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Effects of Species on Nutrient Cycles and Soil Change [and Discussion]

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Effects of species on nutrient cycles and soil change

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The choice of species to be favoured in forest management is subject to several considerations, among them the possibility of adverse effects on site productivity. Information on this possibility is reviewed from three viewpoints: nutrient cycling, soil genesis and classification, and relatively short-term (i.e. within one generation) changes in soil properties and growth rate. Nutrient cycle models describe flows between soil and plant components of ecosystems but generally can reveal little about variation in nutrient supply over the life of a stand. Profound changes in profile characteristics and mineral weathering occur on a time scale of millennia and can scarcely be expected within a single generation of one or another species. Many reported comparisons of species effects on soil profile development, physical structure, or nutrient status are invalid for a variety of reasons, including inadequate perception of inherent soil heterogeneity. Claims of decreased yields resulting from successive generations of conifers are not borne out by recent studies. Finally, maximum changes in soil due to choice of species appear minor in comparison with the mechanical and chemical impacts associated with present day intensive forest management.

A passage from E. M. Crowther's (1953) address, 'The skeptical soil chemist', provides an appropriate preface:

'One of the recurrent troubles in soil science arises from the circumstances that its objectives, methods and findings have to be described and discussed at many different levels of abstraction and thus in many different kinds of language. Forty years ago Sir John Russell...warned us of the dangers: "Illustrations used in farmers' lectures to drive home some important point to an audience before whom lucidity is above all things necessary have acquired the force of established facts; whilst statements and sometimes even substances, have come to be believed in for no better reason than that people have talked a great deal about them."'

The reciprocal influences of soil upon forest and forest upon soil are not easily disentangled, in part because of the long time periods over which these influences act. A unitary view of forest-upon-soil influences is made even more difficult, first, by the limited theoretical framework for understanding soil development (Kline 1973); secondly, by a great abundance of literature dealing with local particulars; and thirdly, by the burden of supposition and lack of rigour that dominates many accounts of soil change in the forestry and ecological literature. The only monograph on this topic is confined to Russian work (Sonn 1960); it intermixes evidence from natural soil–forest associations and plantations, and often makes comparisons within a framework of very broad soil types and of uncertain time spans.

In Britain and much of western Europe, forests are either wholly secondary or greatly modified by man over a period of two to four millennia. For the most part they occupy land that is now marginal or unsuitable for agriculture although a large fraction has been previously

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cropped or pastured, often for very long periods or intermittently. The history of this exploitation is now known in abundant detail (see, for example, Darby 1956). Too often, however, the implications of this history have gone unrecognized or ignored when foresters and ecologists have sought to explain local differences in vegetation or productivity. The soil is an evident source of such differences but the possible explanations and mechanisms are many, and soils are difficult to describe adequately or quantitatively. In consequence, doctrines or generalities that grew up as convenient explanations have continued in use unchallenged. Thus heathlands and the northern coniferous forests have been repeatedly linked together by the fact that both occur on podzols, although the two ecosystems are actually far more unlike than are the European coniferous and deciduous forests. Again, deciduous species, which over the centuries had been encouraged or survived in abundance only on the more fertile soils, became identified as the source or conserver of fertility. Later this designation was reinforced by differences in the composition of litter from coniferous and deciduous species and, often, by evident differences in surface accumulation of organic residues.

It was largely from such premises – not from experiment or comparative growth measurements – that tree species have been designated as 'soil improvers' or otherwise, and their use recommended accordingly. Twenty years ago Ovington summarized the conventional wisdom of previous decades thus: '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 and forestry practice adjusted so as to ameliorate any adverse effects...' (Ovington 1953). Similar beliefs persist today.

Nevertheless, the very definition of soil declares it to be in some measure a product of vegetation, so the significant questions about its responses to forest cover are not whether, but at what rate, how profoundly, and with what consequences. These questions can be examined from three viewpoints, that of nutrient cycling, that of soil genesis and classification, and that of relatively short term changes in soil properties or productivity as reported by foresters and other field biologists.

