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Why do tree species affect soils? The Warp and Woof of tree–soil interactions

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Abstract. Many ideas have been advanced regarding how trees affect soils. Enough evidence is now available to evaluate the strength of these ideas and to consider interactions between tree species and soils in an evolutionary context. Forest floor mass commonly differs by about 20% for different species growing on the same site; differences of up to 5-fold have been reported. Litterfall mass and N content commonly differ by 20 to 30%, but larger differences are also common (especially with N-fixing species). The net mineralizaton of soil N typically differs by 50% or more among species, indicating very strong feedback possibilities. We evaluate the evolutionary context of tree effects on soils by considering 3 degrees of coupling of trees to soils: tightly woven connections where the fitness of the tree is enhanced by its effect on soils; loosely woven interactions where selection for tree fitness unrelated to soil properties leads to indirect effects on soils (either enhancing or impairing fitness); and frayed interactions where the effects of trees on soil derive from features of the ecosystem that do not involve direct selection for tree fitness. Evidence supports each of these degrees of interaction for at least some cases, and no single context explains all the interactions between trees and soils. Important areas for further work include: next-generation assessments of the effects of trees on soil suitability for the same (and different) species, and the role of soil organisms in developing and modifying the effects of trees on soils.

Introduction

The composition and productivity of forests differ strongly among sites that differ in soil properties. For example, sites in southern Utah with soils developed from limestone parent materials support productive forests of ponderosa pine (*Pinus ponderosa*), while adjacent sites with soils from shale support low productivity stands of pinyon (*Pinus edulis*) and juniper (*Juniperus osteosperma*); these parent material boundaries may control species composition even when climate changes substantially (cf. Betancourt 1990). Similarly, the species composition and aboveground net primary productivity of forests in Wisconsin relate strongly to soil texture (Pastor et al. 1984). The large differences in forests that can accompany differences in parent material would make an interesting subject for detailed consideration, including issues of the underlying causes for differences (e.g. water relations, physical impediments to root development, nutrient supplies and balances) and whether site 'conditions' select for species that might engender specific effects on soils. (Do high moisture supplies select for species with high quality litter that increases N turnover?) In the present paper, however, we focus more on the interactions and feedbacks that weave trees and soils together.

How substantially do trees alter soil properties and what are the mechanisms responsible for these changes? A recent review summarized the available evidence for the effects of different tree species on soils (Binkley 1996a), and we use this base to discuss the possible biogeochemical and evolutionary mechanisms leading to these effects. We focus primarily on 'common garden' experiments that have allowed direct comparison of the effects of species on a common soil (with statistical replication). We also examine the processes responsible for and rates of changes in soils, and consider a set of general hypotheses about why these changes occur.

How temperate and tropical forests differ from other vegetation

Forests differ fundamentally from other vegetation types (Table 1). Forests typically develop surficial O horizons, and greatly modify the microclimate at the soil surface and the physical, chemical and biological features of the soil. The scale of spatial variation probably differs for forests; individual trees can affect soils at a scale of 10 m or more (Riha et al. 1986; particularly when trees uproot, Stone 1975), compared with 1–5 m for shrubs (Schlesinger et al. 1990) and 0.1 to 0.5 m for grasses (Hook et al. 1991). The spatial variation around individual trees (reviewed by Rhoades 1997) develops from spatial patterns of stemflow input of water and chemicals; variations in inputs of throughfall water and chemicals (sometimes concentrated near the periphery of the canopy); and variations in litter inputs (both above and belowground).

General mechanisms and magnitudes of differences in effects of tree species on soils

Tree species can differ in their effects on soils by many mechanisms, including rates of nutrient inputs, outputs, and cycling (Table 2, and other papers in this symposium). Some of these differences may have developed from direct selection of traits that increase tree fitness, such as rates of nitrogen fixation or rates of chemical weathering of parent material. Others may have developed with only modest or no connection to plant fitness, such as interception rates of atmospheric pollutants or rates of soil podzolization.

Table 1. Key features that distinguish many temperate and tropical forests from other ecosystem types.

