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Plant–soil interactions: ecological aspects and evolutionary implications

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Abstract. Building on the concept of plants as ecosystem engineers, and on published information on effects of particular plant species on soils, we review the evidence that such effects can provide a positive feedback to such plants. Based on case studies involving dune formation by Marram grass, N supply by N_2-fixing plants, depression of N availability by ericaceous plants, 'islands of fertility' in deserts, mull- and mor-forming temperate forest trees, and formation of peatbogs, as well as similar other cases, we conclude that there is strong evidence for plant–soil feedbacks in a variety of ecosystems. We argue, moreover, that these feedbacks could have played a role in the evolution of the plant species in question. These ideas are based mainly on correlative observations, and need further testing.

Introduction

Jones et al. (1984) defined *ecosystem engineers* as organisms that directly or indirectly modulate the availability of resources to other species by changing the physical state of biotic or abiotic materials leading to the modification, maintenance, or creation of habitats. They defined autogenic engineers as organisms that change the environment via their own physical structures, i.e. their living and dead tissues, and allogenic engineers as those which transform living or non-living materials from one physical state to another. Jones et al. (1994) suggested that the results of ecosystem engineering often feed back to the fitness of the engineers and in that case can be considered as 'extended phenotypes' subject to natural selection (Dawkins 1982).

The chemical and physical properties of soils are influenced by soil dwelling biota, larger animals and plants (Hole 1982; van Breemen 1993) and soils are therefore the products of ecosystem engineering. Many of the soil properties influenced by plants (e.g. acidity and nutrient availability) are also important to plant growth and survival. Therefore, soil can be considered a part of the extended phenotype of a plant and the feedback between a particular plant species and its soil environment could have evolutionary implications. In this paper, first we briefly review the literature on soil–plant feedbacks from pedological and ecological perspectives. Next, we consider six examples from a different ecosystems of plants exerting a strong effect on soil properties. Finally we discuss the possible consequences of the feedback resulting from the effect of those plants on soils with an evolutionary perspective.

Pedological and ecological aspects of soil–plant feedbacks

The study of the effects of organisms on soils is a venerable research area in pedology dating back to Dokuchayev (1879). He recognised biota as one of the five soil forming factors. These were later incorporated in Jenny's (1941) state factor approach, which still forms a major theoretical framework in pedology. Though biota–soil feedbacks were recognised long ago, they were hardly studied by pedologists, probably because these feedbacks frustrated the state factor approach. While the soil is clearly a dependent variable of four state factors (climate, parent material, topography and time), the fifth state factor – biota –, was seen as '*... a real bugbear. ... Like everybody else I could see that the vegetation affects the soil and the soil affects the vegetation, the very circulus vitisis that I was trying to avoid*' (Jenny 1980). In an effort to break this vicious circle, Jenny took the immigration of individuals and input of propagules as the biotic factor.

The study of feedbacks between organisms and their environment received more attention among ecologists. Throughout the 20th century, ecologists attempted to link the theory of evolution to ecological systems (Loehle & Pechmann 1988). Among ecosystem ecologists, there appeared to be two schools of thought with long standing debate among schools. Some ecologists believed that the emergent properties of systems resulted from natural selection at an organisational level above the species (cf. Odum 1983), while others believed that system properties arose from an interaction between the physical environment and intra- and interspecific competition among individual species, with natural selection favouring species capable of filling vacant ecological niches (cf. Gleason 1926; Whittaker & Woodwell 1971).

The idea that plant communities behaved like organisms originated from the work on succession by of Clements (1916, 1936), who argued that a plant community could be analysed as a complex organism which grew, matured, and died. To Clements, the process of succession entailed a continual and reciprocal interaction between a habitat and the life forms comprising the community until finally a stable state, or climax, was reached (Kingsland 1991). By the mid 1950s, Clements's theory had been largely discredited but components of the organismal view of plant communities and succession had been adopted by several ecologists in an attempt to bridge evolutionary biology with systems ecology. For example, Patten and Odum (1981) and Odum and Biever (1984) argued that evolution would provide mutual adaptation of species to form functionally integrated systems (Loehle & Pechmann 1988). The idea of group selection inherent in this work was criticised (cf. Williams 1966) because one could argue that the properties of systems (e.g. net primary production) arose as a consequence of natural selection of individual species, and the individualistic distributions of species and their interaction with the environment (Loehle & Pechmann 1988).