Nutrient cycling

Foresters' awareness of the circulation of nutrients extends back about a century, when Ebermayer investigated the effect of long continued litter gathering by peasant farmers upon forest productivity. Chemical analyses revealed that the quantities of essential nutrients removed in the litter were large relative to the needs of the forest. During the next half century a fragmentary body of information established the magnitudes of nutrient uptake, storage and return in continental forests. Though not unknown to the English speaking world, these results were given renewed currency by Rennie's (1955) compilation. Combined with Ovington's measurements of nutrient circulation in British forest plantations, and the largely independent Russian studies, they stimulated recent interest in terrestrial nutrient cycles.

The simple nutrient cycle diagrams of the past have given way to more complex models, based on fuller data and additional processes, and providing more satisfying insights. Their value is indicated by the readiness with which we apprehend the significance of new findings, such as atmospheric input of nutrients, accelerated decomposition after forest disturbance, or increased removals through whole-tree harvesting. Even as conceptual devices, however, these models have profound limitations in examining the rate of soil change. Their exactness is limited by sampling accuracy and seasonal variation. The quantities are site specific and differ for each combination of soil, species and stand attributes. Moreover, most nutrient flow models simply invoke quantitative expression of conventional explanations about the nature of the processes involved and the ways of measuring them. Only now is the magnitude of the total underground biomass and its overturn being measured effectively. We lack straightforward chemical measures of the rates at which organically bound, non-exchangeable or slowly soluble nutrients become available for plant uptake over decade-long periods. Understanding of the gains, losses and transformations of fixed nitrogen is completely inadequate to write budgets that balance.

The often-emphasized differences in percentage elemental composition of the litter from various species tell little about the actual amounts removed into biomass and organic layers. Differences in organic productivity, especially on less fertile soils, are so great that sheer mass often overrides percentage differences. This is well demonstrated by Ovington's values for 21- to 22-year-old plantations of 13 species at Bedgebury. The range in amounts of nutrient elements (kg/ha) incorporated in the above-ground stands confounds cumulative growth with inherent differences in composition and the availability of nutrients for uptake:

	minimum	maximum
N	175	1590
P	15	110
K	80	790
Ca	100	640
Mg	20	125

(Ovington 1957, 1959; Ovington & Madgwick 1958).

The maximum amounts are found in some fast-growing conifers; the minimum, at this early age of 21–22 years, in slow-starting deciduous species. Although these are only above-ground totals, they suggest that there are large differences among species both in their net annual draft upon the soil and in their capacity to act as a sink for absorbed nutrients. In natural forests these nutrients would return eventually to the soil. In contrast, some currently proposed harvesting methods would remove almost all of the above-ground accumulation. Thus in the managed forest the consequences of growth rate and harvest removals are likely greatly to outweigh the obvious differences among species in litter composition.

What are the sources of the absorbed nutrients? Several attempts to estimate available soil stores have used determinations of exchangeable or readily extractable contents in the upper 20–50 cm layer – that is, instantaneous values in the zone of intensive rooting. Such use ignores the soil chemistry of elements, especially of potassium and phosphorus, and leads to the often erroneous judgement that soil supplies are modest or small relative to content in the biomass.

Again, the extent of downward root penetration is commonly under-estimated except when wholly confined by limiting layers or revealed by measurement of moisture removal in dry seasons (e.g. Russell 1973). There is, however, only meagre evidence concerning nutrient uptake by the sparse root net found at depth, and for this reason estimates of soil supply tend to consider only the uppermost layers. The shortcoming of such restriction is suggested by

Rennie's (1962) account of changes in *total* soil calcium in the upper 50 cm layer of heathland afforested some 80 years previously:

	soil calcium/kg ha^{-1}		
		afforested	
soil depth/cm	control: *Calluna*	*Pinus sylvestris*	*Quercus petraea*
0–30	145	547	730
30–50	795	632	489
sum	940	1179	1219
estimated stand content		400	400

(Rennie 1962.)

The apparent gain in the leached upper layers exceeds net loss from the 30–50 cm depth, and is in addition to withdrawal into the biomass. If antecedent variation and differential addition are precluded, the source of these gains must be removal from the soil below 50 cm. The indicated average removal is small (*ca.* 8 kg/year), but significant in terms of cumulative need.

