The Influence of Tree Species on Forest Soils: Processes and Patterns

Dan Binkley
Department of Forest Sciences
Colorado State University
Ft Collins, Colorado, USA

Abstract

The effects of tree species on forest soils have been discussed for more than a century. The limits of knowledge have often been clouded by conclusions based on weak evidence. Replicated plantations within a single location (common-garden experiments) have not supported many generalisations about the influence of trees on soils. For example, classic expectations often included ideas that conifers degraded soils and hardwoods improved soils. Conifers often do occur on poor soils, but no generalisation about soil impoverishment by conifers is apparent from common-garden experiments. Nitrogen availability is often as high or higher under conifers in common gardens than under hardwoods. Forest floor morphology was thought to relate well with overall site fertility; 'mor' forest floors indicated poorer conditions than 'mull' forest floors. Across wide gradients this expectation may be generally valid; the best sites often have soil communities that mix forest floor materials into the mineral soil. However, the few common-garden experiments that have examined these features found no relationship between forest floor characteristics and tree growth or the availability of nitrogen (N) or phosphorus (P). At present, the best indicator of species effects on soil fertility (particularly N availability) appears to be the lignin:N ratio of aboveground litterfall. New insights about the effects of tree species on soils will come from: 1) re-examination of the soundness of the evidence supporting current expectations; 2) development of clearer, more precise questions; and 3) more comparisons of species effects in common gardens, particularly on the role played by the soil communities.

Key words: nitrogen cycling, mineralisation, nitrogen availability, lignin:N, forest floor, phosphorus cycling, species effects on soils

Introduction

Soils differ dramatically under different types of vegetation and, within forest vegetation, under different species of trees:

> . . . different forest vegetation gives rise to different soil. Local inhabitants have long noted that land formerly under forest has different qualities according to the kind of forest which it bore. Our peasants are extremely conscious of the differences existing between soils formerly under linden, under oak, or under conifers. (Dokuchaev, 1900, cited in Remezov and Pogrebnyak 1965)

From its inception, forestry showed interest in the manner of influence of tree stands on soils; such effects of the canopy and of the litter were regarded by the forester as a means of changing the soil in order to conserve its fertility . . . (Morozov, 1904, cited in Remezov and Pogrebnyak 1965)

These early insights were typically based on observations from natural stands, or from unreplicated plantations. In many cases, it was not possible to infer whether the difference in species composition resulted from prior differences in soils, or whether the differences in soils developed under the influence of the species. Forty years ago, Ovington (1953, cited in Stone 1975) summarised conventional wisdom:

The soil fertility of the marginal lands in the British Isles can be conserved by the correct selection of tree species for afforestation, and where economic conditions necessitate the planting of a species which leads to deterioration of the soil, 'improver' species should also be included in the plantations . . .

Twenty years ago, Stone (1975) concluded that most of the evidence of species effects on soils was in a sense obsolete, and he characterised earlier thinking with words such as 'alchemy of selected species' and 'myth'. He concluded that the strongest evidence showed that species effects on soils were slow or very limited, with the notable exception of major effects of nitrogen-fixing trees. Ten years ago, Miles (1985) suggested that species should indeed be expected to influence soils differently, based on differences in nutrient uptake, litter quality, and growth. Computer simulation models that include the effects of litter quality support expectations that species should have strong influences on the dynamics of soil carbon (C) and N, and that these influences may become important on a scale of decades (cf Pastor *et al.* 1987, Pastor and Naiman 1992).

Impressive examples have become available recently of the very long-term effects of species on soils under similar conditions. In Michigan, USA, the long-term mosaic of forest patches dominated by sugar maple (*Acer saccharum*) or by eastern hemlock (*Tsuga canadensis*) appears to be reinforced (or controlled) by the effects of the species on soil N availability (Frelich *et al.* 1993, J. Pastor, personal communication). Another long-term mosaic of forests on Vancouver Island, Canada, involves patches dominated by western hemlock (*Tsuga heterophylla*) or western red cedar (*Thuja plicata*). Patterns in N and P availability and long-term disturbance patterns tend to perpetuate the dominant species, leading to gigantic differences in soil development (Keenan *et al.* 1993, Prescott *et al.* 1993). What could be the effects of different species over short periods such as decades or centuries? Which is the better null hypothesis, that species should be expected to have different effects until strong evidence indicates no effect, or that the influence of species is negligible until evidence indicates otherwise? In this paper current evidence is examined, and perspectives are provided on the likely differences in effects of tree species on soils. A framework of interactions between trees and soils is also developed, within which their underlying processes can be considered.

THE NATURE OF THE EVIDENCE

Expectations about tree species effects on soils are built from several types of evidence. As noted above, early thinking attributed differences in fertility to the species occurring on a soil, rather than the reverse. Comparisons of adjacent (or nearby) plantations early in this century led to many conclusions in Europe that were commonly based on an assumption that forest floor properties were the keys to site fertility. Norway spruce (*Picea abies*) was considered to be a 'site deteriorating' species, whereas beech (*Fagus silvatica*) was alternately characterised as 'the mother of the forest' or

the 'raw humus producer of the worst type' (Rubner 1932, Tuxen 1932, both cited by Bonnevie-Svendsen and Gjems 1956). Other researchers concluded that the acid-base chemistry of beech and Norway spruce were too similar to drive differences in soil development (Mattson and Koutler-Andersson 1941). Birch (*Betula* spp.) was thought to be a 'soil improver', capable of repairing the 'damage' done by spruce plantations (Siren 1955, McNeill 1955).

From the late 1800s through the 1940s, a phenomenal amount of work was invested in characterising the morphology of forest floors across soil types and under the influence of various species (see Handley 1954 for an excellent review). Most of this work presumed that the morphology and dynamics of forest floors were fundamentally important to soil fertility and site productivity. Romell's (1935) scepticism of these assumptions led to some very insightful investigations on carbon dioxide (CO_2) evolution and N dynamics in forest floors, but most investigators did not accept his views. Van Goor (1985) concluded that sites with poor growth of spruce plantations were simply inappropriate sites for spruce, and that no soil degradation could be confirmed by systematic research.

Better evidence of the different effects of tree species on soils is now available from replicated experimental plantations. However, insights from even well-designed experiments can be limited. For example, such studies often use species typically found on different site types (or even from other continents). Rates of change in soil properties in such studies could be slow initially as the soil community shifts to accommodate the litter of unusual composition. Alternatively, a site that has developed a 'steady state' composition under the influence of native vegetation may change rapidly under the influence of a new species, before settling into a less dynamic phase. This would represent a strong 'species' effect that may represent a transition state more than a simple effect of the new species. Most replicated common-garden experiments have been planted on old agricultural fields; how clearly should differences among species in reforestation trials be interpreted as simply species effects on forest soils?

THE NATURE OF THE QUESTIONS

Much of the confusion about the effects of species on soils results from a lack of clearly articulated questions. A species that acidifies soil may be characterised as degrading the soil, but why is acidification assumed to be degradation? Another species that increases the levels of exchangeable calcium (Ca) in the upper soil may be said to improve the soil, but why is a higher level of Ca necessarily beneficial rather than neutral? Do the levels of soil acidity or exchangeable Ca exert any control on current levels of tree growth or the sustainability of soil fertility?

Similarly, mull forest floors (with fresh litter layers atop well-mixed Ah horizons) are assumed to be superior to mor forest floors (with no mixing between forest floors and mineral soils). Across a wide range of sites, this generalisation may be true. Within a narrower range of environmental conditions, forest floor morphology may be unrelated to soil fertility. As noted later, common-garden plantations show no relationship between net N mineralisation and the accumulation or turnover rates of forest floors. Other studies indicate that P cycling may be much faster on soils with mor forest floors than those with mulls. Comparisons of different species on different sites (rather than within single sites) have led some authors to conclude that species commonly found on poor sites are more efficient at using nutrients than

those typically found on rich sites (cf Hobbie 1992). However, this view confuses site effects with species effects; when planted on the same site, species from typically richer sites may have higher nutrient use efficiencies than those from poorer sites (cf Gower and Son 1992).

Generalisations about species effects are probably not very useful unless tied to questions about specific soil properties or processes. Some evidence does indicate that Norway spruce stands accumulate strongly acidic soil organic matter. No evidence supports generalisations about soil degradation under Norway spruce.

A framework for species effects on soils

To provide a basis for comparing the different effects of tree species, I have included some studies that document rates of change in soil properties for single species case studies. Most of the discussion focuses on projects that examine several species in replicated plantations within single sites (common gardens). A few unreplicated stands with different species composition have been included, where the stands were adjacent and had similar site histories. I have omitted most of the unreplicated studies where confounding effects of site and prior history obscure any effect of species. Almost no common-garden experiments have been replicated on different sites within a single experiment, although the block effect in some experiments has been relatively large.

Although the suite of interactions that characterise the reciprocal effects of trees and soils is more complex than theories can currently encompass, the framework in figure 1 may capture the most important features.

Trees 'filter' the atmosphere, capturing CO_2 and other gases as well as air-borne particulates. This filtering effect is most pronounced in indust-
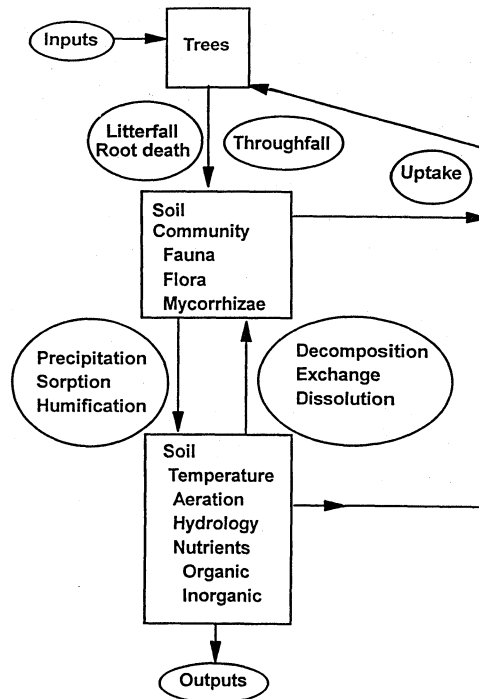

Figure 1: A framework for examining the processes by which species differ in influence on nutrient flows and soil fertility

rialised regions with high atmospheric concentrations of N and sulphur (S) compounds; near oceans with high salt concentrations in the air; and in areas with upwind arid lands that contribute dust particles.

