promote weathering, retard or accelerate erosion, and alter stream channels.

Across all these perspectives and scales, the concept of feedback is frequently invoked. *Feedback* is defined as "the modification, adjustment, or control of a process or system . . . by a result or effect of the process, esp. by a difference between a desired and an actual result" (*Oxford English Dictionary*, http://dictionary.oed.com/entrance.dtl). Feedback describes a sequence of events or interactions in which the result of a process affects the conditions that initially generate the process (Figure 1). In positive feedback, the outcome of the process causes the process itself to increase in magnitude, generating an ever-increasing cascade of effect in a particular direction. In negative feedback, the outcome of the process causes the process itself to decrease in magnitude, resulting eventually in an outcome sufficiently small that it no longer affects the process, which then increases in magnitude until its effect on its own genesis again causes it to become limited. Thus, positive feedback is directional, whereas negative feedback is stabilizing.

Feedback in the context of soil-plant interactions posits that a change in soil conditions causes changes in the plant component, which in turn causes further change in the soil, and vice versa. That is, the results of the process must affect the cause of the process so as to increase (positive feedback) or decrease (negative feedback) the magnitude of the effect (Figure 1). In plant-soil systems, this implies that a plant-induced change in the composition and activity of the soil's biotic, physical or chemical properties, and/or the rates of ecosystem processes, directly affect the plants. Through changes in the demography of the plant population and/or the physiological activity of the individual plants, the plant's effect on the soil conditions increases (positive feedback) or decreases (negative feedback). Strong demonstrations of feedback must include convincing evidence of at least the three steps of reciprocal effect. It is also possible that plant-soil feedbacks could act indirectly by exerting effects on competitors (6), thereby affecting the species initially causing the effect.

Beyond the demonstration that a given interaction between plants and soils yields feedback responses, a number of characteristics of a feedback system can be identified.

1. Specificity: Is the feedback specific to a given plant, microbial species, or functional group—or is it an effect of plants or microbes in general? For
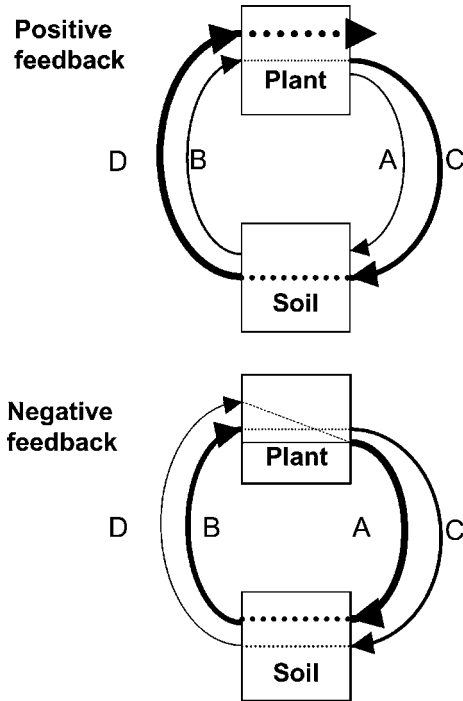
**Figure 1**  In positive feedback, an effect of plants on soil (*A*) causes a reciprocating effect of soil on plants (*B*), which amplifies the effect of plants on soil (*C*), which further amplifies the effect of the soil on the plants (*D*). In negative feedback, an effect of plants on soil (*A*) causes a reciprocating effect of soil on plants (*B*), which attenuates the effect of plants on the soil (*C*), which further attenuates the effect of the soil on the plants (*D*); when *D* reaches some threshold level, it allows the mutual effects to increase back to the original level (*A*), which then starts the cycle of decreasing effect.

example, do different plant species cause different weathering rates, or is weathering affected only by the presence or absence of vegetation?

2. Qualitative/quantitative character: Does the interaction involve a quantitative response in the interacting species (i.e., increases or decreases of population size) or a quantitative change in a process variable (e.g., a mineralization rate) versus a qualitative change (change in species composition; elimination or introduction of a given process, such as hydraulic lift or N fixation)?

3. Response variables: What is the mechanistic basis for the feedback? Through which component(s) of plant or soil ecology, soil physical or chemical properties, is feedback effected? Do the target entities include pool sizes or flux rates or both?

4. Scale: At what spatial and temporal scales does the presumed feedback act? Does it apply to an individual plant, a plant population, or an entire

landscape? Does it act over short (hours or days), intermediate (years to decades), or long periods (centuries to millenia)?

5. Direction: Is it positive or negative?

6. Strength: How important is the posited feedback relative to other biotic and abiotic factors in the given system? This point has been emphasized by Binkley & Giardina (41), who describe a gradient from strong feedback systems ("tight-weave" systems) through weak systems ("loose-weave" systems) to systems with little or no feedback ("frayed" systems).

7. Complexity of feedback pathways: Is the posited feedback described as a simple two-component loop (Figure 1) or are there multiple components and interactions that modify the feedback element of a particular interaction (for example, herbivore-mediated effects on root exudation and microbial activity) (42)?

Although there is abundant evidence for plant effects on soil and the converse, clear demonstrations of feedback are much less abundant. We have sought evidence of plant-soil feedback by surveying the pathways of interaction and clearly established examples of plant-soil feedbacks. We divide the pathways of feedback into those involving the physical properties of the system, the chemical and biogeochemical properties of the system, and the biological components, this last focusing on organisms and questions of species diversity (Figure 2). We recognize that this oversimplification ignores the complex interactions among these three
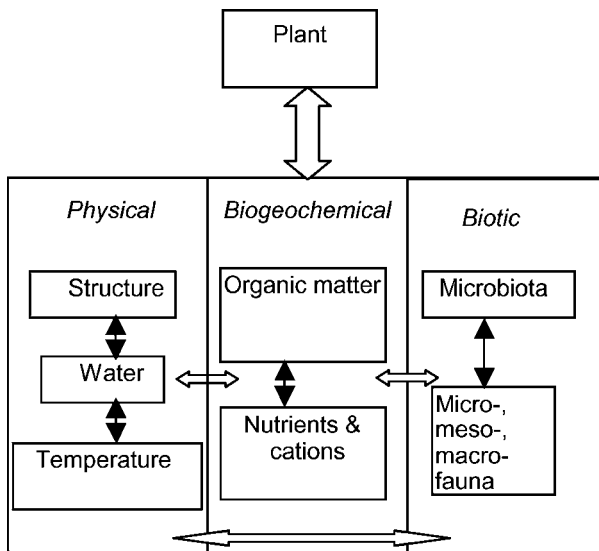


**Figure 2**   Conceptual approach to analyzing plant-soil feedback. Feedback pathways can operate through physical, biogeochemical, and biotic compartments of soil. Arrows describe linkages between the components of each compartment.

major compartments; nevertheless, it provides a way of organizing a bewildering array of data. In each case, we briefly review the nature of the interaction and assess the strength of the evidence for feedback. We finally discuss the factors above in evaluating the weight of evidence for plant-soil feedback.

## SOURCES OF INFORMATION, AVAILABLE DATA, AND THE CONSTRAINTS OF METHODS

The literature from which we explore the extent of plant-soil feedback is highly heterogeneous, as might be expected for a subject covering such a wide range of disciplines and analytic scales. We do not exhaustively examine each pathway of interaction but use recent review articles. The literature relies heavily on correlation and regression, as well as simple observations of large-scale patterns. Experimental approaches include altering species composition, removing key elements of the soil biota with biocides, and a great variety of greenhouse/microcosm studies in which particular plants and soil components are combined in pot cultures. The major limitation of both observational and experimental methods is the timescale of data collection: Very few studies are long enough to verify the reciprocating nature of the feedback interaction. Most studies intend to demonstrate differences in some set of response variables to a given set of hypothesized driving variables, rather than to demonstrate sequential responses of the interacting components, and they commonly rely on a small number of growing seasons, often only one.