Cumulative net removals, as in the table from Ovington (p. 151), probably provide the best medium-term measure of the soil 'supplying capacity' for bases and phosphorus, unless net atmospheric inputs are high. Weathering of soil minerals and the movement of nutrients from less to more easily extractable forms are often small on an annual basis but significant for accumulating plant systems that minimize leakage from the cycle. Even the coarse-textured forest podzols, so often disparaged as 'leached', release a steady flow of nutrients from susceptible minerals through the intensive weathering process that creates the A_2 horizon. This is illustrated by Tamm & Rodes's (Russell 1973) estimates of loss rates from the A horizon: K, 4–8; Ca, 2–3; Mg, 3–6; Fe, 8–18 kg ha^{-1} year^{-1}.

The cycling of nitrogen is of particular interest, because relatively large amounts are immobilized in vegetation and, conspicuously, in any surface accumulation of organic matter, as well as within soil organic matter. Knowledge of sources, storage pools and transformations of this element in arable soils is abundant, but too often forest nutrient cycles are constructed on the same model with little or no exact information. In fact, knowledge of nitrogen additions, aside from atmospheric contributions, in forests lacking nitrogen-fixing plants is inadequate. With rare exceptions, sampling precision is too low to determine whether the accumulation of nitrogen in biomass and litter of new stands represents any additional fixation, or merely redistribution and strict conservation of existing supplies.

One of the exceptions is the classic Rothamsted 'wilderness' – two small areas of old arable land at Broadbalk and Geescroft allowed to revert to deciduous brush and trees in the 1880s. The Broadbalk soil, which contained free $CaCO_3$ and legumes initially, gained in total nitrogen (to 69 cm depth) at an average rate of 52 kg ha^{-1} year^{-1} up to 1904, and 33 kg/year for the next 60 years. Comparable values for the increasingly more acidic Geescroft soil were 21 and 15 kg/ha (Jenkinson 1970). The source of these additions, apart from 4–5 kg/year in rainfall, is unknown.

Other unknown sources may be significant also. Though it is usually supposed that frequent burning must deplete soil nitrogen, studies in loblolly pine forests in South Carolina show modest but significant nitrogen gains in the upper 10 cm of soils burned annually for 20 years. Two of the investigators have now demonstrated that nitrogen-fixation occurs on some portions of the burned surfaces (Jorgensen & Wells 1971).

Thus significant accrual of nitrogen by non-symbiotic fixation is certainly plausible, although the evidence available thus far is merely illustrative, and does not yet point to differences associated with tree species. We must note that despite recurrent speculation appreciable fixation by coniferous root systems or rhizospheres has not been satisfactorily demonstrated. Nor is fixation suggested by the frequency with which pine and spruce respond to added nitrogen in fertilizer trials. It appears, however, that pine, larch and spruce have some capacity to increase the quantities of nitrogen and phosphorus available for plant uptake, even though total nitrogen content of the soil is not significantly altered (Fisher & Stone 1969). This capacity is displayed soon after these conifers are planted on soils that have been under non-forest vegetation, and seems to diminish after some years. The manifestations of this effect probably account for the initial appearance of fixation.

Thus, despite the conceptual value of present day nutrient cycle diagrams, they are far from providing an exact understanding of the nutrient pools in soil and the varying rates at which they become available to plants.

