

## Chapter (non-refereed)

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# What are the effects of trees on soils?

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## 1 Introduction

This paper discusses the tendency for conifers and hardwoods to cause contrasting changes in certain soil properties, and the consequences of these changes for tree growth and for the composition of the field layer, and points out where knowledge is lacking. Because of a dearth of studies in the Scottish uplands, most data quoted will be from sites with similar soils elsewhere in Europe.

All plants influence soil properties, but trees tend to have greater effects than other plant life forms because of their size and longevity. Trees have many direct and indirect effects on the physical, chemical and biological properties of soils. For example, root channels increase soil aeration and drainage, and allow downward mixing of soil particles, while the root mat as a whole inhibits particle erosion by wind and water, and downhill movements of soil. Plant litter and exudates, and animal wastes and corpses are incorporated, with at least two-thirds of the total litter input coming from death of fine roots and mycorrhizas (Persson 1978; Fogel 1980; Ulrich *et al.* 1981). These organic inputs are the energy and carbon source for a great variety of soil-living animals, fungi and micro-organisms that *inter alia* mediate the recycling of mineral nutrients, and thus sustain soil productivity. The litter of different species can vary markedly in content of mineral nutrients and of organic chemicals that influence litter palatability and decomposability (Zonn 1954; Tuszyński 1972; Swift *et al.* 1979). Such variations influence rates of nutrient cycling directly, and also indirectly by causing changes in the populations of decomposer organisms. Different tree species also vary in the degree to which they modify the chemical composition and acidity of rain dripping off their leaves or canalized as stemflow (Ernst 1978).

These and other effects of trees can produce marked changes in soil properties. This paper discusses certain of these changes, but consideration of the mechanisms of change is beyond its scope.

## 2 Effects on soil properties

There is a large but confused literature on the effects of trees on soils. Frequently, the reported effects of particular species are apparently contradicted by contrasting effects noted by other authors at other places. There are 2 main reasons for this confusion. First, many published studies, especially the earlier ones, are seriously flawed (Holmsgaard *et al.* 1961; Stone 1975). They were based on contemporaneous observations of soil under different forest patches, and depended on key assumptions that were never tested,

in particular the supposition of inherent soil homogeneity under the different patches. Second, most studies have dealt with a few isolated examples, so that species, and also provenance, age of stand, soil conditions and past management, insofar as they are precisely stated, vary greatly. Direct comparison between different studies is therefore commonly invalid. However, despite the confusion, certain generalities can be inferred, in particular that effects vary with differing soil type and soil parent material, and vary during the life cycle of the tree stand. Also, there is a tendency for coniferous species to have contrasting effects to broadleaved species, especially on poorly buffered soils.

### 2.1 Effects of soil

The amount and rate of change of particular plant-dependent soil properties by particular species can vary greatly from site to site (Wittich 1972; Howard & Howard 1984), depending in particular on the nature and degree of weathering of the soil minerals (Saly 1965, 1980; Miles 1986). Freshly exposed surfaces weather rapidly. The surface pH of unvegetated avalanche debris on Mt Rainier fell from 8.7 to 6.7 in only 3 years (Bollen *et al.* 1969), while the surface pH of a glacial till in south-east Alaska fell in 20 years from 8.2 to 7.0 under a moss cover, and to 6.8 under grey alder (*Alnus incana*). In contrast, when Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), both species commonly associated with soil acidification, were planted in place of natural stands of beech (*Fagus sylvatica*) and oak (*Quercus robur*, *Q. petraea*) on soils exposed for at least 10 000 years in Europe, pH reductions of only 0.1–1.0 unit occurred in up to 100 years (Miles 1978). Non-calcareous soils with little clay are poorly buffered, and change faster than well-buffered soils. For example, in nutrient-poor sands, the early signs of podzolization may be visible within 100–150 years (Tamm 1920; Ball & Williams 1974), whereas clay soils exposed 10 000 years ago in Britain show no visible signs, and would not be expected to do so.