Feature	Common magnitude and references
Well developed O horizon	O horizons may be thin for tropical forests (<10 Mg/ha), but most temperate forests have 20 to 100 Mg/ha, even more in poorly drained environments.
Moderated temperature and humidity at soil surface	Canopy interception of insolation reduces temperature at soil surface, may increase humidity. Interception and re-radiation of long-wave radiation at night may keep soil warmer. (Hungerford et al. 1980; Cortina & Vallejo 1994)
High water use	Evapotranspiration commonly ranges from 300 mm/yr (with strong water limitation) to 1000 mm/yr. Conversion of forest to grassland or shrubland typically increases water runoff by 100 to 300 mm/yr.
Higher aboveground and perhaps total net primary production	Forests often occupy more fertile environments than other vegetation types, leading to more input of C to the soil surface, and perhaps more within the mineral soil.
Input of high lignin litter	Relatively 'poor' quality of many tree litter types (esp. woody material) may favor accumulation of C in soil more than for other vegetation types. Woody detritus mass is commonly 50 to 250 Mg/ha, occasionally 500+ Mg/ha.
Soil turnover with death of large trees	Mixing of soil horizons may be substantial, especially where root systems tip up as trees fall. (Stone 1975; Schaetzel 1986)
Fire regime	More intense fires may occur than in grasslands or many semi-arid shrublands, with greater heating of soil.
Large scale of influence of single trees	Individual trees may create patterns in soils at scales of 5–15 m, compared with <5 m for shrubs and <0.5 m for grasses.

How substantial are differences among species? We compiled evidence from experimental comparisons of species in 'common gardens,' where climate, parent material, and previous land use were held constant. Most of these studies were summarized in Binkley (1996a) along with newer work (Son & Im-Kyun 1996; Eriksson & Rosen 1996). The stands in these comparisons were at least 50 yr old, and varied in number of true replicate plots from 3 to 12; one tropical case study was only 12 yr old, but had >250 Mg/ha of accumulated biomass (exceeding almost all of the temperate case studies). We examined the relative magnitude of the effect of species by taking the lowest value for any species in a trial as 1.0, and expressing the values for other species as a ratio to this baseline.

Table 2. Mechanisms by which species alter soils.

Process	Common size of effect	Effect on tree fitness	Some references
Atmospheric deposition	Up to doubling of deposition of S, N, and H^+ in polluted areas	Neutral, positive, or negative; probably not driver of plant characteristics	Ulrich 1983; Lovett 1992
Nitrogen fixation	Input of 50+ kg N ha^{-1} yr^{-1} for symbiotic N-fixing species	Faster growth, possible depletion of other soil resources	Hibbs et al. 1994; MacDicken 1995
Mineral weathering by exudates, microflora	Mostly unknown, but some evidence of 0.3 to 1.5 $kmol_c$ ha^{-1} yr^{-1} greater input of base cations; higher P supply	May improve growth	Bergkvist & Folkeson 1996; Gillespie & Pope 1990; Ranger & Nys 1992
Quantity, quality of C compounds added to soil	30%+ difference in quantity, large differences in qualtity	Unclear; increased soil C (within site) have not been experimentally tested. Could be large.	Binkley 1996a
Soil communities	Populations, ratios of functional groups, etc., commonly differ by several fold	Largely unexamined as direct mechanism of effect on soil fertility; likely large effects	Kienzler et al. 1986; Zou 1993; Graham & Wood 1991; Paré & Bernier 1989a,b
Physical properties (temperature, water content, structure)	Moderate to large differences	Feedbacks between trees and soil physical properties documented, but implications not examined	Chapman 1986; Helvey & Patric 1988; Harding et al. 1992
Pedogenesis (such as podzolization)	Some notable case studies of horizon development (esp. E)	No experimental evidence for basis of speculation	Zinke 1962; Nihlgård 1971

Forest floor masses commonly differ by about 20% among species on the same site (i.e., some species had 1.2 times larger forest floor mass than other species in the comparison), but frequently the differences are far larger, ranging up to 5-fold (Figure 1). Rates of litterfall mass and the N contents of litterfall differed moderately among species within each study; most showed about a 20% difference among species, with some differing by as much as 50%. Differences were larger when comparisons included nitrogen-fixing species. The rates of in-field net N mineralization differed more among species than did litterfall parameters; half of the studies showed at least a 60% difference in the rate of net N mineralization among species. In comparing soil pH, we examined direct differences rather than relative differences because of the nature of the pH scale. Most studies found at least a 0.2 to 0.3 unit difference in pH in the A horizon under the influence of different species. The proportion of the cation exchange capacity occupied by so-called base cations (base saturation, %BS) strongly influences pH, and %BS commonly differed by more than 40% in these studies.