Trees influence soils by providing variable quantities of organic matter of varying chemical composition. Aboveground litter is deposited on the soil surface, where fluctuations in microenvironment may affect decomposition. Belowground 'litter' remains in a more moderate environment within the mineral soil. Vegetation litter provides food for incredibly diverse soil communities of animals, bacteria, and fungi. The byproducts of litter processing may be retained in the soil through processes of precipitation

(for P), sorption (for cations), or humification (for recalcitrant organic compounds). Nutrients stored in the soil can be made available to microbes and plants through decomposition (or mineralisation), exchange reactions, and mineral dissolution. Nutrients not retained by plant or microbial uptake may leach from the soil.

Meanwhile, the trees may also influence the physical properties of the soil. Tree canopies tend to moderate soil temperatures, with further insulation by developing forest floor layers. Soil aeration may be altered by the activities of roots, by oxygen consumption during respiration and decomposition, and by changing soil porosity and perhaps structure. Trees typically decrease soil water content and soil water potential (except where peat accumulates, reducing water conductivity). These features are developed in detail in the following sections.

ATMOSPHERIC FILTERING

The filtering effects of tree canopies are phenomenal. Temperate forests typically remove 5 to 10 Mg of C per hectare annually; tropical forests may double this flux. 'Dry' deposition of gases and particles containing N and S is often between 5 and 30 kg ha^{-1} yr^{-1} for industrialised areas. It depends strongly on canopy characteristics, particularly leaf area and aerodynamic roughness. For example, beech forests in Solling area of Germany filter about 25 kg S ha^{-1} yr^{-1} (including wet deposition) from the air, compared with 60 kg S ha^{-1} yr^{-1} in Norway spruce forests (Ulrich 1983). The use of models to estimate dry deposition, as more recent studies have done, relies strongly on both atmospheric concentrations of pollutants and tree leaf area and duration (Lindberg *et al.* 1992, Lovett 1992).

NITROGEN FIXATION

Nitrogen fixation is the reduction of atmospheric N$_2$ to amino N, an energy-demanding process performed only by certain prokaryotes. Some trees species have developed symbiotic relationships with prokaryotes housed in root nodules. These symbiotic bacteria (such as *Rhizobium*) and actinomycetes (such as *Frankia*) receive protection from oxygen and a supply of carbohydrates from the host tree, and produce amino-N for use by the tree. Inputs from symbiotic N fixation can be substantial. Typical N fixation rates for forests with red alder (*Alnus rubra*) run from 70 to 150 kg N ha^{-1} yr^{-1} for 50 or more years, often doubling the N content of ecosystems (Binkley *et al.* 1994). Fixation rates for leguminous trees (such as *Robinia, Leucaena, Albizia* and *Acacia*) typically exceed 100 kg ha^{-1} yr^{-1} (Sprent 1983).

Rates of N fixation in forests that lack symbiotic N-fixing plants typically are thought to be very low, on the order of 1 kg N ha^{-1} yr^{-1}. Several studies have indicated much higher rates of nonsymbiotic N fixation (cf Jaiyebo and Moore 1963, Richards and Bevege 1967, Jenkinson 1971, Day *et al.* 1975). For example, in replicated stands of red oak (*Quercus rubra*), European larch (*Larix decidua*), white pine (*Pinus strobus*), red pine (*Pinus resinosa*) and Norway spruce, Son and Gower (1992) found an apparent N accretion in the red pine and Norway spruce stands of 20 to 40 kg ha^{-1} yr^{-1} relative to the other three species.

A recent experiment by Bormann *et al.* (1993) was conducted with the express intention to test whether such surprisingly high rates of N accretion actually occur, using 'sandbox' ecosystems. These sandboxes consisted of 2.5 x 2.5 m or 7.5 x 7.5 m boxes, excavated to 1.5 m depth, lined with Hypalon polymer, filled with a 15 cm layer of gravel, then with 1.3 m of glacial outwash sand. A 5 cm layer of original topsoil was then added, and tilled to a depth of 20 cm. Bormann *et al.* (1993) reported on the N accretion in sandboxes planted with no vegetation (a nonvegetated control), or with

pitch pine (*Pinus rigida*), red pine (*Pinus resinosa*), black locust (*Robinia pseudoacacia*) or black alder (*Alnus glutinosa*). After 3 to 6 years (varying among sandboxes), the nonvegetated sandbox lost about 95 kg N ha^{-1} yr^{-1}, while the sandboxes with N-fixing species gained from 100 kg N ha^{-1} yr^{-1} (locust) to 270 kg N ha^{-1} yr^{-1} (alder).

Surprisingly, both sandboxes with pines gained about 55 kg N ha^{-1} yr^{-1}. The deposition of N from the atmosphere is about 10 kg N ha^{-1} yr^{-1} at this site (including directly measured bulk deposition and model estimates of dry deposition), far too little to account for the accretion under the pines. The authors performed an unreported number of acetylene reduction assays on fine roots from the pine trees to assay for rhizosphere N fixation. The highest rate measured was 1.8 nmol of ethylene production per gram of root per hour, which led them to conclude that rapid N fixation had occurred in the pine sandboxes. I think their evidence refutes this conclusion. If this maximum observed rate represented a true average for the ecosystems, an estimate of the N fixation rate can be calculated by assuming this rate occurs for 24 hours per day, for a fine root biomass of 3000 kg/ha for a growing season of 180 days, and that each mole of reduced ethylene equals one-third of a mole of N$_2$ fixed (based on mol of electrons for each reaction). This gives 7.8 mol of N$_2$ fixed per hectare annually, or 0.2 kg N ha^{-1} yr^{-1}. Even their maximum rate falls orders of magnitude below the observed rate of N accretion.

The strength of the evidence for N accretion under pines is thus not matched by the inference of rhizosphere N fixation. The mechanism behind any accretion under pines remains elusive. At this point, occult inputs of N to forests with no symbiotic N-fixing plants may occur, but the evidence is too weak to describe an overall pattern or provide a causal explanation.

There have been enough reports of unexplained N accretion to warrant detailed investigations into this possible phenomenon.

LITTERFALL

Many comparative studies have demonstrated large differences in the quantity and chemistry of litterfall in forests of different species composition (Bonnevie-Svendsen and Gjems 1956, Bray and Gorham 1964, Rodin and Bazilevich 1967, Cole and Rapp 1980, Kimmins *et al.* 1985). Comparisons across different sites, however, may not provide adequate information on the differences between species when grown on a single site. A few studies have compared species in common garden plantations (table 1). Most of these studies have simply characterised the total nutrient contents of the litter, but litter decomposition may depend heavily on the nature of carbon compounds in the leaves. A variety of studies have shown that the ratio of ligin:N in litter predicts both decomposition rates (cf Aber and Melillo 1982; but see Edmonds 1980, Berg and Ekbohm 1991 for contrary findings) and N mineralisation rates (Stump and Binkley 1993) better than N concentration alone.

The mechanism behind the relationships among litter decomposition, N mineralisation and litter lignin:N may derive from the effects of polyphenolic or aliphatic compounds rather than lignin (cf Palm and Sanchez 1992). In the comparisons of *Eucalyptus* and *Albizia*, Binkley *et al.* (1992b) found that rapidly decomposed *Albizia* litter had *higher* lignin concentrations (390 mg/g) than slowly decomposed *Eucalyptus* litter (270 mg/g), but the *Albizia* had much lower concentrations of polyphenolics (12 mg/g for *Albizia* vs 63 mg/g for *Eucalyptus*).

As noted above, computer simulation models have shown that differences in litter quality can substantially alter N turnover in soils. Changes in soil N supply can favour some

Table 1: Litterfall mass and nutrient content (kg ha⁻¹ yr⁻¹) for species in common-garden plantations

Location	Species, number of replicate plots, age	Mass	N	P	Ca	Reference
Connecticut, USA	*Pinus strobus*, 8, 50 yr	7565	77	6.4	63	Binkley and
	Picea abies, 8, 50 yr	7460	83	6.4	61	Valentine 1991
	Fraxinus pennsylvanica, 8, 50 yr	6260	63	5.6	70	
Wisconsin, USA	*Quercus rubra*, 3, 28 yr	3960	34			Gower and Son 1992
	Larix decidua, 4, 28 yr	3680	40			
	Pinus strobus, 4, 28 yr	3210	26			
	Pinus resinosa, 4, 28 yr	4460	32			
	Picea abies, 4, 28 yr	4100	40			
Wisconsin, USA	*Pinus resinosa*, 1, 40 yr	2500	12			Nadelhoffer *et al.* 1983
	Pinus strobus, 1, 40 yr	2900	21			
	P. resinosa/P. strobus, 1, 40 yr	3120	16			
Minnesota, USA	*Populus tremuloides*, 2, 40 yr	3980	36	7.4	70	Perala and Alban 1982
	Picea glauca, 4, 40 yr	5480	48	6.0	72	
	Pinus resinosa, 4, 40 yr	6180	40	4.0	32	
	Pinus banksiana, 2, 40 yr	5750	45	4.2	37	
Gisburn Forest, UK	*Quercus petraea*, 1, 30 yr	4780		4.4		Chapman 1986
	Pinus sylvestris, 1, 30 yr	9350		2.5		
	Alnus glutinosa, 1, 30 yr	5460		2.2		
	Picea abies, 1, 30 yr	7820		4.5		
	Picea/Pinus, 1, 30 yr	8920		3.4		
	Picea/Alnus, 1, 30 yr	6340		3.6		
	Picea/Quercus, 1, 30 yr	3180		2.5		
Grue, Sweden	*Larix decidua*, 1, 90 yr	2110	15	1.7	14	Bonnevie-Svendsen
	Picea abies, 1, 80 yr	2036	14	1.7	19	and Gjems 1956
Eidsberg, Sweden	*Larix sibirica*, 1, 45 yr	2530	30	2.2	17	Bonnevie-Svendsen
	Picea abies, 1, 50 yr	3160	32	3.1	17	and Gjems 1956
Hawaii, USA	*Eucalyptus saligna*, 4, 6 yr	9200	40	3.2	60	Binkley *et al.* 1992b
	Albizia falcataria, 4, 6 yr	8400	180	7.0	87	
	50%/50% *Eucalyptus/Albizia*, 4, 6 yr	7000	90	5.2	85	
Washington, USA	*Pseudotsuga menziesii*, 1, 55 yr	4000	9.7	5.2	18	Binkley *et al.* 1992c
	P. menziesii/Alnus rubra, 1, 55 yr	9700	75	10.1	59	
Oregon, USA	*Pseudotsuga menziesii*, 1, 55 yr	6400	30	6.4	19	Binkley *et al.* 1992c
	P. menziesii/Alnus rubra, 1, 55 yr	21300	145	16.2	43	
Washington, USA	*Pseudotsuga menziesii*, 1, 50 yr	1780			15	Homann *et al.* 1992
	Alnus rubra, 1, 50 yr	4480			43	

species relative to others. Further feedback may result; species that perform well with high supplies of N tend to produce 'high quality' litter that further increases soil N supply (Vitousek 1982, Pastor *et al.* 1987).