In upland Scotland, poorly buffered, siliceous soils predominate. Those that are intrinsically freely drained are most susceptible to change. Those that are poorly drained, either intrinsically or because an ironpan (Bf horizon) has developed, show only superficial changes during the lifespan of a tree stand. Peat, which covers almost 11% of Scotland (Jowsey 1973) when defined as a surface organic layer more than 30–40 cm thick, changes most markedly in physical properties, at least during the first tree crop. After afforestation, blanket peat dries progressively and irreversibly, and large

shrinkage cracks can occur (Binns 1959; Boggie & Miller 1976; Pyatt & Craven 1979). All these cases have been reported under lodgepole pine (*Pinus contorta*), which has been used as the pioneer crop, but it seems likely that other species would have similar effects if they could be established. Base saturation and pH have been shown to have decreased under stands of lodgepole pine from 16 to 47 years old (Williams *et al.* 1978), apparently as a result of greater decomposition of the peat as it dried out, leading to a higher cation exchange capacity, thus diluting the base cations present and lowering pH. Again, therefore, any tree species would be expected to have the same effect, provided that the peat dried to a similar degree.

#### 2.2 Effects of conifers compared with broadleaved species

Many studies have now shown that, on susceptible soils, conifers tend to promote more surface organic matter accumulation, greater acidity, and a higher degree of podzolization than broadleaved species, with consequential decreases in base saturation and bulk density, an increase in infiltration capacity, and a repositioning within the profile of organically bound nitrogen and phosphorus. This tendency is well exemplified by Ovington's (1953, 1954) data from Abbotswood (Table 1). There, the amounts of surface organic matter and organically bound nitrogen accumulated under conifers 38 to 46 years old were up to 9 and 7 times greater respectively than under broadleaved species, and topsoil pH was up to 1.3 units less. There was, however, an overlap between the responses of the 2 classes, a feature found by Ovington under experimental planting at 2 other sites, and indeed by other workers generally.

Because of its importance as a timber tree in continental Europe, the effects of Norway spruce on the soil have been widely studied. Published reports from at least 10 countries have shown that on poorly buffered soils this species acidifies the surface soil (Table 2) and causes or accelerates podzolization (Miles 1985). However, these effects are only tendencies, albeit strong ones, and are not always found. Thus, Gennsler

Table 1. Dry weight and nitrogen content ( $\text{t ha}^{-1}$ ) of surface organic matter, and pH in the top 5 cm of mineral soil in a coarse sandy loam, 38–46 years after planting a range of tree species on a former mixed oak/beech woodland site at Abbotswood, Forest of Dean (source: Ovington 1953, 1954)

	Dry weight	Nitrogen content	pH
European larch ( <i>Larix decidua</i> )	0.59	35	4.1
Norway spruce ( <i>Picea abies</i> )	0.44	26	4.0
Corsican pine ( <i>Pinus nigra</i> var. <i>maritima</i> )	0.27	22	4.1
Scots pine ( <i>Pinus sylvestris</i> )	0.19	13	4.0
Beech ( <i>Fagus sylvatica</i> )	0.18	11	4.7
Douglas fir ( <i>Pseudotsuga menziesii</i> )	0.12	8.3	4.6
Sweet chestnut ( <i>Castanea sativa</i> )	0.08	4.1	5.2
Pedunculata oak ( <i>Quercus robur</i> )	0.07	3.7	5.3

Table 2. Increased acidity of natural beech and oak woodland soils after planting Norway spruce and Scots pine (source: Miles 1978)

Country of observation	pH decrease after planting spruce or pine (increased acidity)
i. Norway spruce	
South Sweden	0.4
North-west Germany	0.2–0.5
South-west Germany	0.1–0.8
South-east Germany	0.3
Czechoslovakia	0 –0.9
Czechoslovakia	0.3–1.0
Czechoslovakia	0.2–0.5
West Yugoslavia	0.3–0.8
West Rumania	0.3–0.7
ii. Scots pine	
East Scotland	0.2–0.7
Czechoslovakia	0.5

(1959) found no signs of podzolization after 250 years of spruce culture in the Harz Mountains, though he did record surface acidification, while Saly and Obr (1965) recorded one instance where the pH of the surface soil under planted spruce in Czechoslovakia had increased to 4.2 from a value of 3.9 under the natural beechwood. Variations in these effects reflect varying degrees of soil buffering.