Modeling is also a potent tool in analyzing plant-soil interactions (43–45). Many ecosystem models use a series of equations to describe controls on forcing factors (e.g., temperature sensitivity) and combine these models with mechanistic formulations to describe processes of interest (productivity, biomass, nutrient availability). Others focus on formulations resulting from microbial physiology (e.g., growth based on assimilation efficiencies, stoichiometry, substrate availability) to describe nutrient-cycling patterns (e.g., References 43 and 46). Most of these models do not explicitly incorporate feedback between soil and plant, in part because feedback may be occurring on a temporal time step different from the model formulation (46). Feedback is explicitly incorporated into some models, for example those of Reference 47, which links differential litter decomposition rates and community composition, and Reference 48, which links N availability and mineralization rates from soil organic matter (SOM) to the relative abundance of different plant functional types, defined by their relative growth rates and nutrient use efficiencies. Some recent climate models have coupled climate models with vegetation models (8, 10) and have shown that feedbacks make a large difference in climate scenarios.

Although analyses of the plant and soil components of interacting systems are fairly straightforward, studies of the microbial components have been more problematical. Recently developed molecular and genetic technologies are now opening the "black box" of the soil biota, so that the underlying mechanisms of

plant-microbe interactions are now being elucidated. Methods including reporter genes, fluorescent in situ hybridization (FISH), DNA-based techniques [e.g., extraction and identification of specific genes] enzyme analysis, phospholipid fatty acid (PLFA) analysis, and catabolic profiling allow researchers to visualize and profile the microbial community structure of environmental samples and relate it to ecosystem flux rates.

# PLANT FEEDBACKS WITH PHYSICAL COMPONENTS OF SOIL

The physical properties of soil most important for plant-soil interactions are the behavior of water, the temperature, and the particle structure resulting from the aggregation of mineral grains. These properties not only strongly affect plant growth but are influenced by the nature of that plant growth.

## Water

Soil moisture exerts a primary control on many aspects of plant ecology, from individual plant performance to community dynamics (33), whereas transpiration is a fundamental part of the hydrological cycle. The potential for feedback involving water comes from the capacity of plants to alter the distribution and amount of water in the soil, potentially affecting their growth and reproduction. Plant effects on soil moisture act through the combination of shading and insulating effects of litter and the plant canopy, the amounts of water transpired as a function of root and canopy morphology, and plant adaptations to water stress. Feedback loops involving these pathways can cause successional change driven by plant response to changing soil moisture conditions (positive feedback) (49) or by the maintenance of stable plant assemblages stemming from increased soil moisture (50). Anecdotal evidence suggests another pathway of feedback may involve arbuscular mycorrhizae, which can alter water movement in soils by promoting hydraulic lift, enhancing plant water uptake, modifying soil hydrophobicity, and altering the partition of incident precipitation between surface runoff and infiltration (36).

Hydraulic lift, the nighttime transport of water from depth to fine roots and out into the surface soil, is a widespread phenomenon (51–53), not only in arid ecosystems but also in humid forests. The amount of water moved may be as much as 30% to 40% of the water transpired during the day (51, 52); thus, hydraulic lift can cause a major redistribution of moisture. Possible benefits to the plant include enhanced nutrient cycling in moistened layers of surface soil, maintenance of nutrient uptake functions in surface roots, and maintenance of root vitality in dry soils. Recent reviews stress the lack of firm evidence that these benefits initiate feedbacks. Hydraulic lift also benefits neighboring shallow-rooted plants, whose growth is enhanced by the delivery of water by a deep-rooted neighbor (50), but these effects may be small compared to competitive interactions (54). Deep

roots are also implicated in nutrient uptake from deep soil horizons (53, 55). Another potential pathway of feedback involves hydraulic lift as a factor affecting root herbivores. In one study of citrus trees, an entomopathic nematode's survival and effectiveness against an insect herbivore feeding on roots was enhanced by hydraulic lift (56). Hydraulic lift may be part of complex feedback systems in which deep roots alter both water and nutrient distribution in the soil, which in turn affects a cascade of interactions among the soil biota, co-occurring plants, and the initial plant. The extent of true feedback, however, is not clear; some, but not all, studies find changes in plant performance associated with hydraulic lift (54), suggesting that hydraulic lift is not always a feedback pathway.

Plants may also facilitate the downward movement of water, particularly in desert ecosystems, by using water absorbed at shallow depths to support root growth downward through very dry soil to reach the phreatic zone, or by creating preferential flow paths which serve to channel water from the surface (and competing root systems) to a plant's own deep roots. In deserts, sclerophyllous shrub forests, and tropical savannas, roots extend down as much as 20 m (maximum observed is over 60 m), and are often found to 5 m in most other ecosystems (53). However, there is no specific evidence that deep-rooted plants are altering water movement in soils in ways that promote their own growth.

## Soil Aggregates and Soil Structure

Feedback between plants and the physical properties of soils may also arise from the promotion of aggregates by roots and root-associated microorganisms (57–65), as has long been recognized (66). Soil aggregation results from a variety of root-mediated processes, including wet-dry cycles enhanced by plant water uptake, the physical pressures exerted by roots growing through cracks, and the direct effect of roots and their associated mycorrhizae in binding soil minerals together (58, 59, 62, 64, 67). Roots affect aggregation through plant carbon (C)-based microbial growth, the production of plant and microbial mucilages, the presence of phenolic compounds in root exudates, and the overall input of SOM (57, 63, 65). Species-specific effects on structure are not necessarily seen. For example, Scott (64) found species-specific differences in the aggregate diameter distributions in a sample of trees but not among prairie grasses. In many of these cases, the plant-promoted aggregation is associated with enhanced nutrient cycling (59), which presumably benefits the plant by fueling growth. Angers & Caron (57) emphasize the potential positive effect of root-stimulated aggregation on plant growth, both through improved moisture availability as well as through enhanced nutrient cycling. Insofar as a large body of research demonstrates the positive effects of well-aggregated soil on plant growth, this pathway of interaction may be considered a reasonably well-established feedback; however, specific documentation of the feedback within a particular study system is usually lacking. The data suggest that this pathway may act broadly across taxa within a community and may be a relatively weak ecological force acting in concert with a large number of other factors.

## Temperature

Plants affect soil temperature largely through a combination of shading by litter and aboveground biomass and influence on the color, and therefore the albedo, of the soil (68–70). In regional- and global-scale models, albedo has emerged as the most important factor creating feedback between climate and vegetation (e.g., References 10 and 11). Soil temperature affects root growth, water availability, and microbial activity, thus affecting both nutrient cycling and soil respiration. Eviner (71) has found that species differ in their effects on soil temperature, and these effects are not necessarily well correlated with descriptors of size or litter deposition rates.

At extremes of cold or warmth, the reciprocal interactions of soil temperature and plant growth may constitute a feedback system. In Arctic Alaska, an increase in shrub cover is part of a positive feedback loop mediated by temperature (72). Shrubs trap and retain snow, insulating the soil and increasing microbial activity, whereas little activity occurs in the colder soils lacking deep snow. Shrubs access N mineralized during the winter, fueling more growth during the summer, and therefore trapping more snow the next winter.

Thus, plant-soil temperature feedbacks are well recognized and demonstrated at the spatial scales of biomes and regions as well as temporal scales of years to decades, but it is not clear how important this feedback pathway may be under mild conditions.