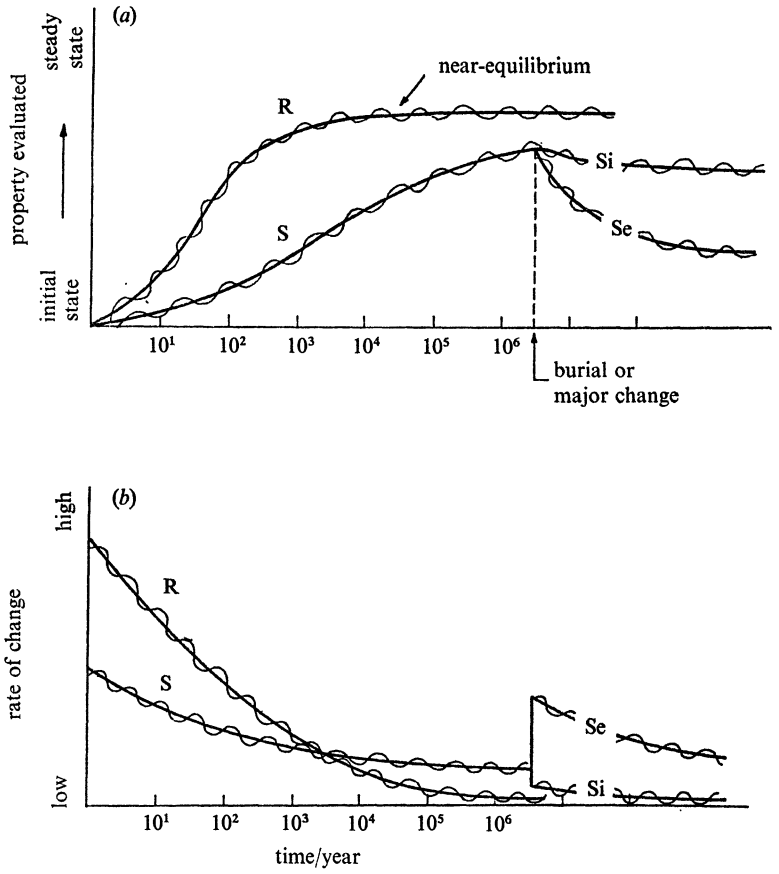

FIGURE 1. Schematic diagram showing soil properties approaching steady state at rapid or slow rate of change. Wavy lines indicate effects due to seasonal or minor fluctuations. If subjected to drastic change in the environment or burial, some acquired features may readjust fairly rapidly (Se), others will remain relatively persistent or irreversible (Si) (Yaalon 1971, Fig. 2). R, rapidly adjusting features; S, slowly adjusting features; i, persistent property; e reversible property.

Soil genesis and classification

As G. W. Dimbleby (1965) mentioned in a similar connexion, development of an apparently 'mature' soil profile on unconsolidated primary materials in this climate requires some 2–4 millenia at least. Development goes faster on previously weathered soil or on deposits consisting chiefly of non-weatherable minerals.

But mature in this sense refers only to attainment of a recognizable and slowly changing gross morphology. It in no way implies that development has ceased. Rather, as Yaalon's schematic diagram (figure 1) indicates, development involves individual properties that change either relatively rapidly or slowly, and reversibly or otherwise. Thus traces of carbonate disappear from the surface of new deposits in a few centuries or much less, whereas in this climate 2 or even 20 millennia suffice to destroy only a small part of the non-carbonate weatherable minerals. In our moderately youthful soils, low total contents of any mineral nutrient are more often the result of initial composition rather than weathering losses. The availability of elements to plants over a span of some decades, however, depends much less on total content than the quantities in slowly replaceable organic or mineral forms. These can be depleted or enriched to some extent, with significant consequences for plants but often without appreciably altering total content, except in the most highly quartzose materials. Low total contents, low rates of weathering or release, and shallow root penetration place sharp limits to what even the most efficient of nutrient cycles might accomplish.

These generalities are well known (Buol, Hole & McCracken 1973). They bear mention only as a perspective from which to appraise claims that particular tree species may have caused major changes in mineral composition or genetic profiles within some brief period, such as a century or less. The probability that such claims are based on valid comparisons seems vanishingly small. Manil (1971), for example, cites an instance in which an old coniferous stand was credited with the formation of a podzolized profile. In fact, the profile was antecedent, and its properties were the reason why the preceding generation of foresters had selected conifers for the site. In other instances the humus podzols characteristic of long occupancy by heath have been mistakenly attributed to the first generation of conifers planted on them.

A second aspect of the soil classification viewpoint is an understanding of soil variability, both coarse- and fine-grained. Most soil landscapes display a greater degree of spatial heterogeneity than generally appreciated in many attempted comparisons of species influence. Variation arises not only from differences in the original materials and slope, but also through differential rates of erosion or deposition and, especially, the consequences of lateral water movement. Map scales of 1:15000 to 1:20000 allow few entities smaller than a hectare or two to be delineated; hence conventional soil mapping represents the larger units but necessarily suppresses detail that cannot be shown conveniently at such scales.