Conifers growing at similar rates to broadleaved species produce similar amounts of litter, at least above ground (Miller 1984). The tendency for greater surface accumulation of organic matter under conifers reflects different decomposition systems from those usual under broadleaves. Decomposition is often slower, but also results in a positional change of organic matter within the soil profile (Nihlgard 1971). Litter is typically comminuted very quickly by earthworms and other soil-living animals under broadleaved stands, and mixed into the mineral horizons (as 'mull' humus) where it continues to decay. Conifer litter, in contrast, tends to lie on the soil surface for many years (as 'mor' humus), being slowly degraded by microbial decay before comminution and soil mixing occurs. One reason is that conifer litter tends to be more acid and to have a higher tannin content, which makes it less palatable to earthworms and other consumers of litter (Satchell 1967).

The soil acidification, surface organic matter accumulations and other associated changes in labile soil properties caused by conifers, or similar changes caused by heather (*Calluna vulgaris*), can be reversed if the decomposition system switches to mull production following a change in the predominant plant cover. Such opposite changes can occur when the main cover is of 'warty' (*Betula pendula*) or 'downy' (*B. pubescens*) birch (Miles & Young 1980; Miles 1981), aspen (*Populus tremula*) (Frank & Borchgrevink 1982) or holly (*Ilex aquifolium*) (Dimpleby & Gill 1955; Malcolm 1957), or, in the absence of trees, under

bracken (*Pteridium aquilinum*) and well-grazed bent/fescue (*Agrostis/Festuca*) grasslands (Miles 1985).

Many other broadleaved species would probably have similar effects to birch, aspen and holly, if they were established on soils where conifer- or heather-induced changes had occurred. They seem to have no features not also found in other broadleaved species, apart from their ability to establish abundantly on poor soils. However, other species that might do this are not planted in such sites, either because they would fail or grow only poorly (eg elms (*Ulmus* spp.) or limes (*Tilia* spp.)), or because they are negligible timber producers (eg rowan (*Sorbus aucuparia*)), or both (eg hazel (*Corylus avellana*)). Oak and beech probably cannot reverse soil changes induced by conifers, except perhaps on less base-poor soils. Although mull soils can be found under natural stands of both, so can mor soils and shallow podzols (Kubienna 1953; Dimpleby & Gill 1955; Mackney 1961; Bublinec 1973). The pedogenic influence of oak and beech seems to lie about midway between the contrasting effects of birch and Norway spruce. It is likely that the nature of the field layer under oak and beech often determines in which direction the soil develops. Herbaceous swards push the system towards mull formation, but abundant bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea*) and, if the tree canopy is fairly open, heather, drive the system towards mor formation (ie

acidification, surface organic matter accumulation, etc). Indeed, Låg (1959, 1971) has suggested that, in Norwegian forests, the composition of the field layer is more important than that of the tree stand in determining the direction of soil development.

### 2.3 Influence of stand age

Soil properties which result from continued plant growth tend to change in a cyclic way during the life of a tree stand. This change was demonstrated graphically by Page (1968) for Sitka spruce (*Picea sitchensis*), Douglas fir (*Pseudotsuga menziesii*) and Japanese larch (*Larix leptolepis*) growing in north Wales. As stands developed, topsoil pH gradually decreased and surface organic matter increased. These changes peaked after canopy closure, when litter input was at a maximum, and when litter decay was slowest, because of relatively cool and dry conditions at the soil surface (because of the heat-insulating effects of the canopy, with maximal rainfall interception by the canopy and evapotranspiration losses). Later, as stands underwent management thinning (or natural self-thinning), and then selective or clearfelling (or ageing and death naturally), pH and organic matter at the surface tended to return to their original values (Figure 1). These cyclic trends have been confirmed elsewhere, notably in Newfoundland (Page 1974). The change in soil pH under birch shows exactly the opposite trend, reaching its peak when the input of readily decomposable birch litter is greatest, but when moisture and temperature conditions at the soil surface are still favourable for rapid decomposition because of the different canopy structure.