## PLANT FEEDBACKS WITH CHEMICAL AND BIOGEOCHEMICAL COMPONENTS OF SOIL

The chemical and biogeochemical interactions between plants and soil are perhaps the most complex to unravel and analyze. Unlike physical and biological interactions, for which the mechanisms of interaction usually can be clearly delineated, chemical and biogeochemical interactions typically involve complex mechanistic pathways that include not only the chemical constituents of soil but also moisture, temperature, and the species composition of the biota. Below we focus on the primary nutrient elements and soil acidity [the "master variable" of soil chemistry (74)].

## Soil Acidity

Plant interactions with soil acidity are well documented in both plant ecology and soil science. Plant communities are clearly differentiated along gradients of pH, particularly at the extremes [e.g., acidophile (pH < 5) and calciphile (pH > 7) communities]. Plant adaptations to high and low pH involve complex biochemical, physiological, and mutualist pathways (34), allowing these species to survive harsh chemical environments induced by the pH. However, these adaptations are not apparently part of feedback systems because they do not result in the modification

of the environmental pH. At intermediate pH values, however, feedbacks may be more important, as small changes induced by particular species differentially affect their growth and that of their competitors.

Plants are an important factor in the acidification of soils through several pathways (73). These include the generation of carbonic acid from root and root-supported microbial respiration, the leaching of organic acids from litter and organic matter, and imbalances in the uptake of positive and negative ions, for which balancing $H^+$ and $OH^-$ or $HCO_3^-$ may be released (74, 75). Plant uptake of $NO_3^-$ can raise, and uptake of $NH_4^+$ can lower, pH by up to 2 units (76, 77). Plants also indirectly affect soil acidity through their promotion of mineral weathering (an $H^+$-consuming process), through the uptake of calcium (Ca) and other base cations from deep soil horizons and deposition of these cations on the soil surface through litter deposition (see below), and through the production of litter whose decomposition products include organic acids. Variations in pH under different co-occurring plant species are well documented (78). Large changes in pH over the decadal scale of plant succession are also well documented; for example, in the Calhoun forest in South Carolina, the transition from agricultural land use to pine forest resulted in a decrease in pH of almost two units in the surface horizon during 30 years (75).

It is generally presumed that the pathways of soil acidification involve feedbacks: Plant-induced acidification promotes conditions under which only acidophiles can live. Plant physiological and metabolic traits provide the mechanistic basis for feedback. For example, acidophiles release polyphenols from their roots that bind to organic N; they can utilize this organic N but nonadapted plants cannot. It is less clear whether calciphile plants actively maintain high-pH conditions conducive to their own growth.

The best example of plant-soil feedback systems involving pH is the effect of mosses in the genus *Sphagnum* (79). Polyuronic acids in cell walls effectively exchange cations for $H^+$, and slow decomposition of plant tissues results in the production of organic acids; together they produce pH values <4.5, even <4.0. When *Sphagnum* first becomes established, pH can rapidly plummet by two or more units over a timescale of years as the moss spreads. The acidity helps eliminate vascular plant competitors that cannot tolerate these conditions. The feedbacks created by *Sphagnum* also include effects on soil moisture (plant morphology induces saturation), the structure of the soil surface (extremely low bulk densities that make root growth difficult for most vascular plants), and the accumulation of peat, which isolates the soil surface from mineral soil water. Thus, the overall feedback process is complex.

Plant-mediated changes in pH are also important in wetlands because the sequence of redox processes characteristic of anoxic soils have strong effects on $H^+$ activity (80). Although these redox-linked effects on pH are well known, linkages to plants and the potential for feedback has been rarely examined. Feedback pathways are likely to involve complex interactions of plants, rhizosphere microbes, and soil chemistry. For example, a possible feedback loop has been described between bulbous rush (*Juncus bulbosus*), a pioneer species on the shores of acidic, iron-rich lakes, and its rhizosphere microbial population (81). Oxygen release by

the roots raises the rhizosphere redox potential, which results in the oxidation of $Fe^{+2}$ to $Fe^{+3}$, the deposition of iron-rich root plaques, and the creation of acidic microsites. Rhizosphere microbial communities associated with the root plaque contain acidophilic microorganisms that produce $CO_2$, potentially an auxiliary C source for a submerged plant in an environment where $CO_2$ diffusion is limited by the acidic conditions.

## Cations

Cations not only control soil pH and acidity but also are a primary factor in plant ecology (33, 34). Plant community composition is especially affected by extreme or unusual concentrations of particular cations. Such soils require highly specialized physiological adaptations, and some plants evolve the capacity to hyperaccumulate cations, including metals. Hyperaccumulation of metals is hypothesized to have multiple effects that could result in feedback; these include inhibition of soil pathogens, allelopathic effects on nonaccumulating plants, and effects on the soil microbial community, including saprotrophs involved in decomposition (82). For example, *Alyssum bertolinii*, a nickel-accumulating species, is a part of a specialized flora that can survive in serpentine soils that have high levels of Ni, Co, and Cr and low nutrient levels (N, Ca, P) (83). Metal-resistant bacterial strains living in the rhizosphere of *A. bertolinii* release organic acids that facilitate solubilization of $PO_4^{-3}$ and enhance the release of Ni from the nonlabile soil phase. Soil microbial community composition is altered up to 5 cm from the plant, suggesting a positive feedback between plant and rhizosphere microbial community that enhances plant uptake of both Ni and P. Even in soils with nonextreme cation concentrations, microbial activities in the rhizosphere solubilize cations and metals, promoting their uptake by plants (84).

Plants alter soil cation concentrations through several mechanisms, which can result in the differentiation of soils under different plant species (78, 85–87). Plants promote weathering of primary soil minerals, in part through their generation of soil acidity (88, 89), but effects may not be species specific (90). In a study of mineral weathering in sandy soils with or without red pine trees, weathering was eight to ten times higher under the pines than in the unvegetated soils (89, 91). Weathering is specifically promoted by ectomycorrhizae, whose hyphal tips excrete organic acids and form conspicuous pores within mineral grains (92, 93). This weathering is particularly important in maintaining Ca for plant uptake (94). It also may be responsible for creating cation-depleted E horizons under ectomycorrhizal trees and may explain the maintenance of forest productivity under conditions of high leaching losses. Thus far, reports of mycorrhizal-based weathering are restricted to ectomycorrhizae; it is not known whether ericoid or endomycorrhizae carry out the same processes. These reports give circumstantial support to the concept of plant-mediated weathering as a feedback process.

Plant-associated promotion of weathering is often assumed to be operating at millennial timescales (75). However, studies such as those of Bormann et al. (91) and Quideau et al. (89) suggest that weathering could be sufficient to affect

growth during the life span of long-lived trees, and it seems reasonable that this mechanism may operate over timescales of decades, allowing a feedback effect on tree growth. However, there is no experimental verification that such feedbacks act at these timescales. It also seems unlikely that short-lived plants would create such feedback systems.

Plants also affect cations through uptake from deep soil horizons and transport to surface soil via the input of cation-rich aboveground litter. Cations with high concentrations in plant tissues relative to their concentrations in soil minerals (e.g., P and K) are highly concentrated in surface soil horizons, whereas cations used as micronutrients are distributed uniformly through the profile (95, 96). Jobbágy & Jackson (95, 96) calculate that the surface pool of K would be one third to one half smaller than its current size without plant-mediated transport. In arid ecosystems, roots extending downward to 10 m access both cations and $PO_4^{-3}$ (55). In temperate zones, sugar maples (*Acer saccharum*) maintain a higher density of fine roots deep in the mineral soil (to 60 cm depth) and absorb more Ca from this pool than do hemlocks (*Tsuga canadensis*). This uptake from deep sources is necessary to balance a greater amount of mineralization of organically bound Ca and higher leaching losses of dissolved Ca from surface horizons (97). Despite this extensive evidence that plants have a major effect on the redistribution of cations through the soil, it is not clear if and how this influence creates or supports feedbacks.