Stone (1975) expected that differences in litterfall mass would be more important than differences among species in nutrient concent-rations. Both patterns can be found in table 1, but differences in litterfall biomass across species are generally smaller than the differences in nutrient concentrations and ratios among nutrients. For example, the white pine stands in Wisconsin had about 70% of the litterfall mass that the red pine stands had (Son and Gower 1992), but higher N concentrations in white pine litter resulted in 80% of the litterfall N content of the red pine stand. In the Minnesota stands, the litterfall mass and N content were the same for white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) (Perala and Alban 1982), but jack pine had much lower P and Ca contents, giving substantial differences in the ratios of N:P and N:Ca in litterfall. For the stands containing N-fixing trees, the litterfall biomass typically is similar to that of the non-N-fixing stands. However, nutrient contents are much higher for the N-fixing stands. The major effects of N-fixing trees on ecosystem production and nutrient cycling probably derive more from the input of high quality litter than from the proportional increase in the ecosystem N capital.

Ideally, table 1 would be accompanied by another table for belowground 'litter' input from fine root death and mycorrhizal turnover, as these belowground dynamics may match or exceed the importance of aboveground dynamics in the effects of tree species on soils. Unfortunately, I know of no studies that have examined these belowground components for common-garden plantations.

SOIL COMMUNITIES

Soil communities exert strong influences on the processing of organic matter and nutrients. Romell (1935) proposed the controversial idea that forest floor morphology depends less on the chemistry of litter than on the dominance of fungi (producing mor forest floors) or bacteria (producing mull forest floors) in decomposition. Other researchers have emphasised that differ-ences in litter chemistry might be the ultimate cause of differences in the fungal and bacterial communities (Broadfoot and Pierre 1939).

Soil animals are important in most soils (Hole 1981). For example, Wolters and Schaefer (1993) showed that disappearance of ^{14}C-labelled organic matter from beech leaves was 77% faster in plots with earthworms (*Aporrectodea caliginosa*) added relative to controls. The worm effect on $^{14}CO_2$ loss was greater than that induced by daily mixing (by hand) or by N addition.

Tree species probably have very strong effects on the composition of soil microbial communities, but little information is available for direct comparisons. A variety of anecdotal experiments demonstrate large differences.

Theodorou (1984) examined soil commun-ities under 20-year-old plantations of *Pinus radiata* and nearby *Eucalyptus* spp. woodlands, at five locations (no site replication within location) in Australia. Soils under pines tended to have greater fungal propagules and lower total bacterial counts than the eucalypt soils. Microbial biomass N (fumigation/incubation) was substantially greater under *Eucalyptus* for four sites, but higher under pine at one site. Differences in mineralisable N (3 weeks at 25°C) and potential nitrification were smaller than the differences in microbial-biomass N, and none was significant.

Mardulyn *et al.* (1993) examined microbial communities under one 92-year-old plantation

of Norway spruce, and an adjacent beech forest aged at least 160 years. One plot (0.012 ha) was sampled in each stand (stand sizes were greater than 8 ha). This study was unreplicated both in terms of species treatments (one of each) and in terms of within-stand sampling (one plot/stand), which unfortunately characterises much of the spruce/beech research in Europe. The plot within the spruce forest showed less than half the N mineralisation rate (6 weeks, 28°C) and nitrification rate in the upper mineral soil (Ah) of the soil from the beech plot. Microbial biomass was also greater for the beech plot, but cellulolytic activity in the forest floor was twice as high in the spruce plot. Despite higher cellulolytic activity in the spruce plot, the authors concluded that they clearly showed a decrease in 'soil global microbiological activity'.

Brown (1992) reported results from one, two, or three replicate blocks of the Gisburn Forest experiment on the effects of tree species in pure and mixed stands. Decomposition of cotton strips was used as a measure for comparing cellulolytic activity among plots, and no substantial differences were found among Scots pine (*Pinus silvestris*), Norway spruce, and black alder. Lumbricid earthworm biomass depended strongly on tree species. Pure spruce stands had only 0.03 g (dry)/m^2, compared with 0.5 g/m^2 for Scots pine and 1.04 g/m^2 for black alder. Enchytraeid worm masses were generally greater than lumbricid mass, and showed less difference among tree species (1.6 g/m^2 spruce, 1.8 g/m^2 pine, and 0.7 g/m^2 alder). Samples from four forest floor layers were incubated in microcosms, and the spruce litter showed much greater release of CO_2 and phosphate than the Scots pine litter. Pine litter showed higher net nitrate production, probably resulting from greater nitrate immobilisation by microbes in the spruce litter, as evidenced by greater CO_2 release. Mixtures of litters generally released more CO_2, phosphate and nitrate than expected based on the simple averages from the two species.

Kienzler *et al.* (1986) examined soil communities in some of the Minnesota plantations that were described by Perala and Alban (1982). The aspen stand's soil had about 10 times more bacteria and twice the fungal biomass in the 0-10 cm mineral soil than under red pine and white spruce. At the 10-25 cm depth, red pine had about 10 times more bacteria than the others (although this quantity was only about 10% of the numbers found in the upper horizon). The aspen stand also had more annelid worms, beetles, beetle larvae, springtails, and arachnids. Total soil organic matter was highest under red pine (0-10 cm depth), and red pine and white spruce had more organic matter in the 10-25 cm depth than the aspen stand. The soil community patterns were unrelated to soil pH, which was lowest under spruce (5.4), and highest under red pine (6.0), with aspen in between (5.6).

Zou (1993) measured earthworm numbers and biomass in plantations of *Eucalyptus saligna* and N-fixing *Albizia falcataria* in Hawaii. Pure *Eucalyptus* stands had 92 worms/m^2 (primarily *Pontoscolex corethrurus*, with a few *Amynthas gracilis*), compared with 281/m^2 for the *Eucalyptus* and *Albizia* stands and 469/m^2 for the pure *Albizia* stands. Soil phosphatase activity and labile organic P both correlated highly with earthworm density ($r^2 = 0.6$, $p < 0.02$). The *Albizia* stands also had significantly more bacterial biomass, and less fungal biomass, than the *Eucalyptus* stands (Binkley, unpublished data).

McClaugherty *et al.* (1985) produced some strong evidence about the importance of adaptation of soil communities to types of litter produced within stands. They sampled litter from stands of sugar maple, aspen (*Populus*

tremuloides), white oak (*Quercus alba*), white pine and eastern hemlock, and followed decomposition (in litterbags) for 2 years. Some bags were placed in the stand of origin, and others were placed in a common plot in the most fertile sugar maple site. Sugar maple litterbags were transplanted into each of the other stands. For litterbags placed in the stands of origin, litter disappearance correlated highly with the rate of net N mineralisation from soil core (buried bag) incubations (r^2 = 0.8). This connection between site N supply and decomposition rate did not hold for transplanted litter; in all cases, litter in the stands of origin decomposed as fast as or faster than it did in the high-N sugar maple site. These results have two implications: decomposition of litter depends on soil communities adapted to specific litter types rather than on the N supply in the soil, and N supply in the soil may derive from patterns in litter decomposition rather than cause them.

PHYSICAL FEATURES OF SOILS

The effects of tree species on soil temperature regimes should derive from differences in canopy leaf area, which attenuates both incoming radiation and long-wave emissions from the soil. A secondary effect may be less snow accumulation under the dense canopies of conifers, leading to greater soil cooling during winter (Kittredge 1948). Evergreen and deciduous species probably differ most markedly in spring, when soils under the open canopy of deciduous stands warm sooner than those under evergreen canopies. Few data are available on the effects of tree species on soil temperatures. Amundson and Tremback (1989) examined temperatures under plantations that were established to stabilise beach dunes near San Francisco, California, USA. In July, soil temperature at 0.5 m for uncolonised dunes was 2-3°C above that of the air, whereas soil

temperatures under radiata pine and *Eucalyptus* (*E. globulus*) were 2°C lower than air temperature. No differences were apparent between species in this study.

Soil moisture should differ between species because of differences in canopy interception (evaporation of precipitation from leaf surfaces) and transpiration. For example, Kaufmann (1985) modelled the interception and transpiration for Rocky Mountain forests of aspen, lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). At a basal area of 25 m²/ha, aspen would transpire 100 mm/yr, lodgepole pine 180 mm/yr, and Engelmann spruce and subalpine fir 330 mm/yr. The differences among species depended on specific conductance of leaves, leaf area and leaf area duration.

At the Coweeta Hydrologic Laboratory in North Carolina, annual water loss from a mature hardwood forest included 230 mm from canopy interception and 660 mm of transpiration, compared with 320 mm interception and 770 mm transpiration from a watershed planted to white pine (Helvey and Patric 1988, Swank *et al.* 1988).

Nihlgard (1971) compared soil water properties under one pair of adjacent beech and Norway spruce stands in southern Sweden. The spruce soil was generally drier than the beech soil, although water supply was considered sufficient for tree growth in both stands. Periods of 'excessive' soil water developed under beech, but not under spruce.

Chapman (1986) followed seasonal trends in soil water content in the Gisburn Forest plantations. Pure stands of Norway spruce had the driest forest floors in summer (40% moisture), followed by Scots pine (50% moisture), sessile oak (*Quercus petraea*; 55% moisture) and black alder (65% moisture). Interception loss of water was about 17% of precipitation for oak, 22% for

alder, 40% for spruce and 44% for pine. These patterns were also reflected in the mean annual depth to the water table, about 45 cm for pine and spruce, compared with 25 to 30 cm for oak and alder.

Gower and Son (1992) found significantly more water in the forest floor plus 20 cm of mineral soil under red oak in Wisconsin than under larch, white pine, white spruce or red pine (which were all similar to one another).

Very little information is available on the effects of tree species on soil structure. Most of the earlier inferences of species effects were confounded with pre-existing differences between stands (see Stone 1975). Indeed, contrary to earlier conjectures, the limited evidence that is available indicates greater soil pore space under Norway spruce stands than under beech stands (cf Miehlich 1971, Nihlgard 1971).

The best experimental evidence of the effect of tree species on soil structure comes from large blocks (5.3 x 5.3 x 2.1 m) of homogenised fine, sandy loam that were planted with various species in southern California (Graham and Wood 1991). After 40 years, soils under the influence of Coulter pine (*Pinus coulteri*) lacked earthworms, had developed a clay-depleted A horizon, and had accumulated enough clay in the B horizon to qualify as an argillic horizon. Soils under oak (*Quercus dumosa*, a shrub) developed a 7-cm A horizon (90% of which was earthworm casts) enriched in humus and clay relative to the underlying C horizon. In this experiment, the plant species affected earthworm activity, which dominated structural development of the soil.