Soil physical and chemical properties change during the course of succession and the effects of plants on these changes dominate, particularly during primary succession. The three models of autogenic plant succession proposed by Connell and Slatyer (1977) are a convenient framework for a discussion of the effects of succession on the evolution of plant effects on soils. In all three models, both early and late successional species colonise at the same time. In their 'facilitation' model, the growth of the late successional species depends on the presence of early successional species which alter resource availability (above- and/or below ground) in a manner which increases the survivorship of later successional species. In the 'tolerance' model, all species grow to maturity in the presence of early successional species but late successional species ultimately outcompete early successional species because they can tolerate the decrease in resource availability during succession. In the 'inhibition model' all species resist invasion by competitors. The first occupant of a site excludes or inhibits later colonists until the former die or are damaged, thus releasing resources allowing later colonist to thrive and mature. In reviewing 150 published studies of primary succession, Connell and Slatyer (1977) concluded that there was considerable evidence for the 'inhibition model', that some cases of succession conformed to the 'facilitation model', but that there was little evidence for the 'tolerance model'.

The work of Grime (1977) serves another framework to examine effects of plants on soils. Grime (1977) distinguished three primary plant growth 'strategies' in response to the intensity of stress (shortages in resources, extreme temperatures and water regimes, growth-inhibiting substances), and disturbance (floods, windstorms, fires, herbivores, plowing, mowing). According to Grime (1977), plants adopt a 'competitive' strategy on relatively fertile, undisturbed sites where intra- and interspecific interactions for light, water, and nutrients regulate the distribution and abundance of plants. In stressed environments, the adoption of a 'stress tolerant' plant strategy is associated with conservative utilisation of water, nutrients and photosynthates (stress tolerant strategy), and on disturbed, productive habitats the 'ruderal' plant strategy is associated with rapid growth, short life span and the production of a large quantity of seeds. An integrated screening programme of 43 common British plants for 67 traits (Grime et al. 1997) found broad support for the existence of the three plant strategies. Three different multivariate methods identified a primary axis with soil nutrient availability separating the ruderals and competitors from the stress-tolerant species. Principal component analysis yielded a tertiary axis separating ruderals from competitors.

We will return to the succession and primary plant strategy models later to discuss them in relation to the case studies we present below.

Effects of plant species on soils

We ask the question of whether the effects of plant species on soil chemical and physical properties influence plant fitness. By focusing on the effects of individual species within a community, this approach implicitly assumes that the evolutionary process occurs at the level of the individual. We will consider a number of cases, some of which are dealt with more extensively later in this volume. They were selected on the basis of specific plant species or of species belonging to a certain functional group of plants with a strong effect on soil properties. In the discussion session we will review the six cases, examine other ecosystems for comparable examples, and see if we can draw general conclusions about the possible evolutionary significance of soil–plant feedbacks. The case studies are: (1) dune formation by Marram grass (Van der Putten 1993), (2) increasing N supply by N_2-fixing plants, (3) depression of N availability by ericaceous plants (Berendse, this volume), (4) 'islands of fertility' in deserts (Schlesinger and Pilmanis, this volume), (5) mull- and mor forming temperate forest trees (Finzi et al.[a,b], in press), and (6) formation of bogs by peatmoss (van Breemen 1995).

Marram grass as a dune former

Ammophila species such as Marram grass and American beachgrass are perennial plants of coastal foredunes. Both species enhance sand deposition by decreasing the wind speed around tillers and tolerate burial up to 1 m per year (Ranwell 1958). Both species are vigorous if buried regularly, but degenerate after sand deposition ceases. Van der Putten et al. (1993) resolved the long standing debate surrounding the mechanisms of *Ammophila* success following sand burial (e.g. Huiskens 1979) by showing that soil pathogens were a major cause of death in Marram grass when sand dunes stabilized. However, with roots constantly colonising recently deposited, windblown sand Marram grass escapes the pathogens. Better ability to increase sedimentation rates surrounding Marram grass plants could increase Marram grass fitness by providing a substrate free of pathogens, increasing plant vigour and reproductive output.

N_2-fixing plants

Symbiotic nitrogen fixation converts unreactive dinitrogen (N_2) in the atmosphere to a reactive plant-available form. Because N is a major mineral nutrient in soils and is essentially absent in soil parent material, N_2-fixation has a potentially important effect on plant growth and ecosystem development. Yet, Walker (1993) who reviewed 150 published primary successional seres found that, while N_2 fixing species were present in all seres, there was no correlation between the presence of N_2 fixers and total N accumulation in surface soils. Moreover, while nitrogen fixers apparently facilitated the growth of some non-N_2 fixing plant species, they often inhibited the growth of other species by competing successfully for other limiting resources.