However, not all plant-dependent soil properties change cyclically during the life of a stand, in particular the horizon differentiation resulting from podzolization. Although the rate of podzolization is increased under many conifers on susceptible soils (Miles 1985), and probably changes cyclically, the results of podzolization are cumulative and stable. The depth of the eluviated horizon in podzols in north Wales planted with Sitka spruce increased steadily as the stands aged (Page 1968). Similar results were obtained from Swedish forests (Troedsson 1972).

Once a podzol profile has developed, it can only be obliterated by mechanical mixing of the horizons. The uprooting of trees in gales causes partial or complete inversion of the upper horizons (Stephens 1956; Stone 1975), and, in areas prone to windthrow, the uprooting will have retarded podzol profile differentiation (Armson & Fessenden 1973). Biological activity in soils constantly mixes particles (Hole 1981), with ants and earthworms being particularly important. When biological mixing is sufficiently intense, effective depodzolization can occur (Lyford 1963; Langmaid 1964). The reported depodzolization under birch (Tamm 1932; Dimpleby 1952; Miles 1981) and herbaceous vegetation (Miles 1985) was probably because of biological soil mixing.

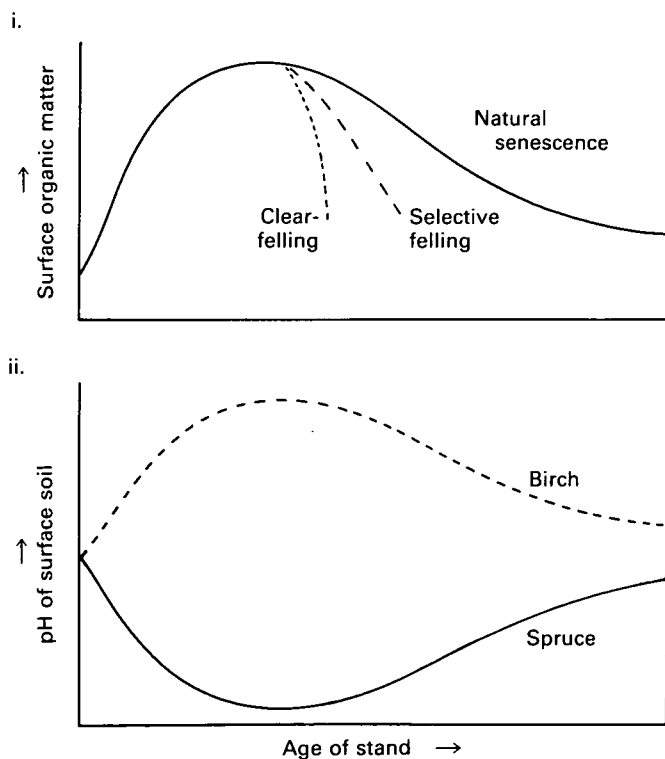


Figure 1. Generalized sequence of change (i) in amounts of surface organic matter under spruce, and (ii) in topsoil pH under birch and spruce, on well-drained, poorly buffered soils (source: Page 1968; Miles 1981)

### 3 Consequences for the field layer

Progressive changes in the composition of the field layer occur during the life of a forest stand, whether the stand arose after disturbance in old forest (MacLean & Wein 1977; Brakenhielm & Persson 1980) or replaced moorland (Hill 1979; Miles 1981; Sakura *et al.* 1985), blanket peat (Doyle & Moore 1982) or farmland (Brakenhielm 1977). Table 3 summarizes the changes in species richness of the field layer between an old Scots pine plantation and part of it that was felled 20 years before and colonized by birch. Soil under the birch stand was significantly less acid (pH 4.4 compared with 3.8 under the pine) and had mull-like humus, whereas under the pine there was mor. Many more species grew under the birch than under the pine stands, while half those under the birchwood did not grow under the pine. The extent to which the changed

Table 3. Changing numbers of field layer species found under an old Scots pine plantation and an adjacent stand of silver birch, established naturally after felling of pine on Dinnet Moor, Aberdeenshire (source: original data)

	89-year-old Scots pine	18-year-old silver birch
Number of vascular species present as growing plants	14	20
*Total number of vascular species present	15	25
Number of pinewood species absent from the birchwood	5	—
Number of species present in the birchwood not occurring in the pinewood	—	11
Number of bryophytes present	5	12
Number of pinewood bryophytes absent from the birchwood	2	—
Number of birchwood bryophytes absent from the pinewood	—	9