Common garden experiments have several limitations, including short time period (though much longer than most ecological experiments), differences in type and impact of prior land use, and use of species that may not occur together naturally. However, the prevalence of large differences in litterfall and soil properties between species should convince reasonable skeptics to reject any null hypothesis that tree species do not differ in effects on soils.

Do these studies collectively support any generalizations about the effects of tree species on soils? Many ideas regarding these effects have been suggested and accepted over the past century, but most were based on evidence from comparative studies that confounded influences of current vegetation with prior differences in site conditions such as parent material or land use. Some of the generalizations developed from these studies are listed in Table 3, along with our evaluation of the evidence. Perhaps the most intriguing generalization supported by empirical evidence is that the lignin:N of aboveground litterfall correlates moderately well with rates of soil net N mineralization (cf. Pastor & Post 1986). Scott and Binkley (1997) reviewed the literature for comparisons of species, and found a reasonable relationship ($R^2 = 0.74$) between lignin:N of litterfall and net N mineralization for forests (Figure 2), particularly within site type or region. No relationship was evident for grassland ecosystems.

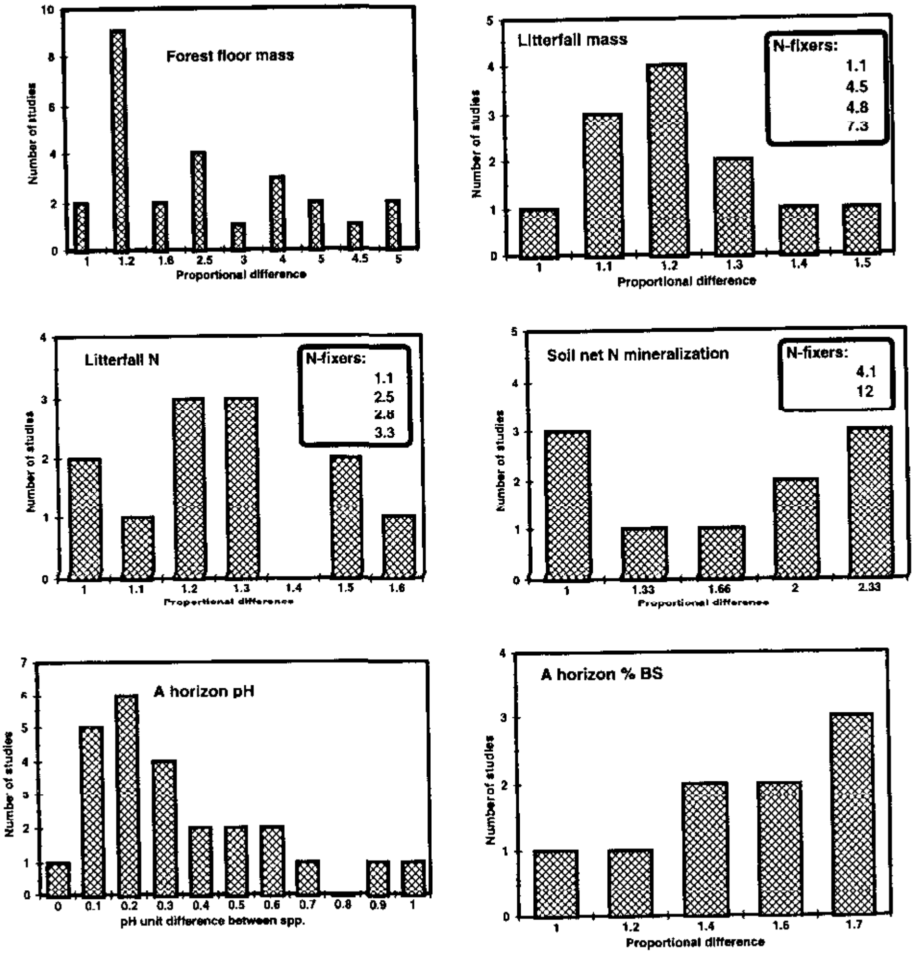

Figure 1. Proportional differences in litterfall and soil characteristics under the influence of different species on the same sites.