Depression of N availability by ericaceous plants

Berendse (1994, this volume) argued that the rate of litter decomposition is an important component of plant fitness in heathland ecosystems subject to high rates of annual N deposition. Following sod removal, the early successional species *Erica tetralix*, could slow down the rate of succession by producing litter which decomposed slowly and depressed nutrient (N) availability as a result of inherently high nutrient-use efficiency. Berendse (1994) showed that *Erica*, by decreasing N availability, transiently increased its fitness by increasing offspring survivorship. Over time however, soil N accumulation facilitated the replacement of *Erica* by the later successional grass species *Molinia caerulea*. He argued that the later successional species *Molinia* replaced *Erica* by producing litter that decomposed more rapidly leading to enhanced nutrient (N) availability required by this fast growing species with lower inherent nutrient-use efficiency. Thus with increasing N availability, *Molinia* outcompeted *Erica* leading to the development of a quasi-stable state until disturbance (sod removal) reset the heathland system to an early stage of succession.

Islands of fertility in the Southwestern USA

Shrubs concentrate soil nutrients (e.g. N, P, K) in 'islands of fertility' that are localised beneath their canopies, while adjacent barren intershrub spaces are comparatively devoid of biotic activity. Islands of fertility are perhaps one of the clearest examples of plants influencing soils and these islands dominate the structure of arid and semi-arid landscapes world-wide (Reynolds et al. 1997). During the last decade, large areas of former grassland in the Southwestern US have become dominated by shrubs (Schlesinger and Pilmanis, this volume). Black gramma (*Bouteloua eriopoda*) has been replaced principally by creosote bush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) (Hennessy et al. 1983; Reynolds et al. 1997).

The mechanisms by which shrubs invade grasslands remain elusive (Schlesinger et al. 1996) but allogenic and autogenic processes appear to be involved. Allogenic processes include climate change, human fire suppression, overgrazing, an increase in small mammal abundance due to the elimination of natural predators, and rising atmospheric CO_2 concentrations (Reynolds et al. 1997, and references therein). Autogenic factors promoting the development of islands of fertility in arid environments include (1) the uptake of soil nutrients followed by their deposition via plant litterfall beneath shrub canopies; (2) symbiotic nitrogen fixation (e.g. *Prosopis glandulosa*) which concentrates N in rooting zones (Virginia & Jarrell 1983); (3) the interception of soil particles from the atmosphere by shrub canopies (Parsons et al. 1992); (4) the funnelling of rainwater and stemflow to the base of shrub stems (e.g. Whitford et al. 1997); (5) greater rates of water infiltration beneath shrub canopies than in shrub inter-spaces due to differences in surface soil structure (e.g. Rostagno 1989); and (6) access to deep soil water (e.g. Hallmark & Allen 1975).

Mull- and mor-forming temperate forest trees

Northern temperate forests are promising ecosystems in which to look for specific plant–soil feedbacks. They are comprised of relatively few species growing on young soils with largely unweathered, glaciated parent material facilitating the measurement of the effects of specific trees on soil properties. Soil properties reported to change differentially depending on tree species that may feed back to the trees include profile morphology (particularly with regard to the organic surface layer, or ‘forest floor’, Muller 1887; Ovington 1953), and related properties such as availability of N (Finzi et al.[a], in press), and soil pH and exchangeable cation concentrations (Zinke 1962; Lefevre & Klemmedson 1980; Alban 1982; Klemmedson 1987; Boetcher & Kalisz 1990; Finzi et al.[b], in press), all of which tend to be lower when organic surface layers are thick (Mor) than when they are thin or absent (Moder- or Mull). Correlations between tree species and soils, however, need not be caused by trees: parent material or soil properties developed under different conditions which predate the extant vegetation could determine the distribution of the tree species. For example, in mature forests in Wisconsin, Pastor et al. (1984) found a dominant effect of texture of the parent material on species distribution and concluded that the cycling of N and P observed in stands dominated by different species had to be attributed to the effects of parent material in combination with effects of tree species.

Unambiguous examples of the species-specific effects of trees on soil properties come from replicated common-garden experiments (Binkley 1995), which, however are confined to short time spans relative to the age of the unmanaged ecosystems. Another approach, followed by van Breemen et al. (1997), and Finzi et al.[a,b] (in press) is to analyse plant–soil interactions by combining measurements of relatively stable soil characteristics not easily influenced by vegetation (e.g. parent material composition) with relatively plastic characteristics more easily influenced by vegetation (pH, C and N content, exchangeable cations).