\*Includes species present only as buried viable seed, which is an important part of any flora

soil conditions were responsible for these differences in the field layer is unclear. Differential shading by tree canopies and competition, particularly for nutrients, do cause change in themselves (Miles 1979), but are confounded with the effects of changing soil conditions. However, soil changes of this order do facilitate the succession in the field layer. For example, Table 4 shows the result of experimentally sowing seeds of a variety of field layer species on moorland and in adjacent successional birch stands of different ages near Advie, Morayshire, where a gradient of soil conditions also existed (Miles 1981). It shows a sequence of species progressively able to establish as the soil changed towards mull conditions.

### 4 Consequences for the trees

The trends of soil change under conifers and under broadleaved species generally would, in an agricultural context, be considered as degradation and improvement respectively. Is there any evidence that such soil

Table 4. Presence of species established 2 years after sowing seed experimentally on bared ground in heather moorland and adjacent successional silver birch stands of different ages near Advie, Morayshire. Brackets indicate that young plants were weak and unhealthy-looking (source: original data)

	Heather		Birch		
			20 years	28 years	40 years
<i>Calluna vulgaris</i>	+	+	+	+	+
<i>Deschampsia flexuosa</i>	+	+	+	+	+
<i>Luzula sylvatica</i>	+	+	+	+	+
<i>Festuca rubra</i>	(+)	+	+	+	+
<i>Holcus lanatus</i>	(+)	(+)	+	+	+
<i>Galium saxatile</i>		(+)	+	+	+
<i>Rumex acetosa</i>		(+)	+	+	+
<i>Ranunculus acris</i>				(+)	+
<i>Rubus idaeus</i>				(+)	+
<i>Geranium sylvaticum</i>					+
<i>Primula vulgaris</i>					+
<i>Prunella vulgaris</i>					+
<i>Viola riviniana</i>					+

changes materially alter tree growth and actual or potential yields of timber? At present, the answer is a qualified 'no', although a more accurate response might be 'answer unknown' because little critical work has been done in this field.

It has often been claimed that deleterious soil changes under conifers cause losses in yield (eg Noirfalise 1968). Certainly, over large areas of Europe, conifers, especially Norway spruce in continental Europe and Sitka spruce in Britain, have been planted in the place of natural broadleaved forest (or, in Britain, on land formerly under broadleaved forest), and many of these soils are showing surface acidification and accelerated podzolization. For example, Marzhan (1959) has estimated that up to 400 kha are podzolizing in Czechoslovakia under Norway spruce and Scots pine. However, early claims about yield depletion as a result of soil change have been shown to be confounded with problems of disease, lack of wind-firmness on surface-water gley soils (an inherent soil property rather than one caused by conifers) and nutrient depletion from litter gathering and sod cutting by peasants (Jones 1965; Stone 1975). Critical studies of the growth and yield of second compared with first generation crops of Norway spruce in Germany and Denmark failed to detect any decreases in yield (Gennsler 1959; Holmsgaard *et al.* 1961; Hausser 1964). Indeed, Hausser (1964) found that the second generation stand grew better than the first. Conversely, tree ring analysis at the birch site near Advie discussed earlier showed that the birch stands there did not apparently grow better as the soils changed from mor- to mull-forming conditions.

The only other direct evidence for progressive yield decline in conifers is Siren's (1955) report that, when Norway spruce established after forest fire in northern Finland, soil changes occurred that slowed down growth of the next generation of trees. However, soil

and climatic conditions there were poorer than at the natural broadleaved woodland sites discussed earlier. The site naturally bore spruce, and lies within the circumboreal zone in which periodic lightning fires are an intrinsic part of the ecosystem. There is evidence that under these conditions periodic fire is needed to maintain high rates of nutrient cycling (Viro 1974).