Weaving hypotheses

Given that tree species differ in their effects on soils, and that some generalizations have more support than others, we consider some hypotheses about *why* species affect soils differently (Figure 3). If the effects of a tree on soil result from direct selection to improve a tree's fitness, then a 'tight-weave' pattern should result from intimate connection and control among the interacting parts of the ecological puzzle. If the effects are secondary from some other process related to tree fitness, this would be a 'loose weave' of indeterminate connections. Loose-weave changes in soil may or may not benefit

Table 3. Some proposed generalizations regarding tree/soil interactions, and supporting evidence (summary based on Binkley 1996a).

Generalization	Evidence and key references
Norway spruce acidifies soils by accumulating strongly acidic organic matter	Five common garden studies supported part or all of this generalization (Binkley & Valentine 1991; Ranger & Nys 1992; Bergkvist & Folkeson 1995)
Norway spruce degrades soils, particularly in comparison with beech	No evidence supports this view. Aboveground net primary production is higher in spruce forests than in beech; studies of adjacent stands show equal or greater net N mineralization and porosity under spruce. (Nihlgård 1971; Bergkvist & Folkeson 1995)
White pine may increase soil N availability	Three common garden experiments found notably higher net N mineralization under white pine. (Nadelhoffer et al. 1983; Binkley & Valentine 1991; Gower & Son 1992)
N-fixing trees increase soil carbon, and rates of cycling of all nutrients	At least 10 studies have documented higher soil C and rates of nutrient cycling in litterfall under N fixers than under non-N-fixers (reviewed by Binkley 1992)
Hardwoods promote soil N availability relative to conifers	Mixed evidence; at least some cases show equal or higher net N mineralization under conifers such as white pine (relative to green ash), larch, or Norway spruce (relative to beech). (Nihlgård 1971; Binkley & Valentine 1991; Gower & Son 1992)
'Mull' forest floors indicate more fertile conditions than 'mor' forest floors	Probably supported regionally (mor forest floors are found on the poorest sites), but not locally (mull forest floors may indicate lower availability of P, for example). (Paré & Bernier 1989a,b)
Increases in soil C represent increased soil fertility	Some evidence, though untrue for Histosols. Common garden experiments do not show greater growth for species that develop greater soil C; but no 'second generation' reciprocal plantings have assessed the legacy of increased C for soil fertility for more productive species. (Gower & Son 1992)
Lignin:N of litterfall is a good indicator of net N mineralization in soil	Moderately strong evidence (See Figure 2) (Pastor et al. 1984; Gower & Son 1992; Scott & Binkley 1997)

a tree, but on balance they should not harm the tree more than the primary trait (such as production of antiherbivory compounds in leaves) benefits the tree. If the effects are byproducts of ecological interactions that were not directly developed in relation to the tree's fitness, a 'frayed' pattern of ecological interactions would pertain, which could lead to positive, neutral, or detrimental effects on the tree.

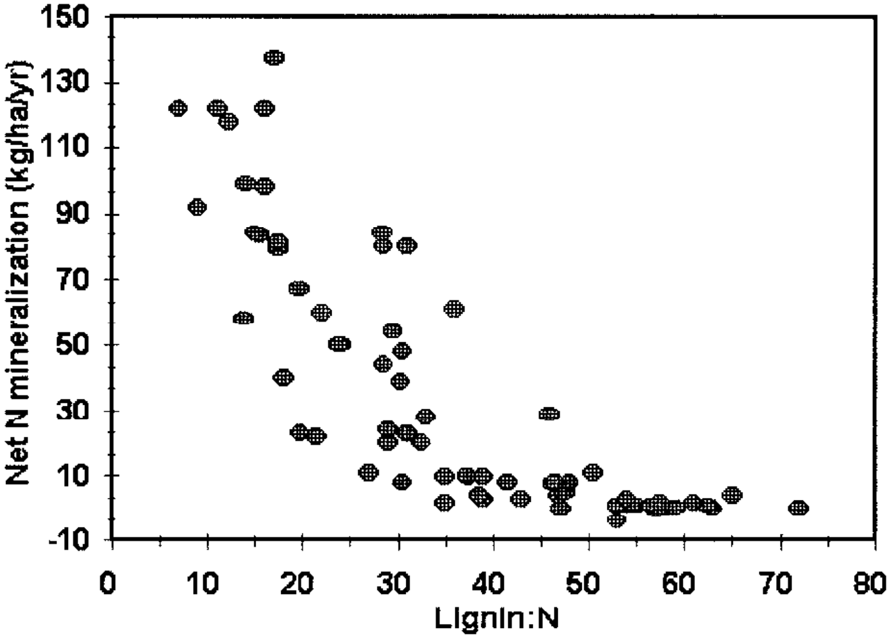

Figure 2. Net soil N mineralization as a function of the ligin:N of aboveground litterfall (from Scott and Binkley 1997).