We used this approach with beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), white ash (*Fraxinus americana*) and red oak (*Quercus rubra*) at two study sites. Soils of both sites were well-drained sandy loams (Typic Dystrochrepts) derived from Wisconsinian glacial till over a mica-schist bedrock, with a similar morphology and nearly identical texture (Van Breemen et al. 1997). There were marked differences ($P < 0.001$) in parent material composition within and between sites, as reflected by significant spatial variation in the contents of (silicate-bound) CaO, MgO and K_2O. These differences reflected differences in parent material composition, as soils were nearly unweathered at a shallow depth, while there was no evidence for effects of differential mineral weathering rates beneath the different tree species.

Forest floor thickness, pH and pools of C, N and exchangeable cations differed significantly beneath the different tree species and sometimes between sites and species (Finzi et al.[a,b], in press). For example, forest floor thickness increased in the order sugar maple < ash < red maple < beech < oak < hemlock while soil pH decreased in the same order at both sites (Table 1, Figure 1), even though the sites clearly differed in mean pH and base content of the parent material (van Breemen et al. 1997). The C/N ratio of the forest floor was lowest under sugar maple (15:1) and significantly lower than under hemlock (20:1). The rate of mid-summer net N mineralisation was nearly two fold higher beneath sugar maple, red maple, and white ash ($\sim$20 kg ha^{-1} 28 d^{-1}), than beneath beech red oak and hemlock ($\sim$11 kg ha^{-1} 28 d^{-1}) (Finzi et al., in press[a]).

The highly reproducible relationship between tree species, soil pH, and exchangeable base cations could be explained by two different mechanisms. First certain tree species were linked to parent material that was either low

Table 1. Mean values of forest floor mass, and of pH and total and exchangeable Ca (mg Ca/g soil) in the 0–7.5 cm mineral surface soil under different canopy tree species in Great Mountain Forest, Connecticut, USA. Species have been arranged in order of increasing or decreasing values of the property in each column. Values with the same letter in a row do not differ significantly at $P < 0.01$.

Forest floor mass g/m^2		pH		Exch Ca mg/g		Total Ca mg/g		Slope of regression of exch Ca to CaO	
S. maple	9 a	S. maple	4.7 a	S. maple	0.93 a	Ash	12 a	S. maple	0.37 a
Ash	13 a	Ash	4.6 ab	Ash	0.55 ab	R. maple	11 ab	Oak	0.20 a
R. maple	25 ab	R. maple	4.5 bc	Beech	0.17 b	S. maple	11 abc	Ash	0.14 ab
Beech	26 ab	Beech	4.3 cd	R.maple	0.17 b	Hemlock	10 abc	Beech	0.05 ab
Oak	44 bc	Oak	4.2 d	Oak	0.17 b	Beech	7.7 bc	R. maple	0.03 b
Hemlock	70 c	Hemlock	4.0 d	Hemlock	0.16 b	Oak	6.6 c	Hemlock	0.02 b

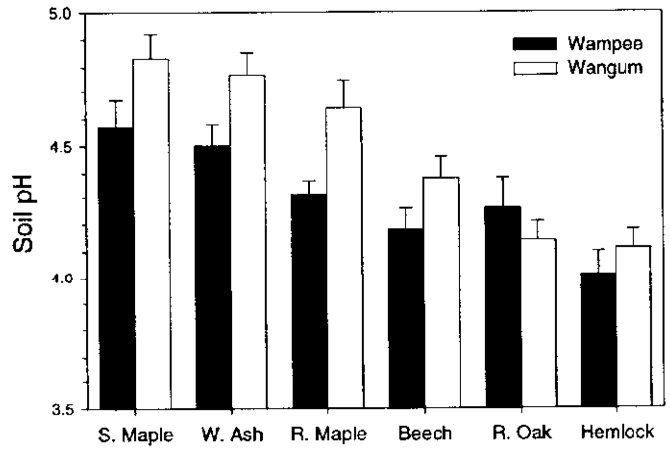

Figure 1. Mean and standard deviation of soil pH (forest floor plus mineral soil) under each of the six canopy trees at two forest sites in the Great Mountain Forest, Connecticut, USA.