NUTRIENT POOLS

In the past 20 years, enough evidence has emerged from well-designed species trials to show that tree species clearly influence the size of nutrient pools and the distribution of nutrients among soil horizons. It is less clear if any generalisations can adequately encompass the diversity found across the case studies.

Forest floor

Afforestation of agricultural fields often leads to rapid accumulation of forest floors. For example, Hamburg (1984) examined a chronosequence of northern hardwood forests in New Hampshire, USA, to evaluate trends over the first 70 years of forest development. The rates of forest floor accretion of biomass and N were 950 kg ha^{-1} yr^{-1} and 19 kg ha^{-1} yr^{-1} respectively, and the timing and quality of woody litter inputs may control the overall pattern with stand age (Hughes and Fahey 1994). Under tropical conditions in Senegal, forest floor accretion during 34 years of development of *Casuarina equisetifolia* stands averaged 3,300 kg ha^{-1} yr^{-1} for mass, and 45 kg ha^{-1} yr^{-1} for N (Mailly and Margolis 1992). Forests clearly have rapid and large effects on the mass and nutrient content of forest floors.

Two patterns are apparent from the species-comparison studies listed in table 2. In some cases, the effect of tree species on forest floor mass and nutrient content is small. For example, the forest floor mass for 40-year-old stands of aspen, white spruce, jack pine and red pine all fell between 24 and 30 Mg/ha in the study by Perala and Alban (1982) in Minnesota, and the N contents fell between 450 and 630 kg/ha. No substantial differences were noted between the hardwood and conifer species. In other cases, the effect of species is much more pronounced. For example, the forest floor masses for 28-year-old stands in Wisconsin spanned a range from 9 Mg/ha for red oak to 43 Mg/ha for white pine, with N contents of 80 and 310 kg/ha respectively (Son and Gower 1992). The forest floor under the hardwood red oak differed greatly from the deciduous and evergreen conifers.

Table 2: Forest floor mass (Mg/ha) and nutrient content (kg/ha)

Location	Species, number of replicate plots, age	Mass	N	P	Ca	Reference
Connecticut, USA	*Pinus strobus*, 8, 50 yr	35.2				Binkley and Valentine
	Picea abies, 8, 50 yr	35.7				1991; Binkley
	Fraxinus pennsylvanica, 8, 50 yr	24.5				unpublished
Wisconsin, USA	*Quercus rubra*, 3, 28 yr	8.7	79	5		Son and Gower 1992
	Larix decidua, 4, 28 yr	37.5	260	18		
	Pinus strobus, 4, 28 yr	33.0	239	16		
	Pinus resinosa, 4, 28 yr	42.8	306	19		
	Picea abies, 4, 28 yr	24.7	225	19		
Minnesota, USA	*Populus tremuloides*, 2, 40 yr	23.5	555	46	810	Perala and Alban 1982
	Picea glauca, 4, 40 yr	29.5	630	50	1075	
	Pinus resinosa, 4, 40 yr	28.0	445	32	470	
	Pinus banksiana, 2, 40 yr	29.0	585	42	570	
Gisburn Forest, UK	*Quercus petraea*, 1, 30 yr	36.7	630	37		Chapman 1986
	Pinus sylvestris, 1, 30 yr	45.1	710	39		
	Alnus glutinosa, 1, 30 yr	25.8	700	35		
	Picea abies, 1, 30 yr	25.7	450	27		
	Picea/Pinus, 1, 30 yr	38.8	620	69		
	Picea/Alnus, 1, 30 yr	32.1	630	33		
	Picea/Quercus, 1, 30 yr	30.0	430	36		
Washington, Idaho USA	*Tsuga heterophylla*, 3, 400+ yr	19.7	200		93	Alban 1969
	Thuja plicata, 3, 800+ yr	25.3	275		335	
Ontario, Canada	*Pinus strobus*, 3, 27 yr	36.8				France *et al.* 1989
	Picea glauca, 3, 27 yr	16.2				
	Betula papyrifera, 2, 27 yr	6.5				
	Acer saccharinum, 2, 27 yr	2.4				
California, USA	*Pinus radiata*, 1, 100 yr	76	2000			Amundson and
	Eucalyptus globulus, 1, 100 yr	54	620			Tremback 1989
Mississippi, USA	*Juniperus virginiana*, 1, 16 yr	4.9	41		52	McClurkin 1970
	Pinus echinata, 1, 16 yr	14.5	130		100	
	Pinus taeda, 1, 16, yr	19.5	146		78	
	Juniperus/P. echinata, 1, 16 yr	9.6	90		68	
	Juniperus/P. taeda, 1, 16 yr	13.7	105		42	
Washington, USA	*Pseudotsuga menziesii*, 1, 55 yr	15.6	104	0.9	96	Binkley *et al.* 1992c
	P. menziesii/ Alnus rubra, 1, 55 yr	29.3	350	1.2	176	

Table 2 continued

Location	Species, number of replicate plots, age	Mass	N	P	Ca	Reference
Oregon, USA	*Pseudotsuga menziesii*, 1, 55 yr	26	153	24	156	Binkley *et al.* 1992c
	P. menziesii/Alnus rubra, 1, 55 yr	21	300	18	126	
Washington, USA	*Pseudotsuga menziesii*, 1, 50 yr	36.7		24	227	Homann *et al.* 1992
	Alnus rubra, 1, 50 yr	98.5		80	831	
Hawaii, USA	*Eucalyptus saligna*, 4, 8 yr	9.2			91	Rhoades 1991
	75% *Eucalyptus*/25% *Albizia*, 4, 8 yr	7.3			61	
	25% *Eucalyptus*/75% *Albizia*, 4, 8 yr	9.8			53	
	100% *Albizia falcataria*, 4, 8 yr	9.0			51	
Puerto Rico, USA	*Casuarina equisetifolia*, 5, 5.5 yr		256		150	Wang *et al.* 1991
	Albizia procera, 4, 5.5 yr		159		77	
	Eucalyptus robusta, 6, 5.5 yr		100		64	
	Leucaena leucocephala K8, 2, 5.5 yr		138		75	
	Leucaena leucocephala, native variety, 5, 5.5 yr		133		45	
La Selva, Costa Rica	*Stryphnodendron microstachyum*, 5, 4 yr	5.6	95	4	41	Montagnini and Sancho 1994
	Vochysia guatemalensis, 5, 4 yr	17.2	240	16	188	
	V. ferruginea, 5, 4 yr	11.1	134	12	170	
	Hyeronima alchorneoides, 5, 4 yr	4.1	39	13	55	

Both patterns also apply to the effects of N-fixing species (table 2). At the Cascade Head, Oregon site, the mass and N content of the forest floor were essentially the same for the conifer and the red alder/conifer stands (Binkley *et al.* 1992c). At the Wind River, Washington site, forest floor biomass in the alder/conifer stand was twice that of the conifer stand, and contained three times as much N. At the Thompson river site in Washington, the forest floor of the red alder forest had 2.7 times the mass of that of an adjacent Douglas-fir forest. Under tropical conditions in Hawaii, no differences in forest floor biomass were apparent under *Eucalyptus* or *Albizia* stands (Rhoades 1991).

The variation in the degree of species effect on forest floor mass and nutrient content may derive from variations in the importance of earthworms. On sites where earthworms can be important, any difference in substrate quality among species may be amplified by worm activity. However, I know of no common-garden experiments that have separated the direct species effects of litter quality from the indirect effects of litter quality on soil animal activity.

Mineral soil

High variation in mineral soil properties makes it difficult to assess the effect of species on pools of nutrients. Available evidence indicates that species effects can be substantial. Son and Gower (1992) found the upper 30 cm of mineral soil ranged from 7.7 mg C/kg soil under white pine to 13 mg C/kg soil under Norway spruce (table 3), a difference of about 30 Mg/ha of organic matter. The N concentration was also much higher under spruce (1.1 mg/kg soil) than

under white pine (0.8 mg/kg), by about 800 kg/ha. For the mineral soil, the hardwood oak values fell between those of the evergreen conifers. Soil P (extractable by sulphuric acid) appeared to differ by about twofold across the species, although the difference was not significant at $p < 0.05$. Differences in exchangeable (ammonium acetate) cations were substantial, amounting to a range of about 140 $kmol_c$/ha, or an impressive rate of divergence among the species of 5 $kmol_c$/ha annually!

Binkley and Valentine (1991) found that soils (0-15 cm in depth) under green ash (*Fraxinus pennsylvanica*) and white pine had significantly more (about double) ammonium-nitrate extractable potassium (K), Ca and magnesium (Mg) in mineral soil than under Norway spruce. In contrast, France *et al.* (1989) found no significant (or even apparent) differences in extractable cations under four species in Ontario.

The patterns of species effects on soil nutrient pools are mixed for comparisons with N-fixing species. In all cases, soil organic matter and N content appear to be higher in stands with N-fixing species, typically by 10 to 40% (Binkley and Sollins 1990, Homann *et al.* 1992). The picture is less clear for pools of soil P. In most cases, labile inorganic pools of P tend to be similar between stands (Zou *et al.* in review), or

lower under the N fixer (Cole *et al.* 1990, J. Compton, personal communication). Labile organic pools and annual uptake of P by trees are consistently higher under the alders. The effects of N-fixing trees on soil cation pools are varied. In Hawaii, soil cation pools were strongly depleted by both *Eucalyptus* and N-fixing *Albizia* in 8 years, but no differences between species were apparent (Rhoades 1991). High leaching of K, Ca and Mg from the alder/conifer stand at the Cascade Head site in Oregon led to much lower quantities of these cations in biomass and on exchange sites than in the pure conifer stand (Binkley and Sollins 1990). At their Wind River site in Washington, the upper soil was enriched in these cations under the alder/conifer stand, whereas the deeper soil was depleted, giving no net difference between the conifer and the alder/conifer stands to a depth of 0.9 m. At another site in Washington, Homann *et al.* (1992) found no substantial differences in exchangeable soil cations under a 50-year-old alder stand compared with an adjacent 50-year-old Douglas-fir stand, despite greater cation leaching losses from the alder stand. (Therefore mineral weathering must have been greater under alder.)

SOIL ACIDITY
Historically, much of the interest in the effects of tree species on soils focused on acidification.