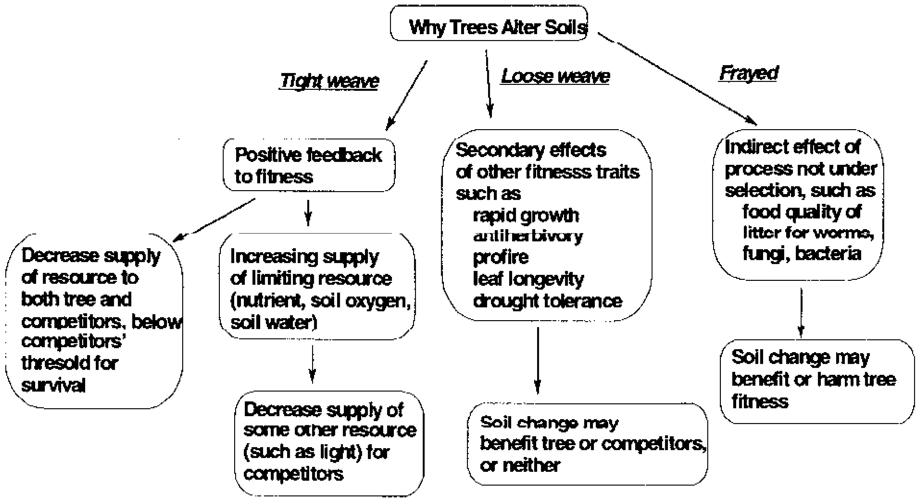

Figure 3. Hypothesis diagram for the types of connections that weave trees and soils together.

The evolutionary fitness of a tree would be defined as the tree's contribution of genes to succeeding generations of that species. In multi-species forests, the fitness of an individual tree could also be viewed in terms of contributing genes to the succeeding generations of the plant community as a whole. If a tree has a trait that alters the soil around it, this trait could increase the tree's fitness only if it enhanced the propagation of genes from this tree (or those of closely related kin). The cumulative impact of thousands of generations of such selection at the tree (or kin) level could lead to substantial differences between species in their effects on soils, and it would be reasonable to consider whether these selection opportunities have led to species-level differences in effects on soils. Therefore we are also using 'fitness' at a level of species, in reference to the success of individuals of one species relative to competitors, recognizing that that species-level 'fitness' is simply a collective property of the individuals.

The tight-weave hypothesis

Soils generally improve in suitability for supporting plant growth over pedogenic time, at least for thousands or tens of thousands of years (Van Breemen 1993). Soil development typically includes accumulation of organic matter and nutrients, development of soil structure, and development of sustained supplies of nutrients through microbial activity. The matter and energy processed by earlier generations of plants and soil organisms results in a state of negative entropy which can benefit later generations. This long-term view may also apply to shorter periods; available evidence shows that within decades, trees can substantially alter soils, which is a short enough time period to produce feedback effects on the fitness of trees (and their immediate offspring).

At a broad spatial scale, some authors have suggested that species characteristic of high nutrient sites should produce high quality litter that fosters high rates of nutrient recycling and species from low nutrient sites should produce recalcitrant litter that retards nutrient recycling (cf. Hobbie 1992; van Breemen 1995). This idea of positive feedbacks is appealing, and is supported by a variety of experimental and descriptive studies (Wedin 1995; Binkley 1996a; Figure 2). However, this bifurcation of expectations about selection opportunities on high vs. low nutrient sites confounds scales. A successful strategy for a tree species on a low nutrient site might include either increasing or reducing the rates of nutrient supply for itself and for competitors. A successful tree on a high nutrient site might reduce the supply of a nutrient for competitors (of the same species and of other species). We also note that a tree or species with intermediate-quality litter may increase nutrient cycling rates if it colonizes a poor nutrient site, or depress nutrient cycling rates if it colonizes a high nutrient site. The basic idea of feedback between litter quality and nutrient cycling rates remains solid, but groupings by site nutrient supply or species traits may not be useful, especially where trees are planted by forest managers rather than developing under natural processes of competition among species for successful establishment.