How do the Scottish uplands fit in the context of the central European situation, where evidence for an effect of conifer-induced soil changes on subsequent growth is lacking, and of the more plausible evidence from Finland that such feedback occurs there? Like Finland, the Highlands are naturally part of the fire-dependent circumboreal forest zone. They have soils mostly formed from base-poor Precambrian rocks, and may therefore be expected to behave similarly. The southern upland soils are derived from more base-rich Silurian and Ordovician sediments, and on freely drained ground are mostly unpodzolized (Muir 1956; Ragg 1960). They are probably more akin to those of central Europe, and feedback effects on tree growth are less likely.

The Finnish hypothesis is that nutrients become immobilized in the progressively thickening layer of surface organic matter, and that this mat inhibits seedling establishment, while growth of the existing trees slows down. A pronounced reduction in the growth of a second generation is unlikely to occur in Scotland because most coniferous forests are regenerated by ploughing and replanting. Ploughing breaks up the surface mat, accelerating its decay and the mobilization of the organically bound nutrients, and also brings relatively unweathered soil minerals to the surface. Only if the proportion of forests being restocked by natural regeneration without site preparative treatments were to increase, might nutrient immobilization become more of a problem. Further, Sitka spruce, the main commercially grown species in the uplands, is adapted to growing on deep surface organic layers, and commonly regenerates on rotting logs within its natural range (Gregory 1960; Franklin & Dyrness 1969). It is thus likely to be relatively uninfluenced by changes in the mineral soil horizons.

Nevertheless, because podzols are normally associated with poorer growth in volume of trees, even of species adapted to such conditions, than unpodzolized soils with mull humus (Låg 1962; Pyatt 1970; Page 1971), concern about the possible effects of podzolization and soil acidification is legitimate. In New England soil pH has been used as an indicator of potential tree growth (Stratton & Struchtemeyer 1968; Mader 1976), while soil pH is closely correlated with the growth of many apple varieties (Kotze & Joubert 1980; Hoyt & Nielsen 1985). However, a confounding factor in Scotland is that most forests have been established on land which was deforested centuries or even millennia ago, when soils were biologically and physically very different from the forest soils of today (Miles 1985).

Differences in many soil properties resulting from past land use can profoundly influence tree growth (Van Goor 1954; Armson 1959; Skinner & Attiwill 1981a, b). Most existing soils are therefore not valid baselines against which to judge change.

The faster rates of decomposition and nutrient release associated with mull-forming birch stands do increase the growth of herbaceous plants in bioassay trials. Table 5 gives an example from the old Scots pine stand and the succeeding birch stand discussed in Table 3. Although there is no evidence as yet that the

Table 5. Mean dry weight (mg) of 8-week-old test plants grown in a glasshouse in soil from an old Scots pine plantation and an adjacent stand of silver birch, established naturally after felling of pine, on Dinnet Moor, Aberdeenshire (source: original data)

	89-year-old Scots pine	18-year-old silver birch	LSD at 5% level
<i>Rumex acetosa</i> (shoots)	2.9	18	14
<i>Luzula sylvatica</i> (shoots)	7.4	26	13
<i>Raphanus</i> spp. (shoots)	10	43	15
(roots)	4.5	53	36

birches respond similarly, the question has often been put: 'would an admixture of birch or similarly behaving broadleaved species benefit the growth of conifers?' There have been claims to this effect (Shumakov 1958; Kovalev 1969; Blintsov 1971; Prudic 1972), but the supporting data are unconvincing. However, more recently, admixtures of Scots pine, lodgepole pine and Japanese larch with Sitka spruce have been shown to increase growth of the spruce (O'Carroll 1978; McIntosh & Tabbush 1981; McIntosh 1983), apparently by increasing nitrogen availability. Similarly, Brown and Harrison (1983) reported that the mean height of 25-year-old Norway spruce in an experiment in the Gisburn Forest in the north-west Pennines was 9 m in pure stands, 10 m with a 50% mixture of alder (*Alnus glutinosa*), and 11 m with a 50% mixture of Scots pine.