## Oxygen and Reduction-Oxidation Chemistry

Wetland plants are well known for their ability to release oxygen from their roots, thereby modifying the sequence of redox reactions that characterize anoxic soils (98, 99). Wetland species vary greatly in the extent of root oxygen loss and their tolerance for reduced chemical conditions (high concentrations of Fe(II), Mn(II), sulfides, and $CH_4$) (98). These plant-generated effects on soil chemistry are presumed to be part of a feedback cycle, as survival under reduced conditions is difficult at best. However, specific testing of a feedback hypothesis is rarely done (but see N inputs and outputs below).

## Carbon

C is perhaps the most prominent chemical component of the plant-soil system; without plant-derived C, soil as traditionally conceived would not exist (100–102). Soil C occurs in multiple forms, including organic and inorganic, solid and soluble, as well as labile and recalcitrant, with residence times of days to millenia. Although we recognize the numerous mechanistic linkages among C forms and between C and other soil components, separation by element helps organize and dissect the anastomosing web of interactions that potentially lead to feedbacks. We separate pathways of potential feedback involving C into three components of the soil C: the litter input, the soluble C derived from plants and microbes, and the solid soil organic carbon (SOC). These compartments each presumably create feedbacks by regulating the supply of nutrients and through the effects of

SOM on moisture retention. We separately consider the interactions of C with N cycling.

SOIL ORGANIC MATTER    Plant-soil feedback in the accumulation of SOC through primary succession has been a fundamental axiom of ecology for more than a century, dating back at least to H.C. Cowles (103). These feedbacks, acting over geological time (101, 102) as well as timescales of decades to centuries of primary succession, are based on the idea that the growth of plants results in accumulations of organic C in soils, which in turn provide a better environment for plant growth in general, leading to the further accumulation of soil C (15, 104–106). Changes in SOC during succession may be associated with both the competitive and the facilitative mechanisms of species turnover (6). Theoretically, this positive feedback reaches an equilibrium; at that point, plant inputs of C are balanced by decomposition and leaching losses, and feedback processes are reduced in importance or eliminated. Large-scale disturbances such as fire or tectonic changes alter the equilibrium point at which the feedback loop decreases in importance.

Plant-induced increases in SOC and its reciprocating effects on plant growth are frequently demonstrated for arid and semiarid ecosystems, in which "islands of fertility" develop beneath both shrubs and tussock-forming perennial herbaceous plants (59, 87, 107–110). Soils beneath shrubs and tussock grasses are enriched in both organic matter and mineral nutrients, but the differentiation from inter-plant spaces is often found only in the surface horizons. Root, stem, and leaf material contributes to the accumulation of organic matter beneath the plants, but physical redistribution processes, themselves reflecting the presence/absence of plants, contribute to the creation of islands (107, 110). Thus, the spatial heterogeneity of SOC is a function of changing vegetation patterns; for example, in a Chinese grassland undergoing desertification, SOC first becomes more spatially heterogenous, as shrubs replaced the bunchgrasses, and then decreases in spatial heterogeneity as the shrubs are replaced by a desert grass (111).

Despite the apparent advantage to the plant of concentrating organic matter and associated nutrients in the vicinity of the roots, there is contradictory evidence of feedback. In grasslands, some studies show little effect of organic matter concentrations on plants (107). In contrast, others have shown that shrub species differentially affect SOC, root growth, nutrient accumulation, and microbial enzyme activity (59, 108). Plant-mediated SOC accumulations facilitate the growth of both patch-forming keystone species and other species, thus increasing the diversity of the plant community (50, 112). As with long-term plant-soil feedbacks, the feedback appears to reach an equilibrium level of C accumulation and plant density (and diversity); at this point, the feedback relationship may be attenuated or switch from positive to negative (stabilizing). Although creation of a high degree of patchiness in soil properties and its association with plants is well established in arid and semiarid ecosystems, the time course of the interaction and possible changes in the strength and direction of feedback over time have not been clearly demonstrated.

On the timescale of years to decades, the relationships between plant growth and C accumulation are not necessarily straightforward. Numerous studies of ecosystem restorations on highly disturbed or nonsoil materials have shown that although soil C increases with time, it does not necessarily do so in a simple linear fashion, and in some cases, soil C has not become equivalent to reference conditions after decades of plant growth (113–119), suggesting that other biotic and environmental factors affect the strength of a plant-SOC linkage. The failure of created wetlands to match reference sites may also be a matter of time; rates of C accumulation are similar, but decades are insufficient to accumulate comparable amounts of C (120), suggesting that feedbacks between plants and SOC act on timescales of centuries. Thus, accumulation of C may be in part a nonspecies-specific feedback (growth of any plants increases C, which enhances more plant growth), and it may be a weak process relative to other environmental and ecological factors that diminish feedbacks.

Similarly, secondary successions do not necessarily result in uniform changes in organic matter. Mitchell et al. (121) examined changes in soil properties following the succession of heathland communities along several different trajectories. Only the trajectory from heath to pine forests showed an increase in organic matter; trajectories toward birch or bracken fern (*Pteridium aquilium*) domination were accompanied by decreases in organic matter, and trajectories towards gorse (*Ulex europaeus*) and *Rhododendron ponticum* communities did not show large changes in organic matter. These trends were observed at multiple sites with different soil types, suggesting that the changes were due to the plant species invading the heath, rather than intrinsic differences in the soil. These varying responses of SOM to successional trajectory emphasize the importance of species-specific effects on SOM accumulation.

Species- and community-specific effects of plant functional groups (grass, shrub, tree) on SOM accumulation are clearly important in rates, amounts, and depth distribution of C (122). But the existence of feedback, a process that could either accelerate directional successional trajectories (positive feedback) or cause successional trajectories to converge (negative feedback) remains speculative and correlative. Other environmental factors, such as soil mineralogy (123) and climate (124), may be at least as important as plant-driven effects on SOM dynamics; how they moderate or override potential feedback interactions is unresolved.

DISSOLVED ORGANIC CARBON    Plant interactions with the dissolved components of the SOM operate at much smaller scales of time and space than interactions with bulk organic matter. The primary pathways of interaction are the exudation of organic compounds from roots, which affect a variety of processes within the soil (125), and the leaching of dissolved components from litter and SOC (126).

The exudation of a wide range of compounds from roots is a well-known phenomenon and has been extensively reviewed (77, 125, 127–132). Exudates contain amino acids, low-molecular-weight organic acids, simple and complex sugars, growth regulators, enzymes, fatty acids, nucleotides, tannins, steroids, flavonoids,

phenolics, terpenoids, alkaloids, and vitamins (127). Root exudation (and deposition of other carbonaceous materials, including mucilages and sloughed cells) accounts for roughly 5% to 33% of daily C fixation (133, 134). Rhizodeposition varies among species and with habitat fertility (135). These compounds directly and indirectly affect both the activity and the community composition of the soil microbiota, including pathogens, parasites, saprotrophs, and mutualists. They also directly and indirectly influence nutrients through the production of enzymes that decompose organic compounds (59, 136–139) and the production of siderophores and chelators that modify the mobility and uptake of metals. In addition, organic acids affect soil pH and facilitate the weathering of soil minerals (140).