The tight-weave hypothesis needs to be addressed on a relative short time scale (of years to perhaps centuries), and at a small enough spatial scale that potential competitors have an opportunity to sample the same soil. At these scales, could the improvement of soil fertility with time result from natural selection? Will plants that improved fertility have advantages in reproductive success (= fitness) over those with neutral or negative effects?

Two general strategies might be successful in a tight-weave situation (based on ideas from Tilman 1988). A tree may benefit from increasing the supply rate of a nutrient in the soil if it could make use of that nutrient to deprive a competitor of some other resource. Higher N supply may be used to create a larger canopy that denies light to competitors. A tree could also benefit from reducing soil nutrient supply rates if the competitors suffered more from nutrient stress.

Strong evidence supporting the tight-weave hypothesis comes from a mosaic of hemlock (*Tsuga canadensis*) and sugar maple (*Acer saccharum*) forests in the Sylvania Woods of the Upper Peninsula of Michigan (Frelich et al. 1993). The parent material and landform appear uniform across the mosaic (Pastor & Broschart 1990), yet the pattern of species dominance has persisted for more than 3 millennia (Davis et al. 1992). Reproduction of hemlock in maple dominated sites appears to be inhibited by the physical influence of the maple forest floor, and reproduction of maple in hemlock dominated sites appears limited by low N supply in hemlock soils. The time frame over which these soil differences developed is unknown, but it is plausible that these effects could develop within the lifespan of individual trees, supporting the tight-weave hypothesis.

Another example involves enhancement of mineral weathering by tree species. The picture is less complete, but some case studies provide insight. Bergkvist and Folkeson (1996) found that Norway spruce (*Picea abies*) stands in Sweden accumulated more base cations in both biomass and soil exchangeable pools than did adjacent stands of either birch (*Betula pendula*) or beech (*Fagus silvatica*). Faster rates of mineral weathering (by about 1.5 $\text{kmol}_c\ \text{ha}^{-1}\ \text{yr}^{-1}$) must have been responsible (assuming the cation budgets are reasonably accurate). Has Norway spruce been 'selected' for higher weathering rates, or are weathering rates simply a byproduct of some other feature? We think too little evidence is available for a clear answer. A fascinating experiment might involve either seedling bioassays of soil fertility from these sites, or harvesting followed by reciprocal plantings of species (including mixed-species plantations) to examine the overall suitability of the various soils for each species.

The influence of some tree species on weathering rates is also supported by acid rain experiments. A classic view of exchangeable cations represents exchange capacity as a 'bank account' that passively receives inputs from weathering, and loses cations to plant uptake and leaching. This view may apply to heavily weathered soils where few primary minerals remain (Binkley et al. 1989; Richter et al. 1994), but probably does not apply to relatively unweathered, young forest soils. The spruce/beech/birch example from Sweden (above) showed that spruce can simultaneously remove larger amounts of exchangeable base cations (relative to birch and beech) and also increase the quantities of these cations in soil. As in economics, the supply is not independent of the 'demand.' Similarly, artificial acidification experiments may deplete the exchange complex of base cations, but the original levels typically recover within a decade after acid additions stop. For example, Stuanes et al. (1992) report on a Norway spruce study, where a total acid addition of 8.8 kmol H^+/ha depressed base saturation from 20% down to 5% in the O horizon, and from 6% to 3% in the E horizon. Within a decade after the acid addition stopped, base saturation recovered in both horizons, despite continued removals of base cations by vegetation. We suggest the bank-account view of exchangeable cations be abandoned (except for highly weathered soils) and a more dynamic, interactive view be developed with vegetation having a positive effect on cation supplies from weathering.

What evidence refutes the tight-weave hypothesis? Only limited information is available on the long-term effects of species on soils in relation to the future performance of the same (or different) species. Nitrogen-fixing trees increase soil N supplies, and generally improve the soil for the growth of non-N-fixing species (based on bioassays with seedlings, cf. Binkley 1986; Brozek 1990; Chapin et al. 1994; Walker et al. 1986). Less information is available on whether the effect of an N-fixer on soil fertility leads to greater future productivity of the N-fixer, but available evidence indicates that N-fixing species *reduce* the suitability of the soil for supporting their own growth (based on seedling bioassays, cf. Walker et al. 1986; Chapin et al. 1994; Binkley 1996b). We know of no studies that have examined the soil legacy of non-N-fixing tree species on soil fertility. No bioassays or second-generation plantations have been conducted to test if trees enhance or impair the soil for future generations of the same (or different) species.