The processes underlying these effects are not known. The soils at Gisburn are surface-water gleys, and are thus not susceptible to major change to any depth. Brown and Harrison (1983) estimated that earthworm biomass was doubled under the spruce/alder mixture, and increased 5-fold under the spruce/Scots pine mixture, an unexpected and inexplicable result. Available nitrogen and phosphorus in the soil increased in proportion to the worm biomass, and Brown and Harrison (1983) suggested that increased earthworm activity under the mixtures increased mineralization of nitrogen and phosphorus, so leading to improved tree growth. Earthworms have long been associated with soil productivity (Russel 1910); their presence has stimulated tree growth in pot experiments (Marshall 1971) and forage yield in field experiments (Hopp & Slater 1948; Stockdill 1966, 1982). Unfortunately, the earthworm populations at

Gisburn were estimated using baited traps, so that densities cannot be calculated. However, if it were assumed that each trap attracted only worms within a radius of 1 m, then the worm population under the spruce/Scots pine mixture might consume only 8–12% of the annual litterfall of needles. On this basis, the increased earthworm numbers under the mixtures are more likely to be a result of the increased availability of soil nitrogen and phosphorus than the cause.

One pointer to possible mechanisms is the finding that there was greater exploitation of the soil profile by roots in the spruce/pine mixture at Gisburn, with pine roots occurring below the mainly surface root mat of the spruces (Brown 1986). This phenomenon might lead to a slight lowering of the water table, and hence to higher mineralization rates of nitrogen and phosphorus, and it could also stimulate nitrogen fixation (Richards 1964, 1973; Fisher & Stone 1969).

### 5 Conclusions

There is good evidence that both conifers and broad-leaved tree species can change many soil properties, sometimes markedly, especially on well-drained, poorly buffered sandy soils. Many conifers, especially spruces, seem to accelerate podzolization, and *inter alia* cause surface acidification and organic matter accumulation, though the latter trends reverse to some extent during the life of a stand. In contrast, birch, aspen and probably some other broadleaved species are associated with reduced soil acidity, mull formation and a different soil fauna which may tend to depodzolize soils by physically intermixing the A and B horizons. Soil changes induced by trees significantly affect the composition of the field layer, but as yet there is little evidence that they materially affect the growth of the trees that brought about the changes. There are, however, grounds for suspecting that tree performance of naturally regenerated conifer stands might be affected by acidification and podzolization in the Scottish Highlands, though perhaps not in the usually more base-rich soils of the southern uplands. If there is ever a swing to restocking forests by natural regeneration without ploughing the soil, then this point should be further investigated.

At a more fundamental level, there is still little detailed information about the extent to which different species, and perhaps different genotypes, can alter soil properties when growing on different soil types. Is there a threshold level of soil base status below which mull soils undergo acidification, mor formation and perhaps podzolization, and how does this threshold vary for different species? What is the role of the field layer in promoting mull or mor soils, and what are the pedogenic effects of different field layers in relation to different tree canopies? A degree of acidification can occur by a dilution effect, when increasing surface organic matter increases cation exchange capacity. Profound acidification (excluding pollution effects)

occurs only when the leaching of soil bases exceeds the supply from mineral weathering and from atmospheric inputs. The answers to the questions posed above can only be found through studies of nutrient fluxes.

The old debate about the yield of mixtures compared to that of pure stands has recently been given new emphasis by the finding from various experiments that the growth of Sitka and Norway spruce can be markedly improved by admixtures of other species, conifers as well as hardwoods. This increased growth seems to result from increased availability of nitrogen and phosphorus, but the underlying mechanisms are unknown.

### 6 Summary

On the poorly buffered, sandy soils that predominate in the Scottish Highlands, conifers tend to promote soil acidification, podzolization, and surface accumulations of mor humus. In contrast, broadleaved species tend to reduce soil acidity, to form mull humus, and to have a soil fauna which may depodzolize soils by intermixing the surface horizons. Some of these changes reverse, at least in part, as the tree stands senesce.

Any role of the field layer in helping to bring about such changes is only conjectural, as are the threshold levels of soil base status that permit gross change to occur. Soil changes induced by trees can significantly affect the composition of the field layer. They would be expected to influence the growth of the trees themselves, especially if sites were restocked by natural regeneration without ploughing the soil. Increased growth of spruces grown in mixture with various other species, apparently because of increased availability of nitrogen and phosphorus, has recently been noted in several experiments, but the underlying mechanisms are unknown.

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