or high in Ca and Mg. The high-pH soils under ash and red maple had parent material that was markedly richer in CaO and MgO, than the low-pH soils under oak and beech (Table 1). Thus, pH differences between ash, red maple, red oak, and beech appeared to be attributable to differences in base content (and acid neutralising capacity of) the parent material. This implies that the successful establishment of individuals of these species depends in part on the composition of the parent material (i.e. the species differed in 'site preference'). Second, species changed soil chemistry independently of the composition of the parent material. Despite large differences in soil pH, the parent material of soils under sugar maple and hemlock did not differ

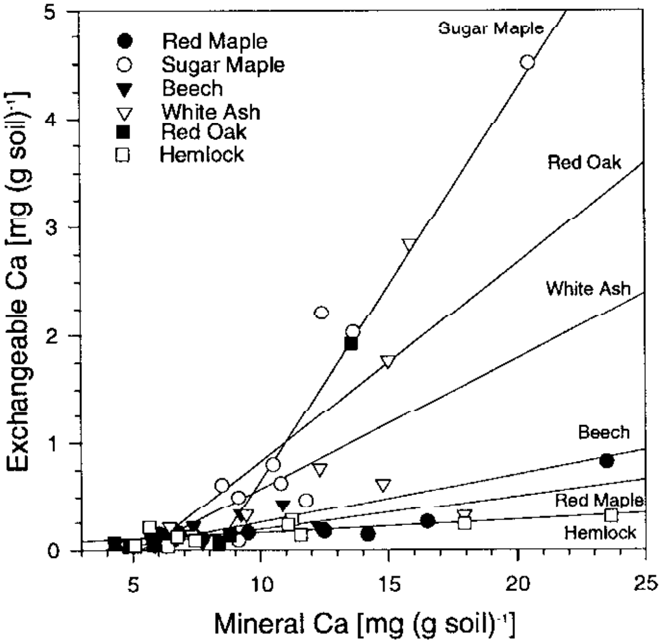

Figure 2. Species specific linear regressions of exchangeable Ca as a function of total soil CaO in the upper 7.5 cm of mineral soil for six canopy trees studied at Great Mountain Forest, Connecticut, USA (after Finzi et al., in press[b]).

significantly in CaO and MgO content. Although exchangeable Ca was a small fraction of mineral Ca, there was a positive correlation between exchangeable and mineral bound Ca (Figure 2). This suggests that the size of the CaO pool reflects the amount of Ca available for weathering. The slope of the regression of exchangeable Ca as a function of mineral bound Ca was highest for sugar maple, and lowest for hemlock, and highly significantly different between the two (Table 1). These last two findings suggest that the late-successional, shade-tolerant species sugar maple and hemlock influence exchangeable Ca, soil pH and available N in opposite directions, regardless of the nature of the parent material.

The differences in soil chemistry and nutrient availability beneath sugar maple and hemlock appear to be causally related to the presence of the these trees regardless of the soils' parent material composition. The question arises of whether the changes in soil chemistry and nutrient availability beneath these species confer some competitive advantage or disadvantage to each of these species. Frehlich et al. (1993) showed that patches dominated by sugar maple or hemlock in an old-growth forest in northern Michigan are stable for thousands of years. They concluded that seedbed effects (burial of hemlock seedlings beneath sugar maple leaf litter, and low N availability to sugar maple beneath hemlock) explained the development and maintenance of the patches over long periods of time. Kobe et al. (1995) observed that deeply shaded sugar maple saplings survived better in calcareous than in non-calcareous soils implying that the small size of the exchangeable pool beneath hemlock competitively displaces sugar maple. Walters and Reich (1997) found that nitrate availability to sugar maple seedlings increased growth under low light.

Whatever the mechanisms by which the tree species change soil conditions, a number of conclusions may be drawn. Sugar maple, through its effect on soil chemistry and nutrient availability, appears to create habitats that favour self replacement while inhibiting hemlock seedlings by burying them under leaf litter. Through its effect on soil, sugar maple probably also favours itself vis-à-vis other late successional species such as American beech and red oak, which either prefer more acid sites, or are outcompeted by sugar maple in more base-rich soils (Kobe et al. 1995). Hemlock appears to influence seedbed conditions favouring offspring success while hampering the establishment of sugar maple. The low soil pH beneath hemlock appears to be created by the production of highly acidic, slowly-decomposing leaf litter because of high lignin and tannin contents (e.g. White 1986, 1991; Millen 1995). The low pH depresses the rate of net N mineralisation and the rate of net nitrification which could dramatically reduce the growth rate of sugar maple seedlings beneath hemlock. While low N availability and low soil pH may not be an optimal growth environment for hemlock, hemlock tolerance to such conditions (Godbold & Huttermann 1994, and references therein) may be sufficient to give hemlock seedlings a competitive edge over sugar maple (and other) seedlings that germinate beneath hemlock.