We conclude that the Sylvania case study of hemlock and maple supports a tight-weave pattern; each species modifies soil environment to the disadvantage of the other species. The evidence from N-fixing species appears to be more of a loose-weave pattern. More evidence would be needed for clear insight.

The loose-weave hypothesis

Many lines of evidence support at least some loose-weave connections between trees and their effects on soils. The simplest case would be nutrient removal from soils into rapidly accumulating tree biomass. This may reduce soil fertility and work against the future fitness of the tree, but the overall balance may favor faster growth in the short term. The decrease in soil nutrient supply may appear to reduce the suitability of the soil for the tree, but the overall effect could be an increase in tree fitness.

Another loose-weave explanation may involve the protection of tree tissues from herbivory. Tissues with high concentrations of digestion-inhibiting polyphenolics (lignins and tannins) (Rosenthal & Janzen 1979; Horner et al. 1988; Loehle 1989; Tuomi 1992) may discourage feeding by herbivores, with an indirect effect on the later decomposition of the tissues. Decomposition could be slowed (fostering accumulation of soil C) as an indirect effect of selection for resistance to herbivory. A review of this subject is beyond our scope, and at least some authors argue that accumulation of decay-resistant secondary compounds results from low nutrient supply rather than selection to deter herbivory (cf. Bryant et al. 1989). In any case, these ideas involve a loose-weave connection between trees and soils.

The litter of some tree species may enhance the occurrence or intensity of fires (cf. Mutch 1970). Changes in fire regimes could benefit individuals of species that tolerate fire and compete with fire-intolerant species, or benefit individuals of species that regenerate well after fire. For example, Kellman (1984) suggested that the pine savannas of Belize may be maintained by the synergistic effects of fire and low soil fertility. The understory vegetation and the litter of Carribean pine (*Pinus caribaea*) promote frequent, low-intensity fires. Fire supression leads to invasion of the mono-specific pine stands by hardwoods. Carribean pine tolerates surface fires and uses nutrients more efficiently than local hardwood trees, and pine fitness may be enhanced by the partly self-induced stresses of fire. Therefore, a loose-weave selection opportunity could favor increased likelihood or intensity of fire under the influence of pine, even if fires may reduce long-term soil fertility. In these loose weave situations, the effects of species on soils may derive from tree species effects on litter, the effects of tree litter on fires, and the effects of fires on soils. We know of no conclusive experiments that have examined all the pieces of this puzzle, but the logic is appealing.

Many other connections that have loose-weave consequences for soil are possible, including adaptations for longevity (investing more herbivory defense compounds into longer-lived tissues), for drought tolerance (such as recalcitrant organic compounds in sclerophytic leaves), and simply structural support (lignification of wood). In all these cases, the effects of trees on soil would not be the result of selection for traits that improve soils for the tree, but rather the result of adapting to other ecological aspects that improve the tree's fitness.

The frayed hypothesis

The fabric of interactions in ecosystems may not be perfectly woven of tight and loose connections. Interactions, disturbances, random events, trophic dynamics, and evolutionary contingencies should ensure some fraying in the interactions of soils and trees. For example, the direct effects of trees on soil are mediated by soil organisms, that include an indeterminate number of functional groups, thousands of species, and millions of individuals per m^2 of soil. Any soil enhancement that benefits a tree species unavoidably depends upon the reactions of the complex soil community. For a tree's 'strategy' to work, the soil community must go along with it. Is the soil community a helpless black box that passively interacts with trees, or does it interact with trees in diverse ways that may fray the connection between trees and soils?

Kienzler et al. (1986) examined the soil community beneath experimental plantations of 3 species in Minnesota. The aspen ecosystem produced 30% to 40% less aboveground litterfall than those dominated by red pine or white spruce, and apsen litterfall cycled 10% to 25% less N than the other species (Perala & Alban 1982). In the top 10 cm of mineral soil, the aspen site had 10 times more bacteria and twice the fungal biomass of the stands with red pine or white spruce. The aspen stand also supported more annelid worms, beetles, beetle larvae, springtails, and arachnids. Did the microbial community and the processing of organic matter under aspen represent a high-fitness soil for aspen, or did these simply derive from opportunistic responses of the diverse community? The role of the soil communities in mediating (or altering) the effects of trees on soils needs much more investigation.