Table 3: Mineral soil (0-0.3 m) effects of tree species in Wisconsin, USA (from Son and Gower 1992). Means followed by the same letter do not differ at $p < 0.05$

Property	Red oak	European larch	White pine	Red pine	Norway spruce
Carbon (mg/kg)	8.3a	8.6a	7.7a	10.1b	12.9c
Nitrogen (mg/kg)	0.9ab	0.9ab	0.8a	1.0bc	1.1c
H_2SO_4 extractable P (mg/kg)	21a	36a	41a	28a	21a
pH_{water}	5.4a	5.3ab	5.4a	5.5a	5.2b
Exchangeable K + Mg + Ca (ammonium acetate, $mmol_c$/kg)	143b	115a	105a	140b	110a

Common expectations included greater acidification of soils under conifers than under hardwoods. These views were derived from comparisons where pre-existing differences in soils were attributed to the current species (Stone 1975). In this section, I discuss the factors that account for differences in soil pH, and then tabulate the findings from repeated-measurement studies and from common-garden plantations.

Factors controlling soil pH

Soil acidity is a complex phenomenon that includes very large pools of stabilised acids (typically more than 1000 $kmol_c/ha$) and very small pools of H^+ free in soil solution (typically less than 1 $kmol_c/ha$; Binkley and Richter 1987). A tree species may lower soil pH by four basic processes (Binkley *et al.* 1989), assuming no change in soil aeration and redox:

- increasing the quantity of anions in soil solution, some of which will be balanced by H^+, lowering the soil solution pH;
- increasing the quantity of acids stored in the soil, particularly humified organic matter. Such an increase is typically measured as an increase in both soil organic matter and cation exchange capacity. A given quantity of soil water will have more H^+ ions if it is in contact with a greater quantity of soil acids;
- increasing the degree of protonation of the stabilised soil acids. The proportion of the exchange complex occupied by so-called 'base' cations is a measure of the degree of deprotonation of the exchange complex, whereas the proportion occupied by H^+ and Al^{3+} indicate the degree of protonation. Increasing the 'acid saturation' (or decreasing the 'base saturation') of the exchange complex leads to greater concentrations of H^+ in soil solutions;
- increasing the acid strength by accumulating soil humus that is more strongly acidic (has a lower pK_a). Stronger humic acids donate H^+ to soil solutions more readily. (Kaolinitic clays are also stronger acids than smectite clays.)

Tree species might differ in the quantity of ions in solution by capturing more ions from the atmosphere (particularly in polluted or dusty regions), or by favouring greater within-ecosystem ion generation (particularly nitrification). Species may differ in the accumulation of stabilised soil acids (humus). In the past, some species were said to acidify soils by producing acidic litter; however, the acids contained in fresh litter are degraded rapidly and contribute little if anything to the acidity of the soils (Nykvist 1959, 1963, Binkley and Richter 1987). Any effect of species on the accumulation of acids depends on the creation of organic acids through the partial decomposition of litter, which may depend strongly on the soil community as well as the tree species. Changes in the protonation of soil acids (the soil exchange complex) may derive from removal of nutrient cations that are sequestered in biomass or leached from the soil, or from the addition of nutrient cations that were taken up from deeper horizons or released by mineral weathering. The strength of the acid complex may differ if the byproducts of litter decomposition have stronger acid groups under one species (or soil community) than another.

Changes in soil pH over time

A wide range of studies have documented changes in soil pH over time (reviewed by Johnson *et al.* 1991), although few have evaluated the importance of various factors in driving the observed changes. One of the best illustrations of the magnitude of changes over time comes from southeastern Sweden, where C O Tamm and Hallbacken (1986) relocated

soil pits (within 1 m!) in 11 stands of Norway spruce and 17 of beech that had been sampled 55 years earlier by O Tamm (figure 2). The comparisons showed no apparent differences among species for any depth, but for all species a strong acidification (about 1 unit in the top soil) across time was evident. Soil pH was measured in water, so any of the factors described above could have contributed to the observed acidification.

In the northeastern USA, Anderson (1988) sampled 48 hardwood forests in the Adirondack Mountains about 50 years after a prior sampling. Between samplings, forest floors with pH of 4 or less in the original sampling had not changed, but those with higher pH had declined by 0.3 to 0.5 units. The declines in exchangeable soil Ca averaged about 0.4 kmolc ha^{-1} yr^{-1}, which was about 70% of the Ca accumulated in the vegetation over this period.

In Ontario, Canada, Brand *et al.* (1986) resampled soil pits in 20 stands, 46 years after an earlier sampling which had been conducted

55 yr acidification in Sweden
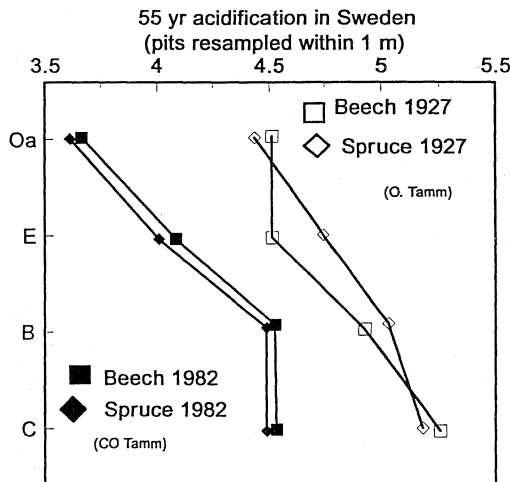(pits resampled within 1 m)

Figure 2: Fifty-year declines in soil pH under Norway spruce and beech in southern Sweden (after Tamm and Hallbacken 1986)

within 10 years of afforestation of old agricultural fields. In one stand of Scots pine and another of jack pine, the pH had not changed. For five stands of red pine, pH declined on average from 6.0 to 5.3. Thirteen stands of white spruce declined on average from pH 6.0 to 4.7. The causes of the acidification under spruce were not examined, but I suspect the accumulation of strongly acidic organic matter in the upper mineral soil was a major factor. In Quebec, Roberge (1987) found that the pH of forest floors and mineral soils in nine stands (all over 50 years old) of sugar maple, balsam fir (*Abies balsamea*), jack pine and black spruce (*Picea mariana*) had increased by 0.0 to 0.6 units during periods of 5 to 20 years. Again, no mechanisms were addressed, but the pH measurements were in deionised water, and the increase over time could have resulted from a decrease in total ion concentrations.

C Wells sampled soils from eight plots in a 5-year-old plantation of loblolly pine (*Pinus taeda*) on an old agricultural soil, with further sampling at 5-year intervals through age 30 (Binkley *et al.* 1989, Richter *et al.* 1994). The pH of 0-15 cm depth soil dropped by 0.3 units in just 5 years, and by another 0.3 units in the next 10 years. The 0-5 cm depth soils declined from 4.8 (in 0.01 *M* CaCl$_2$) to 3.8 after 30 years, and the pH at 0.5 m depth declined by 0.3 units in 30 years. Binkley *et al.* (1989) developed an empirical titration approach to evaluate the importance of factors that might explain the changes in pH. The majority of the decline resulted from increasing the acid saturation of the exchange complex (decreased base saturation), driven by cation nutrient accumulation in biomass.

In plantations of *Casuarina equisitifolia* in Senegal, Mailly and Margolis (1992) documented a decline in soil pH from 7.4 to 6.4 after 34 years. Mechanisms were not investi-

gated, but the concentrations of exchangeable cations changed little, while the pool of soil organic matter more than tripled. Therefore, the acidification probably resulted from organic matter accumulation.

Changes in soil acidity under the influence of different species

Soil pH appears to diverge under the influence of different species, typically by a few tenths of a unit over some decades. In some cases, changes are even faster. For example, Sanchez *et al.* (1985) reported that soil pH in the upper soil increased from 3.9 in an intact primary rainforest to 4.9 after clearing and burning. Six years later, the pH had declined back to 3.9 under plantations of *Pinus caribaea*, but continued to climb to 5.5 under *Gmelina arborea*.

In the Connecticut plantations (Binkley and Valentine 1991), soil pH was substantially lower under Norway spruce than under green ash (table 4), in both water and dilute $CaCl_2$ solutions (respectively 4.6 and 3.8 in water, 4.0 and 3.7 in dilute $CaCl_2$). The importance of ionic strength was not directly assessed, but the difference in pH in dilute $CaCl_2$ demonstrated that this factor alone could not account for the difference in soil pH. If the quantity of soil acids (organic matter) under the ash were increased to match that of the spruce, while other factors were held constant, the pH under the ash might decline by about 0.1 unit. If only the protonation of the soil acids (the acid saturation, or base saturation) under ash were adjusted to match that of the spruce soil, the pH decline would be about 0.15 units. If the strength of the acids under the ash were shifted to match those under the spruce, a 0.4 unit decline in pH might result. In this case, the primary factor driving the acidification of the Norway spruce soil was the accumulation of strongly acidic organic matter.

The same approach was used to examine the effects of alder on soil acidity (Binkley and Sollins 1990). At the Wind River site in Washington (table 4), the soil pH in water was 5.4 under Douglas-fir compared with 5.1 under red alder/Douglas-fir. This 0.3 difference in pH represents 3.6 umol$_c$/L more H^+. The alder/Douglas-fir soils had 160 umol$_c$/L more nitrate, so the increase in H^+ concentration represented just 2% of the extra anion concentration. The pH measured in dilute $CaCl_2$ showed no difference between stands, indicating that the ionic strength effect accounted for the observed difference in the soil pH measured in water. Interestingly, the acid saturation of the exchange complex was lower (ie higher base saturation) in the mixed stand (0.55, vs 0.68 for the Douglas-fir stand), indicating that pH should have been *higher* in the mixture with alder. In this case, the similarity in soil pH between stands resulted from the offsetting effects of lower acid saturation but greater acid strength under alder. At the Cascade Head site, the alder/conifer stand had much greater acid saturation (0.91, vs 0.71 for the conifer stand), accounting for the majority of the decrease in soil pH. In both of these studies, the effects of species on soil acidity extended from 0 to 10 m away from the stand boundaries, with the greater distances observed downslope from the alder/conifer stands.