Sphagnum peat bogs

Sphagnum spp. may be one of the best examples of an ecosystem engineer (Jones et al. 1994; van Breemen 1995[a]). Well developed *Sphagnum* bogs are characterised by a nearly treeless landscape, with only few stunted xeromorphic trees on the better drained parts of the bog. The poor tree growth is due to a combination of low soil temperatures, locally dry hummocks over waterlogged, anoxic hollows, high acidity and low nutrient supply. Van Breemen (1995[a]) recently reviewed how *Sphagnum* creates acidic, nutrient-poor, cold and anaerobic peat bogs (Figure 3), mainly in temperate and cold climates. Once *Sphagnum* gets established (Figure 3, top dashed box) it may start bog formation because of specific organo-chemical, morphological, anatomical, and physiological properties (ovals in Figure 3) which enable it to form acidic, nutrient poor, heat-insulating, and slowly permeable peat.

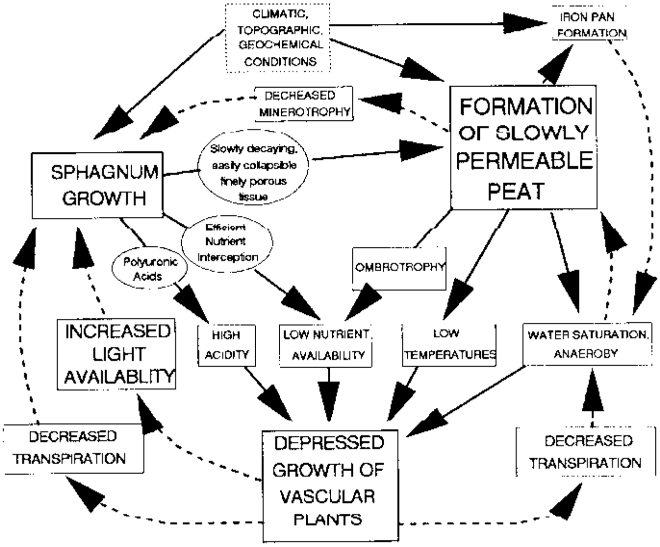

Figure 3. Feedforward (solid arrows) and feedback (broken arrows) processes contributing to growth of *Sphagnum* and peat formation (reproduced by permission, after van Breemen 1995).

'*Almost nothing eats Sphagnum*' (Clymo & Hayward 1982), in spite of its high content of polysaccharides and its lack of lignin. Its low palatability to herbivores and decomposers alike may be caused mainly by its high content of polyphenols, which partly form a polymeric network that is probably covalently linked to the cell wall polysaccharides (Van der Heijden 1994). Due to the pliable nature of the material, and its many open, porous ('hyaline') cells, dead *Sphagnum* collapses to a finely porous material, which holds large quantities of water, yet is extremely slowly permeable to water. High nutrient-use efficiency in *Sphagnum*, the presence of polyuronic acids in plants cells, and anoxia contribute to a very slow rate of litter decomposition. As a result, *Sphagnum* peat tends to build up above the original ground water layer (raised bogs), or on top of mineral soil (blanket bogs). The resulting bogs are increasingly dependent on nutrients deposited from the atmosphere (ombrotrophy), and are subject to even greater nutrient limitation.

Collectively, high acidity, low nutrient availability, and water saturation in bogs reduces the competitive ability of upland, vascular plants because of their requirement for the uptake of nutrients by roots and the difficulty in doing so. The absence of vascular plants in bogs increases light availability, decreases the rate of evapotranspiration, and increases water availability. High acidity, low nutrient availability, water saturation, and the absence of upland vascular plants favours the development of a positive feedback loop by promoting Sphagnum growth and peat formation (Figure 3, broken arrows).

Sphagnum also competes with species of its own genus. Compared to *Sphagna* of the low, wet pools in the bog, the capillary movement of water up stems of *Sphagna* of the higher hummocks is more efficient because of a different pendant branch morphology. *Sphagnum* also has higher productivity under nutrient-poor conditions, higher uronic acid content, and more slowly decomposing litter than *Sphagna* (Johnson & Damman 1991). In bogs, these properties allow hummock species to outcompete hollow species, in the dryer portions of the peat bog.