Numerous studies demonstrate linkages between these inputs of soluble C and nutrient availability (for a review, see Reference 125). Root-linked C stimulates the decomposition of SOC and litter (141, 142) and increases the activity of soil enzymes associated with nutrient mineralization (143). However, not all studies find species-specific differences in soil responses to rhizodeposited C. Species-specific effects can vary among environments; for example, the effects of two grass species on microbial activity were different in improved agricultural soils versus unimproved meadows (144). The quality, quantity, and effects on soil functions such as N mineralization also vary with plant nutritional status (145, 146). Grazed plants have been shown to transfer more C to the soil, stimulating more N mineralization in comparison with ungrazed plants and increasing plant growth (147). Thus, in this case, a rapid feedback loop between plants and soil involving exudate C is mediated by aboveground grazing, forming a complex feedback system.

Secondary plant chemicals also are well-known components of exudates and affect microbial activity in a variety of ways (148). Phenolic compounds are often a C source for rhizosphere microbes but are used differentially, thus driving differentiation of communities among plant species (149–151). Higher microbial biomass, respiration rates, and N immobilization result from phenolic exudation (152, 153). Polyphenols are also implicated in sequestering N in organic form (154, 155), thereby reducing N availability to plants unable to take up organic N compounds. Other secondary compounds, including alkaloids, terpenoids, and flavonoids, have inhibitory effects on particular components of the microbiota, although the effects of such antimicrobial activities for nutrient cycling are unknown (156–158).

Root exudates affect nutrient availability through a variety of other pathways. As described above, organic acids originating from roots are effective in promoting weathering of soil minerals, thus increasing the supply of nutrient cations (as well as toxic forms of Al) (159). Organic acids can react with iron compounds, facilitating the release of P (140). Roots (and their associated mycorrhizae) release enzymes, including phosphatases, proteases, and others involved in the mineralization of N, enhancing availability (140, 160). Exudates may also affect nutrient availability indirectly by altering soil pH.

Although these studies clearly show that the input of dissolved C from roots has profound effects on the availability of nutrients, there are few direct demonstrations of feedback. In a recent review, Paterson (125) emphasizes that interactions of root

exudates with the microbiota and soil minerals are readily demonstrated but that their relative significance in the control of both plant and microbial ecology is neither clear nor easily determined.

The other main source of plant-derived soluble C is the leaching of litter. Significant inputs of C in leaf leachate are found in throughfall, amounting to about 1% of total net primary production (126). Leachate from the forest floor (litter plus organic soil materials) may equal 15% to 18% of the total litterfall (126, 161). This material is important to weathering processes, soil pH, microbial community composition and microbially mediated nutrient cycling, but there have been few suggestions that the leached dissolved organic carbon creates feedbacks. Indeed, there are apparently few differences in the soluble C originating from different species (162).

LITTER   The role of litter inputs has been perhaps the mostly widely examined and cited source of plant-soil feedback (15, 30, 43, 134, 163–168). This feedback system is thought to operate primarily through the chemical composition of the litter (i.e., the stoichiometric relationships of C, N, P, and lignin as well as the content of secondary plant chemicals) and the effects of this chemistry on microbial activity and nutrient mineralization. Litters with low C:N ratios, low ratios of N:lignin, and/or low concentrations of polyphenols decompose more rapidly and completely, resulting in the mineralization of N (and other nutrient elements), whereas litters with the opposite qualities tend to decompose slowly, resulting in low rates of nutrient mineralization. These patterns are paralleled by vegetation patterns: Plants on soils with low nutrient-cycling rates tend to have a suite of traits including low N concentrations, high polyphenol and lignin concentrations, and low relative growth rates (15, 31, 169), and vice versa.

A good example of these relationships with regard to feedback is the change from heathlands dominated by the ericad shrubs *Calluna vulgaris* and *Erica tetralix* to grasslands dominated by *Molinia caerula* and *Deschampsia flexuosa* (15). The shrubs produce litter that decomposes slowly, a correlate of the long life span of the leaves and slow growth rates of the plants, whereas the grasses grow more rapidly and produce litter that decomposes more quickly. Exogenous inputs of N allow the grasses to outcompete the shrubs and, over intermediate-term timescales (decades), cause nutrient mineralization rates to increase. Grass-dominated systems with high N-cycling rates and shrub-dominated systems with low N-cycling rates are thus alternate stable states, each maintained by negative feedback loop between plant growth characteristics and N-cycling rates. Berendse (15) suggests that slowly decomposing litter is an adaptation evolved to reduce nutrient losses in nutrient-poor environments, and such adaptations not only affect soil development but also the competitive interactions that shape plant communities. Similar relationships among species, litter quality, and nutrient availability have been widely documented (e.g., References 170 and 171).

Litter, as a component of the soil surface, can also affect plant communities through direct and indirect effects on seed germination and seedling establishment.

Litter affects light penetration and temperature profiles on the ground surface, affects nutrient supply and acidity, and may inhibit either germination or growth through phenolics in leachate (172–175). However, the effects of litter leachates on seed germination vary among studies (176–178). Physical interference with seedling ecology may affect germination, overall growth, or growth of some portion of a plant (roots, leaves, stems) (179). The multiplicity of effects, both within and between ecosystems, makes it difficult to determine whether there are potential feedbacks possible between the structure and composition of the soil surface horizons and plant communities as mediated by effects on seeds and seedlings.

In summary, there are multiple pathways of feedback between plants and soil C, operating over a wide range of temporal and spatial scales and often operating through complex (multifactor) pathways. However, the existence of a particular pathway of feedback in any given system cannot be assumed.

## Nitrogen

The interplay among plant species, plant communities, N and C cycling has generated more discussion of feedback in the soil-plant system than any other topic. Frequently proposed feedback mechanisms include the linkage of decomposition and mineralization rates, the linkage between chemical forms of N and their uptake by plants, competition between microbes and plants for N, and plant-mediated effects on ecosystem inputs and outputs.

NITROGEN MINERALIZATION AS A BASIS FOR FEEDBACK    Extensive research has been devoted to the linkages between plant species composition, plant productivity and biomass, plant morphological and physiological traits, and N mineralization rates. Net N mineralization rates are strongly linked to chemical properties of litter (134), particularly lignin content (or more specifically, N:lignin ratio) (166, 180), C:N ratios (43, 125, 181), and the polyphenol content of the tissues (155). Wardle & Lavelle (182) specifically address the issue of feedback; they note that there are likely to be multiple scales of feedback between litter quality, nutrient release, and other ecosystem components. The complexity of interrelations among litter quality, the trophic structure of soil food webs, and N mineralization are emphasized in References 182 and 183.

Although litter chemistry has well-established relationships with N mineralization, the devil, not surprisingly, is in the details. Linear relationships between various indices of litter quality (e.g., C:N, lignin:N, polyphenol:N) and N mineralization only hold over fairly narrow ranges of values, and above or below these ranges, other controls appear to operate (184). Litter chemistry also affects the temporal pattern of N release (184). Plant residue amendments and mixtures of materials do not always behave as expected or in a linear fashion (185). Tissue constituents other than C, N, and lignin also affect mineralization rates (186–188). Nitrogen mineralized from SOM may not be affected by differences in the input leaf litter (189). These results suggest that while feedback between plant chemistry

and N availability is likely, feedback pathways are complex and variable among species and communities. Furthermore, although plant tissue N content is clearly linked to rates of N mineralization and its dependence on litter chemistry, there are few studies specifically demonstrating changes in plant demography or growth to plant-induced changes in N availability.

There are broad correlations between observed rates of N mineralization, plant community types, and a suite of plant traits, including tissue contents, growth form, and growth rate (31, 41, 181, 190). For example, Craine et al. (191) examined multiple traits in a set of 33 grassland species and found that low rates of N mineralization occurred in the soils of species with low N concentrations, high C:N ratios, high root:shoot ratios, and high biomass, a combination of traits observed in a range of other studies (32, 167, 192). These associations between N mineralization rates and plant traits provides strong circumstantial evidence of both an evolutionary-scale feedback process and feedback changes in vegetation over successional time.