The Thompson site in Washington also showed soil acidification under red alder relative to Douglas-fir (Van Miegroet and Cole 1984, Homann *et al.* 1992). Lower pH in water resulted in part from greater ion concentrations. The lower pH in dilute salt resulted from an increase in organic acids. Soil C was about 45% greater with alder, and cation exchange capacity at pH 7 was about 20% higher. The quantity of exchangeable Ca + Mg + K was similar between sites, so the increase in exchange capacity

Table 4: Soil pH under the influence of tree species

Location	Species, number of replicate plots, age	Horizon (cm)	pH in water	pH in dilute salt	Major cause of species differences	Reference
Wisconsin, USA	*Quercus rubra*, 3, 28 yr	0-30	5.4		nd	Son and Gower 1992
	Larix decidua, 4, 28 yr	0-30	5.3			
	Pinus strobus, 4, 28 yr	0-30	5.4			
	Pinus resinosa, 4, 28 yr	0-30	5.5			
	Picea abies, 4, 28 yr	0-30	5.2			
Wisconsin, USA	*Pinus resinosa*, 1, 40 yr	0-10		5.3	nd	Nadelhoffer *et al.* 1983
	Pinus strobus, 1, 40 yr			4.4		
Connecticut, USA	*Pinus strobus*, 8, 50 yr	0-5	4.55	4.36	Primarily acid strength	Binkley and Valentine 1991
		5-15	4.34	3.97		
	Fraxinus pennsylvanica, 8, 50 yr	0-5	4.20	4.06		
		5-15	4.21	3.94		
	Picea abies, 8, 50 yr	0-5	3.81	3.64		
		5-15	3.99	3.67		
Ontario, Canada	*Pinus strobus*, 3, 27 yr	Forest floor	5.3		Forest floor, acid saturation	France *et al.* 1989
		0-15	6.7			
	Picea glauca, 3, 27 yr	Forest floor	5.9			
		0-15	6.4			
	Betula papyrifera, 2, 27 yr	Forest floor	4.8			
		0-15	6.6			
	Acer saccharinum, 2, 27 yr	Forest floor	3.7			
		0-15	6.3			
Oregon, USA	*Pseudotsuga menziesii*, 10 trees, > 300 yr	Forest floor	3.6		Hemlock forest stronger floor, organic acids	Turner *et al.* 1993
		0-10	3.8			
	Thuja plicata, 10 trees, > 300 yr	Forest floor	3.7			
		0-10	3.8			
	Tsuga heterophylla, 10 trees, > 300 yr	Forest floor	3.4			
		0-10	3.6			
Southern Sweden	*Fagus silvatica*, 3, 60-120 yr	0-10	4.0	3.3	nd	Nihlgard 1971
		20-30	4.4	3.5		
	Picea abies, 3, 40-55 yr	0-10	3.8	3.0		
		20-30	4.0	3.4		
Grue, Sweden	*Larix decidua*, 1, 90 yr	Forest floor	4.23		nd	Bonnevie-Svendsen and Gjems 1956
		0-15	4.15			
		15-38	5.0			
		38+	5.3			
	Picea abies, 1, 80 yr	Forest floor	4.18			
		0-19	4.25			
		19-30	5.1			
		30+	5.3			

Table 4 continued

Location	Species, number of replicate plots, age	Horizon (cm)	pH in water	pH in dilute salt	Major cause of species differences	Reference
Eidsberg, Sweden	*Larix sibirica*, 1, 45 yr	Forest floor	4.86		nd	Bonnevie-Svendsen and Gjems 1956
		0-24	5.1			
		24-30	5.3			
		30+	5.5			
	Picea abies, 1, 50 yr	Forest floor	4.40			
		0-22	4.6			
		22-42	5.3			
		42+	5.7			
Washington, USA	*Pseudotsuga menziesii*, 1, 55 yr	0-15	5.4	4.3	In water, pH lower with alder because of higher ionic strength. In salt, no difference from offsetting high base saturation and stronger acid with alder	Binkley and Sollins 1990
		15-40	5.3	4.3		
		40-65	5.2	4.1		
		65-90	5.2	4.1		
	P. menziesii/Alnus rubra, 1, 55 yr	0-15	5.1	4.3		
		15-40	5.1	4.2		
		40-65	5.0	4.1		
		65-90	4.9	4.0		
Oregon, USA	*Pseudotsuga menziesii*, 1, 55 yr	0-15	5.4	4.4	Lower base saturation under alder	Binkley and Sollins 1990
		15-30	5.4	4.4		
		30-60	4.2	4.3		
		60-90	4.9	4.1		
	P. menziesii/Alnus rubra, 1, 55 yr	0-15	4.3	3.7		
		15-30	4.8	4.1		
		30-60	4.8	4.2		
		60-90	4.7	4.1		
Washington, USA	*Pseudotsuga menziesii*, 1, 50 yr	0-7	5.0	4.3	Organic acid accumulation under alder, leading to lower base saturation	Homann *et al.* 1992
		7-15	5.6	4.7		
		15-30	5.5	4.8		
		30-45	5.5	4.8		
	Alnus rubra, 1, 50 yr	0-15	4.3	3.8		
		15-30	4.8	4.3		
		30-60	5.2	4.5		
		60-90	5.5	4.7		
Hawaii, USA	100% *Eucalyptus saligna*, 4, 8 yr	0-15	4.95	4.54	Acid strength weaker, but acid saturation higher with Albizia	Rhoades 1991
	75% *Eucalyptus*/25% *Albizia*	0-15	4.85	4.37		
	25% *Eucalyptus*/75% *Albizia*	0-15	4.77	4.39		
	100% *Albizia falcataria*	0-15	4.62	4.27		

resulted in a decrease in base saturation (ie increased acid saturation) and a drop in soil pH. The contribution of the strength of the acids under the alders was not examined.

Collectively, these studies indicate that the pH of forest floors may diverge by up to 2 units within a few decades under the influence of different species. The maximum rate of divergence for mineral soils is slower, up to about 1 unit in a few decades. The mechanisms underlying differences in soil acidification have been examined in only a few cases, and each of the four factors listed above have been implicated in one or more case studies. The implications of the differences in acidification remain even murkier. In fact, no association between acidification and nutrient availability is apparent; the availability and turnover of both N and P do not follow the patterns of soil acidification from common-garden plantations.

NUTRIENT IMMOBILISATION PROCESSES

Figure 1 lists three general types of processes within soils that remove nutrients from the soil solution: precipitation, sorption, and humification. Precipitation of minerals is generally unimportant in forest soils, with the possible exception of secondary mineral formation and sorption of P by sesquioxides (similar to precipitation). Ion sorption is very important, particularly for cations in younger soils and for cations and anions in older soils.

Species probably differ substantially in the quantity, forms and location of humus accumulation. As noted in table 2 and discussed above, species can differ by twofold or more in forest floor accumulation, and by 25% or more in humus accumulation within the mineral soil. Less is known about differences in the chemical quality of the humus produced from litter of different species. Classic expectations of greater

podzol formation under spruce may depend on solubilisation of iron and aluminum through chelation by soluble humic compounds. Recent developments in nuclear magnetic resonance have been used to examine differences in the quality of humus under western hemlock and redcedar forests on Vancouver Island, Canada (deMontigny *et al.* 1993, Prescott and Preston, in review). Redcedar needles are relatively low in tannin, but the redcedar humus was higher in tannin, resulting from the contribution of ericaceous understorey salal (*Gaultheria shallon*). The redcedar humus also had higher ratios of carbohydrate:lignin, indicating poorer decomposition. These techniques need to be used to examine soil humus in common-garden plantations, particularly with thorough characterisation of the soil communities, soil enzyme activities, and root dynamics.

NUTRIENT RELEASE PROCESSES
Nitrogen release

No method of assessing N availability in soils is perfect, as all involve some degree of disturbance and artificial conditions (Binkley and Hart 1989). Two methods have been used in common-garden plantations to examine the effects of tree species. Buried bag incubations place soil cores in gas-permeable bags which are then reburied and incubated typically for 30-day periods. The initial content of ammonium and nitrate are subtracted from the post-incubation contents to obtain a net flux value. The month-long incubations are repeated through the growing season or a whole year, and the values summed to estimate annual net N mineralisation. The resin-core method is similar, except the soil core is incubated in an open plastic tube, with a bag of ion exchange resins on the bottom to trap any ammonium and nitrate that leach from the core during incubation. Both methods examine only the net

fluxes, and do not account for differences among soils in the amount of N that was mineralised but reimmobilised by microbes (see below). Both methods also involve unavoidable artefacts (of unknown size) from the severing of fine roots and fungal hyphae.

Tree species have very large effects on N mineralisation rates, but the results of common-garden plantations do not match classic expectations of higher N availability under the influence of hardwood species (table 5). The highest net N mineralisation rate among the species in the Wisconsin plantations (Gower and Son 1992) was for European larch, followed by white pine. Net N mineralisation under red oak was matched by that under red pine and

Table 5: Tree species effects on net N mineralisation rates (kg N ha^{-1} yr^{-1})

Location	Species, number of replicate plots, age	Method, Soil depth (cm)	Sum, net N mineral- isation	Proportion as nitrate	Reference
Wisconsin, USA	*Quercus rubra*, 3, 28 yr	Buried bags, forest floor+0-20	55	0.42	Gower and Son 1992
	Larix decidua, 28 yr	Buried bags, forest floor+0-20	117	0.95	
	Pinus strobus, 4, 28 yr	Buried bags, forest floor+0-20	87	0.93	
	Pinus resinosa, 4, 28 yr	Buried bags, forest floor+0-20	51	0.63	
	Picea abies, 4, 28 yr	Buried bags, forest floor+0-20	46	0.50	
Wisconsin, USA	*Pinus resinosa*, 1, 40 yr	0-10	32		Nadelhoffer *et al.* 1983
	Pinus strobus, 1, 40 yr	0-10	80		
	P. resinosa, P. strobus, 1, 40 yr	0-10	50		
Connecticut, USA	*Fraxinus pennsylvanica*, 8, 50 yr	Resin cores, forest floor+0-15	40	0.96	Binkley and Valentine 1991
	Pinus strobus, 8, 50 yr	Resin cores, forest floor+0-15	84	0.80	
	Picea abies, 8, 50 yr	Resin cores, forest floor+0-15	56	0.70	
Southern Sweden	*Picea abies*, 1, 40-55 yr		100		Nihlgard 1971
	Fagus silvatica, 1, 60-120 yr		100		
Washington, USA	*Pseudotsuga menziesii*, 1, 55 yr	Resin cores, forest floor+0-15	1	0.00	Binkley *et al.* 1992a
	Alnus rubra/P. menziesii, 1, 55 yr	Resin cores, forest floor+0-15	126	0.79	
Oregon, USA	*Pseudotsuga menziesii*, 1, 55 yr	Resin cores, forest floor+0-15	30	0.49	Binkley *et al.* 1992a
	Alnus rubra/P. menziesii, 1, 55 yr	Resin cores, forest floor+0-15	124	0.93	

Norway spruce. Net nitrification was also high under white pine at another site in Wisconsin (Nadelhoffer *et al.* 1983). In the Connecticut plantations, soils under white pine showed more than twice the rate of net N mineralisation of the green ash soils (Binkley and Valentine 1991).