Discussion

First we discuss the evidence that soil–plant feedbacks favour the individual species responsible for soil changes and how these effects fit within Connell and Slatyer's (1977) succession models and Grime's (1977) primary plant strategies. Then we address the possible role of such feedbacks in the evolution of the plant–soil interactions.

Feedbacks from soil to plant

In all 6 cases reviewed here plant species strongly change soils, with potential effects on plant growth. *Erica* in heathlands, *Tsuga* in temperate forests, and *Sphagnum* in peatbogs all decrease or depress the availability of a number of soil resources, notably N. All three mediate the reduction in N availability through an effect on litter chemistry and on the environment in which the litter decomposes. Because the reduction in N availability appears to have a greater negative effect on potential competitors than on the causative species, this effect on soil favours the causative species in an indirect manner. *Sphagnum* and *Tsuga* also depress minerotrophy (e.g. the concentration of Ca^{2+}) to levels which may be required for their optimal growth (as in the case of *Sphagnum*, cf. Clymo & Hayward 1982) and/or may hamper competitors more than themselves. The ability to decrease soil pH and nutrient availability to a level below which competitors are able to tolerate may be common. For example, Kauri pines (*Agathis australis*) produce a thick organic surface layer and nutrient-poor podzols with impermeable Spodic horizons. These 'basket-podzols' are common under large individual trees (Swindale 1955) and may be an important mechanism inhibiting the colonisation of broad-leaved trees that dominate on adjacent, relatively fertile, non podzolized soils (Orbell et al. 1980). *Rhododendron maximum* (eastern US forests) litter is recalcitrant to the decomposition process and depresses earthworm activity. This property facilitates the development of a thick forest floor which could confer a competitive advantage to their seedlings over other understorey vegetation (Boetcher & Kalisz 1990, 1991).

Species that depress soil fertility and the growth of competitors clearly fit Connell and Slatyer's (1977) 'inhibition model' and follow Grime's (1977) stress-tolerant strategy typical of slow-growing plants on nutrient-poor soils with low foliar nutrient concentrations and low palatability to herbivores. The results in this paper expand Grime's (1977) model to include an active component (i.e. creating stress) as part of the competitive strategy of mid- and late-successional species. This is consistent with Grime's (1977) definition of competition: 'the tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space . . . '.

N_2 fixing plants could either fit the 'facilitation' model of Connell and Slatyer (1977) (where they increase the supply of mineral N for other plants), or their 'inhibition' model (if a competitive strategy prevails). Although N_2-fixation increases the N-status of the fixing plant, a resultant increase in soil N availability is unlikely to favour the plant symbiont itself for at least two reasons. First, the positive effect of N_2-fixation on available soil nitrogen would be disadvantageous to the same plant in the long-term by increasing interspecific competition. Second, rates of N_2-fixation are often negatively correlated with the availability of inorganic N in soils (Boring et al. 1988), which could reduce the overall N capital of the plant symbiont leading to an overall decrease in plant growth rate and reproductive output.

Other early- to mid-successional plant species that stimulate the supply of soil resources fit Connell and Slatyer's (1977) 'facilitation' model (e.g. *Molinia* in heathlands, desert shrubs and 'islands of fertility'). While islands of fertility are clearly important in helping shrubs persist at the expense of grasses (Schlesinger et al. 1990), it is not clear if they favour certain species of shrubs over others. Despite the well documented effects of shrubs on seedling establishment across generic boundaries (e.g. Franco-Pizana et al. 1995), the effect of islands of fertility on replacement by conspecifics remains elusive. According to McAuliffe (1988) *Larrea tridentata* seedlings were more abundant under *Ambrosia dumosa* adults rather than conspecific adults in the Sonoran desert of Arizona, but Boyd and Brum (1982) found that *L. tridentata* seedlings were commonly found beneath conspecific adults.

Islands of fertility are not confined to shrubs, but have also been observed in semi-arid grasslands and beneath canopy trees in savannahs. Under grasses the effect may be small: for patches of bunch grass (*Boutelona gracilis*) in shortgrass steppe, Kelly and Burke (1997) found that enriched nutrient-supply zones under dead plants did not persist beyond several months. The effects trees on soil beneath them in savannah-like landscapes is likely to be more substantial. Dahlgren et al. (1997) showed that blue oak (*Quercus* *douglasii*) significantly increased organic C and N, cation exchange capacity, exchangeable bases and pH in the soils under their canopies in California. Similarly, *Quercus robur* invading *Calluna* heathlands increased soil pH, decreased the thickness of the organic surface layer, and decreased the contrast between albic and spodic horizons in podzols in Denmark (Nielsen et al. 1987). In addition to physical and chemical changes in soils, balsam fir tree islands in dry, alpine areas influence microclimate – snow cover, water supply and weather-related stresses – that tend to increase plant growth (Van Miegroet & Hysell 1995). In all these cases the soil effects, which are likely to result from particular physical and physiological properties of the tree species, may well have a positive feedback to individuals that cause them.