Soluble C inputs from plants also affect N cycling, primarily through their C:N ratio (125). Because most such materials are either compounds with no N content (e.g., sugars, organic acids, phenolics) or have a high C:N ratios, root-associated organic materials are most frequently found to immobilize N (153, 193, 194). The presence of clay minerals that adsorb DOC may also modify the release of N from soluble root C (150, 195). Alternatively, soluble root C may preferentially affect some components of the microbiota. For example, some phenolic compounds specifically stimulate the growth of ammonia-oxidizing bacteria (196). Rhizodeposited organic matter may "prime" the microbial community, stimulating the mineralization of SOM in the bulk soil (125, 141). This latter process may result from plant-stimulated increases in microbial biomass, which in turn affect the size, composition, and activity of consumer meso- and macrofauna. Interactions based on the effects of soluble C on N immobilization are thus diverse, and feedbacks based on these processes are likely to be operating at a shorter timescale than litter-based processes.

Polyphenols in leachates and exudates are implicated in the direct complexation of proteins and reductions in N mineralization rates (127, 155, 197, 198). Northup et al. (155, 197) have proposed that this is the basis for a feedback system over evolutionary timescales on very acidic, nutrient-limited terrains, involving the plants, their mycorrhizae, and the development of the soil profile. The plants that grow best on these sites have high concentrations of polyphenols in their tissues, and they support ectomycorrhizae that are capable of absorbing organic N, thus "short-circuiting" the N cycle and giving these species a competitive advantage over species incapable of utilizing organic N. They point out that polyphenols also form complexes with soluble Al, reducing its toxicity on very acid soils, and with Fe, releasing P and increasing its availability. Polyphenol concentrations in plant tissues increase as soil nutrient concentrations decrease (199), supporting the existence of feedback. Polyphenols are thus implicated in both short-term simple feedbacks and long-term complex feedbacks.

Recently, the importance of plant tissue N content and N use efficiency as a basis for feedback was questioned by Knops et al. (200). They point out that SOM develops a much higher N concentration (3.75%) than the original litter (<1%). This suggests that all the N in the litter is retained in SOM, primarily in soil microbial biomass through immobilization processes, and that changes in litter quality are slow to influence N cycling. They suggest that plants affect N cycling through differences in microbial immobilization, and these differences stem more from differences in the amount of belowground input than differences in quality and quantity of aboveground litter. They predict that sites with high net primary production will have larger litter inputs to the soil, which will drive immobilization and therefore a reduction in N availability, whereas low net primary production will fuel more net mineralization and higher N availability. These trends are, however, the opposite of what is commonly observed (rich sites have higher rates of N mineralization and support larger plants, i.e., plants with higher annual productivity than poor sites). Clearly, the connections between litter quality, plant traits, and feedback to N mineralization rates require further clarification. Feedback processes between plants and N availability may vary among environments and biomes.

PLANT UPTAKE OF NITROGEN    Plants vary in the form in which they preferentially absorb N (as $NO_3^-$, $NH_4^+$, or organic N). There is some evidence that nitrification rates are higher under species that can utilize $NO_3^-$, and lower under species that preferentially use $NH_4^+$ or organic N (29). Differences among plants in the form of N utilized may promote species diversity within communities (201, 202). Plant uptake of organic N involves amino acids that are not preferred by microbes (202), thus alleviating both competition among plants and between plants and microbes (203). If plant preference for different forms of N both structures plant communities and affects plant-microbe interactions, it could form the mechanistic basis for a feedback pathway. It should be noted, however, that uptake of organic N and its role in structuring plant communities is primarily known for heathlands, conifer forests, and alpine or arctic communities; knowledge of the role of organic N uptake in structuring other communities is much weaker.

INPUTS AND OUTPUTS    Feedbacks involving inputs and outputs have been less frequently addressed than feedbacks involving mineralization and uptake rates. The presence of N-fixing plants profoundly alters N cycling, differentially affects the growth of plant species, and alters many other properties of the soil. Forests in which N-fixing alders (*Alnus* spp.) are present provide a well-documented example (204, 205). Invasions of N-fixing species into communities lacking such species also clearly demonstrate feedback. The most frequently cited example is the invasion of *Myrica faya* into Hawaiian forests (206, 207). Vitousek and colleagues showed that the introduction of an N-fixing tree caused an increase in available N in the soil, which preferentially supported the growth of the introduced species compared to native species that were N limited. Similar feedback processes have

been observed in other cases in which an N-fixing plant invades communities lacking such species (208–210).

Plants may also affect inputs through their effects on amounts and chemical properties of throughfall (200, 211, 212). However, there is little evidence that this supports a feedback process.

Feedbacks based on losses of N involve plant control over leaching and gaseous losses. In wetlands, where denitrification is a major component of the N cycle, plant effects may create clear and strong feedbacks. For example, in nutrient-poor wetlands occurring on the sandy soil of barrier islands, low-productivity early successional plants release large amounts of oxygen from their roots, which promotes nitrification in the rhizosphere soils and linked denitrification in the bulk soils as excess nitrate diffuses from the root surface. The enhanced loss of N in sites dominated by these plants is thought to prevent succession to other species, thus stabilizing the community in the initial species composition and inhibiting the development of larger stature communities of higher productivity (213).

In summary, feedbacks between plants and N cycling have been widely explored and invoked, most frequently with respect to the effects of litter input quantity and chemical quality on microbial mineralization processes. Although there is broad support for the existence of such feedback in general, there is not necessarily a tight relationship between litter characteristics and N mineralization rates or N availability, and some have questioned the existence of a true feedback linkage through this route. Despite the numerous studies linking plant traits to litter decomposition and N mineralization rates, there are relatively few studies that complete the loop by examining responses of plant species or communities to litter decomposition patterns. Feedback based on this pathway is likely to be operating on an intermediate timescale of years to decades because of both the time necessary for litter to influence the quantity and quality of SOM and the time necessary for plant community dynamics to result in dominance of a particular plant species or type. Feedbacks operating through the effects of rhizodeposited root material on N availability operate on a much faster timescale, corresponding to population growth rates of microbes and/or the soil fauna. Although there are abundant data to demonstrate how these interactions occur, there is a paucity of data demonstrating that a given plant's growth, survival, or reproduction responds to changes in N cycling that it has caused.

## PLANT FEEDBACKS WITH BIOTIC COMPONENTS OF SOIL

Numerous studies illustrate interactions between the activity and composition of the soil biota and the quantity and quality of plant inputs. Feedback has been frequently proposed to result from interactions between plants, the microbiota, and the soil fauna (29). We focus on studies exploring the linkages between plants and

soil community composition as well as the evidence that changes in communities result in changes in function in either party to the interaction.

## Microbial Community Structure

Numerous studies demonstrate both a nonspecific increase in total microbial biomass in the rhizosphere (by one to two orders of magnitude) and the induction of species-specific microbial assemblages (107, 130, 136, 137, 214–220). It is generally presumed, and sometimes demonstrated, that these effects on microbial communities translate into functional changes, which can directly affect plant growth (136, 147, 221). However, plants do not always create species-specific microbial communities (222–224). Although new microbial and molecular methodologies have greatly expanded knowledge of plant-microbial interactions in the soil, the lack of knowledge of the functional significance of altered microbial community structure for plant (and ecosystem) function is still striking (217, 221).