Stands that contain N-fixing species typically show greater rates of soil N mineralisation (table 5), and greater net nitrification. Preliminary evidence indicates that heterotrophic nitrification may be particularly important under red alder stands (S Hart, personal communication). The greater net N mineralisation is associated with higher rates of N return in aboveground litterfall, and the residence time of N in the forest floor may or may not be shorter than in adjacent conifer stands (Binkley 1992).

Historically, the accumulation of thick organic layers under some species (such as 'mor' humus under spruce) was interpreted as a sign of low nutrient supply relative to other species with thinner organic layers (such as 'mull' humus under beech). For this to be true, several conditions would need to be met:

- the comparisons would need to be on the same site;
- the rate of litterfall input of nutrients would need to be the same;
- the thicker forest floor must still be accruing mass rather than be in steady state; and
- forest floor dynamics would have to be a good indication of overall nutrient supply.

It appears from the partial evidence available that these conditions are not met. Indeed, forest floor accumulation (in terms of mass or nutrient content) has shown no relationship with N mineralisation in common-garden plantations. For example, the comparisons of five species by Gower and Son (1992, Son and Gower 1992) provided information on the N content of litterfall (similar across species, table 1) and forest floor (very different across species, table 2). N mineralisation did not correlate with N content of litterfall or the forest floor. Moreover, it did not relate to the accumulation of the forest floor. The turnover time of N in the forest floor can be calculated by dividing the forest floor N by the annual litterfall N (figure 3). This calculation assumes the forest floors have steady state masses; any sites with continued accretion of forest floors would have longer turnover time than calculated. The small pool of N in the red oak forest floors turned over quickly, but was associated with only a moderate rate of N mineralisation. The larch stands had moderate turnover times, but very high rates of N mineralisation. The turnover time for forest floor N (and for mass, not shown) also did not correlate with litterfall lignin:N; the lignin:N ratio was not a good predictor of forest floor turnover time. However, lignin:N appeared to be a good predictor of N mineralisation (though note that the strength of the relationship [$r^2 = 0.75$] depends strongly on larch). In comparisons of Douglas-fir, western hemlock, and western redcedar, Prescott and Preston (in review) also found that the lignin:N ratio of litter explained the differences in soil N mineralisation very well.

The 50-year-old plantations in Connecticut, USA (Binkley and Valentine 1991; see tables 1 and 2) show the same patterns: no effect of species on N content of litterfall; moderate range of forest floor biomass (N content not measured); and no relationship between forest floor mass or litterfall N and net N mineralisation in the forest floor + 0-to-15-cm mineral soil.

It is also important to note that lower pH was not associated with lower net N mineralisation in the Wisconsin and Connecticut plantations (table 3; see also Prescott *et al.*, this volume). Inclusion of the results from N-fixing stands, where acidification is not unusual, would skew the relationship in favour of enhanced N
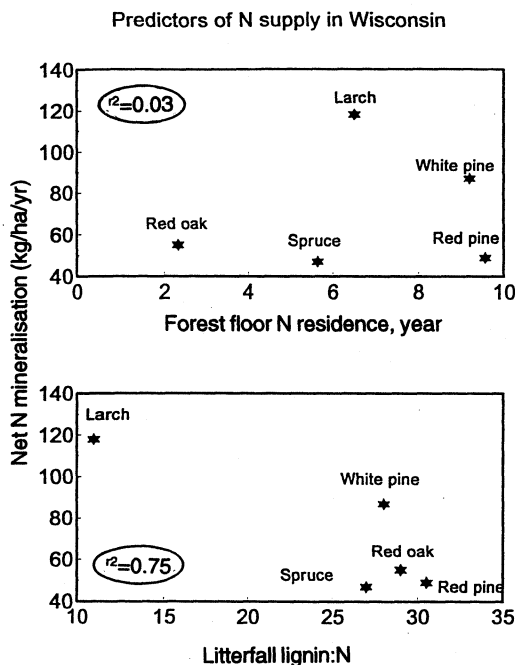
Predictors of N supply in Wisconsin

Figure 3: Net N mineralisation was unrelated to the residence time of N in the forest floor, but related well to the lignin:N of litterfall in these Wisconsin plantations (after Gower and Son 1992)

supply at lower pH. Any acidification effect of a species should not be construed as evidence of declining soil N supply; as noted above, available evidence indicates no relationship between these two soil properties.

Current evidence suggests that classic inferences of nutrient supply from forest floor accumulations, acidity and morphology are probably invalid. Other factors, such as chemistry of fresh litter, dynamics of organic matter within the mineral soil, and perhaps the activities of soil macro- and microbiota prevent these simple expectations from being fulfilled. At present, the lignin:N of litter (or forest floor) seems to be the best indicator of the connection between current litter production and nutrient

supply. This relationship has also been used for simulating the effects of tree species on soil N availability (cf Pastor *et al.* 1987, Rastetter *et al.* 1991, Pastor and Naiman 1992). The usefulness of this relationship probably does not derive from any direct effect of N or lignin, *per se*, on decomposition. Increasing the N content of a single litter type typically does not increase decomposition rates (Prescott 1994) and, as noted above, the value of lignin as an index of decomposition may derive from covarying chemistry of polyphenols or aliphatics. More experimentation in common-garden plantings is clearly warranted, with mechanistic manipulations of litter.

White pine was included in three of the species comparisons in table 5, and net N mineralisation appeared high in all cases. Thick, mor forest floors under white pine have been thought to indicate very fertile sites in the past (Wilde 1964). Perhaps white pine enhances soil N turnover relative to some other species.

Red pine was included in three of the species comparisons as well. In all cases larger pools of soil organic matter resulted than for the other species. Future common-garden experiments in the USA should include white pine, red pine and larch species.

Phosphorus release

Single-species studies have documented very strong changes in soil P pools and transformations with stand age. For example, Polglase *et al.* (1992) found that labile inorganic P declined from over 30 ug/g dry soil in young stands of *Eucalyptus regnans* to less than 3 ug/g at age 16 years and beyond (pH declined from 5.2 to 4.1). At the same time, labile organic P was increasing, along with microbial-biomass P and phosphatase activity.

The effects of tree species on P cycling has received even less attention than in single-species studies. At this point, we know that the effects

may be substantial, and that a wide range of interacting processes may be involved.

Trees may differ in effect on the P supply in soils by several mechanisms. The simplest would be rooting distribution; a deeply rooted species may tap pools of P that were simply not accessed by another species (cf Comerford *et al.* 1983, Malcolm *et al.* 1985). In a more active way, differences in the pH of soils and rhizospheres may lead to differences in rates of solubilisation of P bonded with Ca (Gillespie and Pope 1989, Gahoonia and Nielsen 1992, Illmer and Schinner 1992). The supply of P from organic pools may be driven by differences in the activities of phosphatase exoenzymes, produced either by the trees or by microbes in association with the trees (Jayachandran *et al.* 1992; see an excellent paper by Fox and Comerford 1992). Finally, some plants have been shown to produce low-molecular-weight organic acids that can chelate iron or aluminum, releasing phosphate (Ae *et al.* 1990).

The best comparisons of species effects on soil P supply come from studies with N-fixing tree species. Zou (1992, Zou *et al.* in review) examined the replicated plantations of *Eucalyptus* and *Albizia* in Hawaii, and found no species effect on resin-extractable P or bicarbonate-extractable inorganic P. However, plots with *Albizia* had about 80% greater bicarbonate-extractable organic P, and 50% to 100% more phosphatase activity than pure *Eucalyptus* plots. Zou *et al.* (1992) also developed a new method to separate resin-extractable P into components that depend on microbial and enzyme-mediated reactions from inorganic geochemical reactions. These methods revealed no substantial differences among species.

Zou (1992, Zou *et al.* in review) also examined some P pools and transformation at the Cascade Head, Oregon stands with red alder, Douglas-fir, and the mixture of species.

The bicarbonate-extractable pool of organic P, and the phosphatase activity were again the most sensitive measure of species effects. Both measures averaged about double those for stands with alder. The stands with alder also had much greater rates of inorganic-P release from organic pools, and microbial immobilisation of released P.

Giardina *et al.* (1995) examined pools of P under replicated, 22-year-old plantations of pure Douglas-fir and Douglas-fir mixed with red alder near the coast of Oregon. Pools of labile P (resin-extractable P, NaOH-soluble organic and inorganic P, and HCl soluble P) were substantially higher under the stands with alder.

J Compton (personal communication) is describing the differences in soil P between adjacent stands of 50-year-old Douglas-fir and red alder at the Thompson Research Site in Washington, USA. Extractable inorganic P is much lower with alder, whereas extractable organic-P and phosphatase activities are higher under alder (B Caldwell, personal communication).

Paré and Bernier (1989a, b) demonstrated that P supply is higher on sites with mor-type forest floors than on sites with mull forest floors. They examined five sites of each type in sugar maple stands from the Quebec Appalachians, where the foliar concentrations of P ranged from 0.85 to 2.36 mg/kg. The mor sites had about four times more P in the forest floor than the mull sites, yet the mor sites also had about twice the P concentrations in foliage than the mull sites. The Ah horizon of the mull sites had about eight times the P content of the mor sites. The P content of the B horizons did not differ among the forest floor types. Although the mor forest floors were more acidic (pH 3.6 to 4.2) than the mull forest floors (pH 4.9 to 5.5), the concentration of extractable iron and aluminum was far greater for the mull forest floors (by factors

of about 3 to 5, depending on method). The higher concentrations of iron and aluminum in the mull sites apparently bound the P in forms that were less available (or unavailable) to the sugar maple trees. This excellent pair of studies again demonstrates that classic expectations of greater fertility on sites with mull forest floors may be ill founded, and the reality may even be the reverse of what was thought.

NUTRIENT UPTAKE

Surprisingly little is known about the importance of differences among species in nutrient uptake, by either microbes or trees.

Some authors (eg Nadelhoffer *et al.* 1983) believe net N mineralisation estimates represent good measures of soil N availability to trees, but others are more sceptical. The N that is measured as net mineralisation is what remains after microbial immobilisation, and this immobilisation may not be a constant proportion across sites. For example, Davidson *et al.* (1992) found that net N mineralisation in the 0-10 cm mineral soil of a young mixed-conifer forest was higher than that of an old-growth forest (10 and 7.5 mg N g^{-1} soil day^{-1} respectively). However, the gross release of N from organic pools was far lower in the young forest (180 vs 400 mg N g^{-1} soil day^{-1}). Differences in both the gross mineralisation and immobilisation rates were very important in determining the differences in net N mineralisation between these stands.

The only data available for common-garden experiments come from the Wisconsin sites studied by Gower and Son (1992). N Scott (personal communication) used ^{15}N techniques and found that gross-N mineralisation was between six and nine times greater than net N mineralisation across the five species. Differences in net N mineralisation rates, therefore, could derive from either differences in the release of

N from organic matter, or differences in microbial immobilisation of the released N.