The case of Marram grass stands apart from the other examples in that its effect on soils is physical (e.g. an increase in sedimentation) rather than chemical (i.e. changes in nutrient availability). Nevertheless, the development of a positive feedback exists not because of greater success in competition with other species but because of its ability to stimulate the accumulation of a new substrate free of soil-borne pathogens.

Do soil–plant feedbacks influence the evolutionary process?

With the exception of N_2 fixing plant species, whose stimulation (if any) of soil N availability appears to unfavourable for the plant symbiont, the five cases discussed in this paper involve feedbacks favourable for the plant in question, at least in part of the range of soil conditions that are under influence of the plant.

The changes in soil properties mediated by the plants species reviewed here could be pre-adaptations which increase plant fitness. If so, the effects of plants on soils are heritable and soil formation and the changes in element biogeochemistry associated with soil formation could, in part, be driven by Darwinian evolution. Furthermore, if these processes are typical in plant communities with species that have a dominant effect on soil properties, then this analysis might help to explain the mechanisms behind what appear to be functionally integrated systems, without resort to group selection (Odum & Biever 1984; Williams 1966).

So far, this idea is based on descriptive case studies and clearly needs to be tested. First, we need to test specific hypotheses regarding the mechanisms involved in plant species effects on soils. Second, we need manipulative studies to assess whether or not soil changes mediated by plant species influence intra- and intergeneric establishment and survivorship. Third, we need to establish that individuals within a species vary in the attributes that influence soil properties and confer a competitive advantage to offspring. Additional suggestions along these lines were made by Binkley and Giardina (1998).

The soil changes induced by the plant species discussed can have marked and significant effects within the lifetime of a single individual (Binkley 1995; Berendse 1994). This increases the probability that changes in soil properties influence the growth and survivorship of the causative individual, as well as its offspring. This may even be true for *Sphagnum*: although centuries may be needed to build ombrotrophic bogs, long-lived individual clones of *Sphagnum* could form the bulk of individual raised bogs, as illustrated by paleoecological studies showing that the same species may be present for thousands of years (Tolonen 1967).

The apparently common syndrome of plant species depressing nutrient availability via low quality litter production may be linked to herbivore deterrent properties in live tissues of the same species. As suggested by Chapin (1991), elaborated by Hobbie (1992), and experimentally confirmed by Grime et al. (1996), characteristics of plants in nutrient-poor ecosystems that deter herbivores also decrease litter decomposability and nutrient mineralisation from organic matter (e.g. carbon based secondary plant compounds such as lignin). The dual-property of these compounds (anti-herbivore, nutrient depression) may have facilitated their evolution.

One could argue that a soil change caused by a certain plant species, e.g. depression of nutrient availability, alters soil conditions beyond a tolerable range to itself and therefore facilitates the invasion by a different species. While possible, this scenario does not necessarily argue that the soil effect has no evolutionary benefit. The only requirement for adaptive value is that the effect lasts long enough and recurs often enough to markedly increase the fitness of the individual. While long-term site monopolisation associated with specific soil conditions linked to a particular tree species (e.g. Sylvania Woods, Frehlich et al. 1993) may provide strong circumstantial evidence of an evolutionary benefit, shorter-term, less dramatic effects could also be evolutionarily significant.

Time is also important. The two-species, soil-vegetation patch system at Sylvania is relatively old (~3000 yrs), but far too young to have been significant in terms of the evolution of the species. However, hemlock and sugar maple (1) probably coexisted during earlier interglacials, and perhaps since the Tertiary, leaving time for evolutionary processes to sculpt the differences among these species; while (2) their opposing positions on the primary axis of Grime et al. (1997) would provide them with opportunities to evolve the same strategy in competition with other plants.

Clearly, the question of what regulates plant fitness and whether plant fitness is adaptive over the course of succession needs further study. Much of this discussion goes beyond what can be inferred from the ecologically oriented data obtained on the effects of plant species on soil properties presented here. Nevertheless, these questions need to be highlighted and addressed if we are to begin linking ecological studies to broader questions of evolution especially with recent concerns over rapid environmental changes associated with human activity.

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