In Quebec Paré and Bernier (1989a,b) examined five P-deficient stands of sugar maple and five stands with no P-deficiency (the stands were located on sites with various parent materials across a 9000 km^2 region). Sites with low P in maple foliage were characterized by low quantities of total P in L and F horizons (Oi+Oe), and large accumulations of P in Ah horizons (a mull-form forest floor). Those with high P in foliage had larger quantities of P in L and F horizons, and much lower quantities of total P in H horizons (Oa, a mor-form forest floor). They concluded that the key difference in P nutrition of the maples was the degree of mixing of the litter layers by soil animals. Well-mixed layers (mull forest floor) allowed inorganic P to bind with Fe and

Al into unavailable forms. Where the organic horizons decomposed without mixing with mineral soil, P cycled at higher rates through organic pools. The connection between the trees and their soil P supplies was frayed in this case by the intercession of soil animals that processed soil organic matter for their own needs. Earthworms lowered P availability by allowing an increase in the entropy of P molecules that precipitated into insoluble salts when exposed to Fe and Al in mineral soil.

In Hawaii, Zou (1993) measured the density of exotic earthworms under plantations of exotic *Eucalyptus saligna* and N-fixing *Albizia facaltaria*. The food quality of albizia litter was apparently superior, supporting more than 450 worms/m^2, compared with just 90/m^2 for eucalyptus plots. Along with these differences in worm densities, the albizia soils had half the fungal biomass of the eucalyptus soil, but 20% more bacterial biomass (Garcia-Montiel & Binkley 1998). Soil phosphatase activity and labile organic-P correlated highly with worm densities. In this case, the effect of albizia on the soil may have been mediated in part by the suitability of its litter as worm food. It is possible that an assemblage evolved for mutual increases in fitness: the albizia evolved high-quality litter to promote earthworms which would increase cycling of organic-P from litter, which increases the P supply to Albizia, increasing Albizia growth and fitness. We are skeptical, however, of such long chains of logic about evolutionary adaptations, and suspect that this is simply a frayed connection between albizia and the soil.

We also note that the 'connection' of trees to soils is mediated substantially by symbiotic microbes (such as mycorrhizal fungi), and the initiation and development of these symbioses may include random (or non-deterministic) features that might fray any chance for a tight connection between trees and soil nutrient cycling processes.

Parting threads of thoughts

Trees substantially alter soils on a time scale of decades, which is well within the time frame needed for these changes to feedback or affect the fitness of the tree. If changes in the soil increase fitness, then the connections between a tree and soils represent a tightly woven tapestry. However, a number of examples indicate that these interactions may be loosely woven, involving side effects stemming from other aspects of a tree's fitness. Strong evidence also indicates that many ecological interactions may not optimize a tree's fitness, and the fraying of connections between tree and soil may either benefit or impair a tree's growth and reproductive success. Additionally, the tightness of the weave between a tree and the soil may change over time, with opportunities for fraying (by invasion of other plants), or tighter weave (by cumulative improvement of the soil). We conclude that all three levels of connection are woven into the ecological interactions between trees and soils, with some interactions being more important in some cases.

The first step to developing better insights into the relative importance of the feedbacks between trees and soils might be second-generation studies on sites where monoculture plantations of different tree species have resulted in substantial differences among soils within a common garden. We know of no such studies yet, but the wide variety of first-generation studies that have been reported indicates the opportunities exist for the next installment.

We also think that the role of soil communities as the implementors of tree effects on soils needs a great deal of descriptive and experimental work. The sugar maple case studies of Paré and Bernier (1989a,b) and eucalyptus/albizia case study of Zou (1993) show that the 'black box' of the soil community can strongly affect the supply of nutrients. A black box which sometimes decreases and sometimes increases the strength of a signal clearly needs to be taken apart and examined in greater detail!

We close by noting that most forests are not comprised of a single tree species, and that mixtures of species produce litter that commingles, fosters novel soil communities, and generally complicates attempts to determine simple effects of the species. For example, Zou et al. (1995) found that a mixture of conifers and N-fixing alder greatly increased P turnover relative to monocultures of conifers or alder. Ineson and McTiernan (1992) used a microcosm study to examine the decomposition and N release from litter from single species, and from mixtures of litter from different species. They concluded: '. . . litters rarely decompose in mixtures in a manner which can be predicted from their behavior as a pure litter.' We suspect this statement applies generally to the biogeochemistry of mixed-species forests, but this remains largely uncharted territory.

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