Differences in nutrient uptake among tree species also remain relatively unexplored. For some elements, such as N and P, tree uptake has often been assumed to match the supply rate. However, tree uptake of nutrients may affect supply. For example, depletion of K from exchange sites may enhance release from less-available pools (Comerford *et al.* 1990, Nowak *et al.* 1991). Another possibility would be uptake of nutrients from subsoils, followed by accumulation of nutrients in the upper soil horizons where biotic processing results in faster nutrient turnover. Tree species are often characterised as pumping cation nutrients from deeper soil horizons, and depositing them in litter at the soil surface, resulting in a net increase (net sorption) of these ions in the upper soil (cf Fisher 1990). Unfortunately, I know of no common-garden experiments where nutrient uptake has been quantitatively estimated by individual horizons. The role of mycorrhizae in 'increasing' P supply through more efficient uptake could also have substantial impact on later cycling of P. Again, I am not aware of common-garden experiments that have examined these mechanisms, or the importance of differences in nutrient uptake in generating differences in soils under various species.

NUTRIENT OUTPUTS

Almost no information is available on the effect of tree species on nutrient outputs from ecosystems. Nadelhoffer *et al.* (1983) found that nitrate leaching below the rooting zone appeared high under white pine (about 10 kg-N ha^{-1} yr^{-1}) compared with red pine (near 0). The high leaching loss under red pine might result from both a high turnover rate of soil N, as a legacy from a previous hardwood forest, and rapid decomposition of organic matter under white

pine, which impairs opportunity for N retention (K Nadelhoffer, personal communication). The red pine stand should have had the same soil legacy before it was established 40 years ago. Uptake of N in the red pine stand was slightly more than half the flux for the white pine stand, yet the red pine stand had accumulated 30% more soil organic matter. Poor litter quality in the red pine stand may have depressed N turnover, increased organic matter accumulation and prevented N leaching losses. These intriguing comparisons did not have the benefit of replication of stands, but the pattern is consistent with the replicated comparisons of white pine and red pine from Son and Gower (1992), who found significantly more soil C and N under red pine in a common-garden experiment.

More information is available for unreplicated comparisons of adjacent conifer and N-fixing red alder stands. Van Miegroet and Cole (1984) estimated that nitrate leaching removed about 50 kg N ha^{-1} yr^{-1} from a red alder stand, compared to negligible leaching from an adjacent Douglas-fir. High nitrate leaching led to high leaching losses of nutrient cations. Homann et al. (1992) estimated that Ca losses were about 5 kg ha^{-1} yr^{-1} from the Douglas-fir stand, compared with 40 kg ha^{-1} yr^{-1} from the red alder stand. Despite the high losses from the alder stand, the pool of exchangeable Ca was not depleted. Mineral weathering must have kept pace with the leaching losses.

Binkley et al. (1992c) examined N losses from two pairs of conifer and conifer/alder stands. On a poor site, they found about 5 kg ha^{-1} yr^{-1} of N loss from the conifer stand compared with 26 kg ha^{-1} yr^{-1} of N loss from the conifer/alder stand. Dissolved-organic N accounted for about 80% of the loss. On a more fertile site, the conifer stand lost 21 kg ha^{-1} yr^{-1} and the conifer/alder stand lost 50 kg ha^{-1} yr^{-1}.

One could hypothesise that denitrification might be particularly high on alder sites with high supplies of water, C and nitrate, but denitrification rates appeared to be negligible in these sites.

Some fascinating types of feedback could exist among soil nutrient supply, litter quality, subsequent nutrient supply, and nutrient losses from soils. Unfortunately, current information is so limited that only speculation and computer simulation are possible.

Conclusions

Understanding of the effects of tree species on forest soils has been heavily clouded by premature inferences based on limited information and by unwarranted extrapolation from these inferences. A person who 'knows' that spruce degrades soils may be unlikely to develop experiments to test this possibility. Confusion has also resulted from use of vague terms like 'degradation'. If soils under spruce have more organic matter but a lower pH, is the net effect good or bad? Species clearly have different effects on soils, and these effects span the gamut from nutrient pool sizes to acidity to nutrient supply rates. No study has shown that any species uniformly pushes all soil variables in unfavourable directions.

Classic expectations that forest floor structure and turnover should be good indicators of soil fertility are logical and appealing. Greater accumulation of undecomposed litter would logically seem to indicate low fertility. However, common-garden plantations have clearly contravened this expectation for species compared on the same site. Open questions about forest floor structure and turnover remain. For example, would the manipulation of the soil community (such as the addition or removal of earthworms) emphasise the connection between forest floors and site fertility?

Several other major questions remain, all of which are amenable to experimentation:

1. Can a species lower soil fertility to the point that a second generation of the same or a different species will be less productive? Many people have discussed declines in soil fertility in response to monoculture plantations, but all available evidence seems to indicate that any decline in later rotations results from poor management (such as compaction, fire, nutrient removal in biomass, and weed competition) rather than any species effect *per se* (cf Will 1984, Innes 1993). Despite a total lack of evidence of substantial soil degradation by species, this remains a viable hypothesis that should receive more testing. In particular, areas formerly under a particular species should be replanted to a variety of species, with manipulations designed to test hypothesised mechanisms of soil degradation (cation supply, acidity, N availability).

2. To what extent do soil communities differ under different tree species? How does the composition of the soil community relate to overall soil biogeochemistry? How malleable are the composition and functioning of the soil community? For example, Binkley *et al.* (1992b) documented major differences in replicated plots with *Eucalyptus*, *Albizia* or mixtures of the species, and attributed the effects to higher litter quality in the presence of the N-fixing *Albizia*. However, Zou (1993) found such large differences in earthworm biomass among the plots that the improved nutrient cycling under the influence of *Albizia* may have resulted from the palatability of *Albizia* litter to worms, with the worm activity being the proximal cause of increased nutrient cycling. How different would the tree species effects have been if the (exotic) earthworms were absent? A host of creative experiments are waiting to be done, where one or a few features of the soil community are varied to examine the direct mechanisms that result in the observed effects of tree species on soils.

3. Do some forests experience 'occult' inputs of N that may exceed 30 kg ha^{-1} yr^{-1} and, if so, what is the source? It is tempting to conclude that the components of N cycles in forests are very well known, with few surprises remaining. Most scientists assume that N inputs are relatively well characterised, even under polluted conditions. However, isolated studies continue to point toward unexplained increases in forest N content. This occult N could be an artefact of measurement approaches. If real, the unexplained N must come from unexamined pools (such as subsoils), from poorly measured but well-understood processes (such as nonsymbiotic N-fixation) or from an unknown process (although this may be unlikely).

4. How important are understorey species in determining the overall effect of an overstorey species? In many cases, differences in resource use among overstorey species leads to differences in the composition of the understorey community. Often, too, the contributions of the understorey may match or exceed those of the overstorey. At present, no common-garden experiments with overstorey species have manipulated the understorey species. It is time to begin such experiments.

5. How far does the influence of one species extend into an adjacent area of another species? This question is important for the ecotones between stands of different species, and for the mosaic of effects of each species in mixed-species stands. Studies which focus on sampling transects across the boundaries between plots in existing common-garden experiments (cf Rhoades and Binkley 1992) could provide insight into this issue very soon.

6. How important is the input and decomposition of woody materials in the long-term effect of species on soils? All of the common-

garden experiments described here use sites that are too young for woody litter to have had much effect on the soils. Would increasing amounts of woody litter in the future substantially alter the patterns that have developed from non-woody inputs?

Our best insights about the effects of species on soils have come from plantations that our predecessors established decades ago. The answers to the questions posed above (and others) will require a new generation of more extensive, replicated plantations of tree species in monoculture and in combination, with a variety of treatments that manipulate the soil communities. Some creative approaches may depend on integrating such research into normal forestry operations. Research budgets may be too small or too short-term in focus to cover the expense and time of such plantations, but collaborations with colleagues in operational forestry may cover some of the costs of plantation establishment as part of normal operations. This approach might also facilitate replication of studies on a variety of site types, and this level of replication is sorely lacking in current common gardens. Research funds could be invested as they come available, perhaps waiting until the next generation of forest soil scientists begins looking for sites to answer questions we have not imagined.

Addendum

Eriksson and Rosen (1994) examined the influence of four species on the chemistry of a Typic Dystrochrept soil in southwestern Sweden: silver fir (*Abies alba* Mill.), grand fir (*Abies grandis* (Lindl.)), Norway spruce (*Picea abies* (L.) Karst.) and Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Endl.). The experiment included a randomised block design, with three blocks and nine species (the other five species were not sampled in this study), with 400-m^2

plots. At 35 years, the grand fir plots had the greatest volume (470 m^3/ha) and silver fir the least (175 m^3/ha); larch (375 m^3/ha) and Norway spruce (340 m^3/ha) were similar. The plots had been thinned three times, with the most recent thinning just 2 years before soil sampling. The intensity of thinning varied across species, influencing both the current volume and the number of stems per hectare. Only boles were removed, with slash left on-site. The understorey composition and biomass differed substantially, with a dense sward of grass under larch (and some naturally regenerated hardwood trees), and almost no vegetation under the firs and spruce. The forest floor of the larch plots averaged 86 Mg/ha (based on 20 samples per plot, and three plots per species), compared with about 70 Mg/ha for the other three species. The mineral soil of 0-15 cm depth also had more organic matter under larch (87 Mg/ha) than under the other species (about 75 Mg/ha). Only minor differences in pH of the forest floor and mineral soil were evident. The mineral soil under larch had the highest pH (5.2, compared with 4.9 to 5.0 for the other species), and the lowest base saturation (18%, compared with 21% to 29% for the other species). Declines in base saturation should reduce pH, unless the acid strength of the soil organic matter decreased. Therefore, the higher pH under larch, coupled with the significantly lower base saturation, indicated that the organic matter accumulated under larch probably had a weaker acid strength than the organic matter under the other species. The largest soil difference among the species was in the N and C content of the 15- to 95-cm depth soil. Only one pit per plot was sampled in the deeper soil, and the significance of the differences among species was not discussed. In this depth interval, the larch plots had only half as much N and organic matter as the silver fir, a difference of about 1.6 Mg N/ha, and 55

Mg organic matter/ha. These rates of divergence between the species (45 kg N ha^{-1} yr^{-1}, and 1.6 Mg organic matter ha^{-1} yr^{-1}) appear very high, so the one pit per plot may have been inadequate for characterising the effects of species in the deeper soil.

Acknowledgments

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