Microbial communities are sensitive not only to the species of plant occupying the soil, but also to a variety of ecological influences on the plants, including growth phenology (144, 225, 226), soil fertility (144, 227, 228), insect defoliation of the aboveground biomass (227), total plant net primary productivity (229), C input chemistry and timing (230), as well as plant community diversity (214, 229, 231). Although rhizosphere microbial communities have larger numbers and biomass than bulk soil, they may have lower diversity than bulk soil communities (214). Some rhizosphere microbes carry plasmids with genes responsive to plant exudates, suggesting a tight functional connection (37, 232). It is clear that plant biology affects microbial communities in many ways, but the effects of these variations on plant function are not well documented.

## Mutualisms

Feedback between plants and microbes is perhaps best expressed in the sequence of signals that result in the establishment of symbionts and mutualists (38, 39). Usually the plant initiates a positive molecular feedback loop that results in better nutrition, thus increasing fitness for both the plant and the microorganism. In legumes, the same plant genes are apparently needed to establish both fungal and rhizobial infections (233). Although the plant initiates a molecular dialogue with its own particular "cocktail" of compounds, the microorganisms respond with release of "Nod factors," which initiate genetic and morphologic responses in the plant. Two localized plant proteins, contained on a plastid, possibly derived from an ancient cyanobacterial symbiont, initiate a cascade of genetic events that result in establishment of the mutualism (233, 234). Establishment of mycorrhizal symbioses in other plants entails similar complex molecular signaling feedbacks (235).

Not only do plants and their symbionts communicate through a system of molecular and genetic feedback, but plants appear to be able to use similar molecular feedback systems to deter bacteria that are nonbeneficial or pathogenic. Bacterial

community activities are coordinated through detection of population densities via a mechanism known as quorum sensing. Specific quorum-sensing molecules [N-acyl homoserine lactones (AHLs)] build up, enable resident microbial populations to sense the density of their neighboring microbes, and regulate expression of beneficial or pathogenic traits. *Medicago truncatula* has been shown to respond to both symbiotic (*Sinorhizobium meliloti*) and pathogenic (*Pseudomonas aeruginosa*) AHL concentrations as low as 1–50 $\mu$M by producing over 150 different proteins (236). Legumes also cause the rapid disappearance of AHLs, whereas nonlegumes do not have this effect (237). Some plant-produced proteins mimic AHLs, potentially disrupting the molecular dialogue between pathogenic bacteria and plants. The plant proteins formed can either enhance or inhibit AHL-regulated bacterial responses. Not surprisingly, the research on molecular feedbacks in mutualist relationships focuses on crop plants; the significance for wild plants is unknown.

Some components of the rhizosphere community are effective in suppressing pathogenic organisms (238). Saprophytic pseudomonads can improve plant health through the production of antibiotics (239). Pseudomonads also activate certain gene sequences involved in nutrient acquisition, stress response, and secretion pathways specifically in the rhizosphere (240). In one of the few studies of noncrop plants, Holah & Alexander (241) found that unspecified fungi altered competitive relationships between two grasses from a tallgrass prairie because of the suppressive effects on parasitic fungi. It is assumed that specific root exudates promote the growth of the disease-suppressing bacteria, thus creating a feedback loop. Although the phenomenon of disease suppression by rhizobacteria is well established for crop plants, its significance for natural ecosystems is unknown.

Mycorrhizal mutualisms have marked effects on both ecosystem function and plant community structure, suggesting the potential for fungal-plant feedbacks. Leaf litter decomposability and relative growth rates are correlated with the type of mycorrhizal symbiont (arbuscular, ectomycorrhizal, or ericoid); arbuscular plants have rapid growth and highly decomposable leaves, whereas ericoid plants have slow growth and slowly decomposing leaves, and ectomycorrhizal plants are intermediate (242). These patterns correspond to ecosystem-wide properties, suggesting a feedback between plant type, mycorrhizal growth, and ecosystem process. Mycorrhizal diversity promotes plant community structure and productivity, which in turn apparently maintains the diversity of the fungal community (243). Plant community diversity is also affected by the relative benefits conferred by different species of arbuscular mycorrhizae, and negative feedback between growth of fungal and plant partners is thought to promote community diversity (244). Mycorrhizal-plant feedbacks thus operate at the level of individual plants and also plant communities, and over timescales of years to decades.

Mycorrhizal-plant feedbacks are complicated by other ecological processes. The establishment of the mutualisms can be affected by co-occuring rhizosphere microbes (245), aboveground grazing, and belowground consumption of fungal biomass (246–248). This evidence suggests that studies restricted to the plant and fungal partners may fail to reveal the details of feedback pathways.

## Pathogens, Parasites, and Herbivores

Interactions between plants and organisms that attack or consume root tissues provide some of the best-documented examples of feedback interactions. Clear demonstration of reciprocal effects on plant growth and the abundance of below-ground plant pests supports a theoretical analysis of feedback in the plant-soil system (249–252). Numerous studies have shown that the development of below-ground pest populations relative to the growth of particular species can (*a*) drive succession (e.g., replacement of native *Ammophila* on coastal dunes with other vegetation) (253, 254), (*b*) affect tree seedling recruitment near parental trees (255), (*c*) promote the invasion of exotic plant species by allowing them to escape from belowground enemies (14, 241, 256–260), and (*d*) alter competitive relationships and community structure (14, 241, 260). Many of these studies rely on soil sterilization to demonstrate positive and negative effects on plant growth, so that it is not known whether the effects are due to pathogenic bacteria or fungi, plant parasitic nematodes, or other direct consumers of plant tissues. However, these studies more clearly demonstrate reciprocal effects of the composition of the soil biota and plant growth than most other plant-soil investigations.

## Invertebrates

It has long been known that the soil food web has profound effects on plant growth and community dynamics, as was first clearly demonstrated by Coleman and colleagues (261) and subsequently demonstrated in numerous studies (262, 263). A full consideration of the nature of feedbacks between plants and the components and function of soil food webs is beyond the scope of this paper, but this has been extensively documented and analyzed by Wardle (29). Soil invertebrates interact with plants indirectly through their predation on soil microbes and through the effects of this predation on nutrient mineralization rates. There is extensive evidence that the species composition, trophic structure, and function of soil food webs can affect plant growth through alterations in nutrient mineralization rates, which in turn alter the quality, quantity, and timing of the C resources, which support the fauna (46, 182, 264–267), as well as affect successional and community dynamics (246). Soil invertebrates are thus part of the complex feedback loops linking C, N, microbial communities, and plants.

## COMMUNITIES AND BIOMES: A FEW EXAMPLES

Following are a few representative examples of well-documented feedback systems, illustrating both simple and complex pathways.

- Mangrove swamps: The oceanfront boundary of mangrove swamps dominated by *Avicennia marina* is modified by a simple feedback between the physical structure of the plant and the physical structure of the shoreline.

The plant's pneumatophores trap sediment and prevent erosion, decreasing the amount of seawater inundation by raising the level of the ground. This facilitates further mangrove expansion seaward (268).

■ Arctic and alpine shrubs: As described above, shrub-snow-soil feedbacks involving soil temperature create a positive feedback that promotes the growth of the shrubs and moderation of soil temperatures (72). The change in soil physical conditions results in altered biogeochemistry as soil microbes remain active under warmer temperatures. Because the biogeochemical change in soil benefits shrubs more than other tundra plants, the positive feedback loop is completed. Snow trapping by the shrubs results in thinner snow cover in the interspaces between shrubs, so shrub patch boundaries are likely to remain stable. Thus, this feedback produces stable patch boundaries (a situation predicted to be a result of feedback by Wilson & Agnew (18). Similar processes are active in maintaining montane treelines (269) and alpine shrub communities (270).

■ Arid biomes—islands of fertility: As discussed above, in arid and semi-arid biomes, plants are patchily distributed, and soil properties reflect their distribution (110). Shrubs produce fertile patches because the shrub's physical structure is able to intercept nutrients and water, both as precipitation and as overland flow from the inter-shrub spaces (271, 272). The increased water availability and nutrients in trapped sediments increase shrub productivity while depleting the interspaces of nutrients. Shrubs deposit above- and belowground litter and root exudates, increasing SOM and fertility, and hydraulic lift may augment the moisture differences between shrubs and interspaces. The result is a stable distribution of shrub patches and unvegetated interspaces. Although the causative mechanisms are based on water flow, the feedback system involves complex interactions with soil microbes, soil chemistry, and plant growth.

In some arid systems, over gentle elevational gradients, banded or patterned vegetation develops by the same feedback mechanisms as those forming islands of fertility. These vegetation bands have been observed in Nigeria (273) and other arid areas in Africa, the Middle East, Mexico (272), Spain (274), and Australia (275). Below rooting depth (30 cm), soils in vegetated and unvegetated bands are indistinguishable, strongly suggesting that feedbacks, not microsite or soil characteristics, are important in regulating the distribution of vegetation in bands.

■ Wetlands and *Sphagnum* bogs: Feedbacks involving the effects of *Sphagnum* mosses on pH were discussed earlier. Here, we note that the feedbacks involving the creation of such large landscape features as raised bogs, patterned peatlands, and blanket bogs involve complex, multifactor feedbacks (79, 276). In addition to the pH pathway, *Sphagnum* produces litter with low decomposability and high phenolic content, thus reducing nutrient availability, and it dramatically alters soil moisture (by creating persistent

saturated conditions), which also radically affects soil chemistry by promoting reductive biogeochemical pathways. All of these effects enhance its own growth and inhibit the growth of most vascular plants, thus establishing a positive feedback system.

In many other kinds of wetlands, plant-generated hummocks alter soil conditions so as to promote further plant growth. Hummocks are produced by both graminoid plants (98) and woody plants (277, 278); they create more aerobic, better-drained soil conditions that permit the growth of plants that cannot tolerate continuous flooding (279).

■ Pygmy forests and heathlands: Dwarf conifer (*Pinus contorta* var. *bolanderi* and *Cupressus pygmaea*) forests on coastal sands in California have litter with very high concentrations of polyphenols (155, 197). As described above, phenolics reduce N-cycling rates and decomposition, increasing forest floor thickness, sequestering N in organic form, and ensuring that only plants with ectomycorrhizal symbionts, which can absorb these organic materials, can obtain sufficient N. The polyphenols also affect the biogeochemistry of other nutrients (Fe, P) and toxic forms of aluminum. This feedback thus involves both microbial and chemical soil components. A similar set of feedbacks is thought to promote the spread of ericaceous plants at the expense of forest trees (280).

## CONCLUSIONS

The potential for plant-soil feedback is vast, ranging in scale and scope from the molecular signaling of plants and their mutualists to global-scale climate change. There is abundant evidence for mutual effects of plants on soil and vice versa, acting through mechanisms involving all aspects of plant growth, morphology, and physiology, and all the physical, chemical, and biological components of the soil. However, clear demonstrations of feedback—a reciprocating sequence of effects—are much less common than the unequivocal demonstration of one-way effects.

Several general patterns emerge from our survey of the literature. We offer them as stimuli for further research.

1. Strong evidence of feedback is more commonly reported for extreme environments—hot or cold, dry or wet, acidic or calcareous, or extreme soil chemistry due to metals—than for moderate environments. It may be that feedback emerges as a structuring element of ecosystems from the welter of other ecological processes when communities are simple. Stressful environments may also promote the evolution of plant characteristics that induce feedback processes with the soil (6), much as facilitative interactions among plant species are more commonly observed in highly stressful environments.

2. Strong evidence of feedback is also more commonly reported for systems involving trophic interactions between live plant tissues and plant consumers (pathogens, parasites, root herbivores) or plant mutualists (symbiotic N fixers, mycorrhizae). In trophic interactions based on detrital plant C, there is abundant evidence of interaction, but not necessarily of feedback effects.

3. Most studies of interaction demonstrate either plant effects on soil properties or soil effects on plant growth, but these studies only speculate that a feedback will result. There is a strong need for studies that attempt to trace the reciprocating effects, which are a hallmark of feedback. The most notable weakness of much of the literature on plant-soil feedback is the lack of data on those plant responses that would demonstrate the feedback process, especially changes in demography. Few studies test whether plant responses to changing soil conditions contribute to an amplification (or attenuation) of the signal generating the soil response. Fewer still demonstrate that a plant-generated change in soil conditions will affect the survivorship and reproductive capacity of the plant. We note that such studies have been most frequently carried out with respect to soil-based enemies; plant population ecologists should be enlisted to work with community ecologists, biogeochemists, microbiologists, and geologists, investigating other pathways of feedback.

4. Many of the presumed feedback pathways act over successional (decades to centuries) or even geological timescales. For such pathways, investigators are forced to use space-for-time observational models and correlational approaches to data analysis. This may be one reason why feedbacks acting over short spatial and temporal scales (mutualists, enemies) are so much better demonstrated than those acting over large temporal and spatial scales. Innovative approaches to determining feedbacks over these timescales are needed to generate unequivocal evidence of feedback, such as the greater use of paleoecological methods for reconstructing histories of plant growth, community composition, and the physical and biogeochemical status of the environment.

5. The role of plasticity in both the plant and microbial or faunal partners needs to be better explored. It is frequently implicitly assumed that the plant and microbial components of a particular experimental system are invariant, whereas the high degree of phenotypic plasticity among plants and the extraordinary physiological and functional plasticity of most microbes are well known in other contexts. The presence of this plasticity could either enhance or attenuate feedbacks, but conclusions about the importance of plasticity must await specific tests of its importance.

6. In spite of the rapid increase in number, type, and availability of molecular and genetic tools in plant and microbial science, these methods are still rarely used in exploring plant-soil feedback (with the exception of

pathways affecting agronomic plants). These methods could greatly enhance knowledge of the mechanisms behind apparent feedbacks.

7. Many of the studies of plant-soil interactions involve observations of experimental systems, including greenhouse pot cultures, planted micro- or mesocosms, or monocultures such as plantations or crop fields. However, in natural ecosystems, plants typically grow intermixed with each other, with a high degree of overlap of both canopies and especially roots. Thus, in order to evaluate the significance of the numerous demonstrations of species-specific effects on physical, chemical, and biotic properties of soil, observations are needed under conditions in which a unit of soil is affected by multiple species simultaneously and plants are interacting with each other.

8. Few studies of plant-soil interactions account for the role of other nonplant, or soil-based, factors in the system of interest or try to evaluate the importance of plant-soil feedback relative to other ecological factors. Studies of the effects of aboveground herbivory on root exudation and on mycorrhizae testify to the importance of placing plant-soil feedbacks in a larger ecological context. We suggest that analyses of the relative strength of various ecological factors, operating in tandem with plant-soil feedback and undoubtedly interacting with each other, are essential to evaluating feedback as an ecological force of its own.

In sum, feedback between plants and soil is undoubtedly an important phenomenon, but it should not be assumed on the basis of evidence of a one-way effect. As Heraclitus reminds us, such an important process demands more than arbitrary conjecture.

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# CONTENTS

## IV. Emerging Integrative Themes

## Indexes

## Errata

An online log of corrections to *Annual Review of Environment and
and Resources* chapters may be found at http://environ.annualreviews.org