Figure 2 from Lyford (1974) illustrates the fine scale pattern within a 1.6 ha tract of native forest, resulting from moisture regimes on initially uniform glacial till. The range in internal drainage embraces the soils termed pseudogleys in continental Europe. Obviously any realistic examination of the influence of planted species upon soil properties in such a landscape would first have to distinguish the intrinsic pattern of heterogeneity. Some of the soil units are small enough so that even comparisons of soil beneath single trees, as between old oak standards and surrounding spruce (Werner 1958), would not escape the possibility of antecedent differences. I have personally seen instances where soil differences attributed to species were in fact simply those that occur naturally in such a drainage catena, and one can readily infer similar confusion in some published reports.

Perception of natural soil variation also facilitates recognition of features due to man's previous use of land, either recent or in the remote past. Single or successive episodes of cultivation or erosion, with depletion or enrichment can create large differences within short distances, even within the same soil type. Crampton (1970) has provided an illuminating example of the extent and persistence of old cultivation and erosion effects, which might easily be confounded with topography or soil type. Even so, he did not assess the variation in residual soil phosphorus often associated with past habitations of man and his animals.

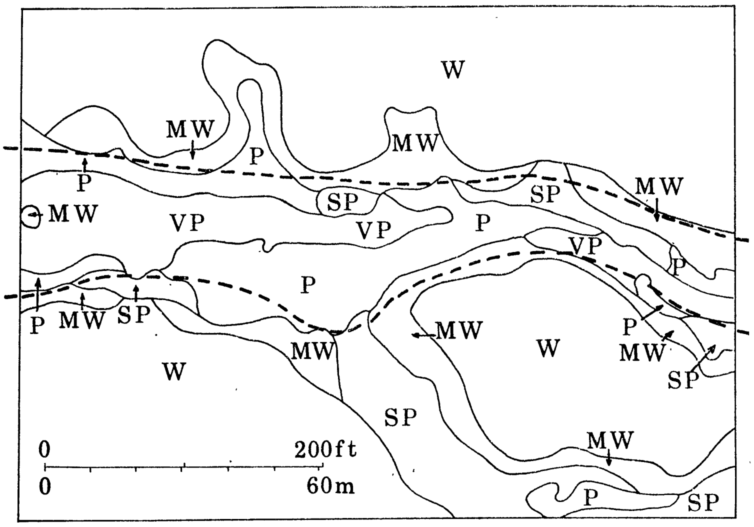

FIGURE 2. Highly detailed soil map of 1.6 ha area of glacial till, made at a scale of 1:300. Letters indicate drainage class: W, well; MW, moderately well; SP, somewhat poor; P, poor; VP, very poor. Dashed lines are the soil boundaries shown on the published soil map (Lyford 1974, Fig. 5).

It is not only prehistoric land use that goes unnoticed. Again at the risk of over-emphasizing personal observation, I have frequently been surprised at European foresters' indifference to many marks of past cultivation, such as plough horizons, field boundary berms and reduction of micro-relief. Too often the evidence of use written so plainly in the soil is ignored in favour of inference from scanty historical records.

SHORT TERM CHANGES

In contrast to the time scale of the pedologists, foresters and ecologists interested in soil changes under forest commonly think in terms of measurable changes within some decades or at most a century or two.

Much of the interest in adverse soil changes stems from the concerns of continental silviculturists faced with managing great areas of planted conifers that had replaced degraded woodlands, heaths, pastures and unprofitable agriculture. Not surprisingly, these plantations encountered numerous biotic and abiotic problems such as beset any new crop. A little noted paper by E. W. Jones (1965) describes how such problems helped shape attitudes towards pure conifers.

Many problems of poor growth, lack of wind-firmness, and difficulties in establishing regeneration after clear-cutting were related to soil factors in some degree. Others were attributed to soil for lack of alternative explanations. Even 40 years ago, foresters' knowledge of soil development and soil variability was decidedly limited. By some transmutation, adverse soil properties found in conifer stands became identified as consequences of the conifers themselves, even though these trees had occupied the land for only a small fraction of the total period of man's use.

It is neither feasible nor particularly instructive to detail the abundant literature on supposed soil changes. Much of the earlier major work has already been reviewed in somewhat devastating fashion by Holmsgaard, Holstener-Jørgensen & Yde-Anderssen (1961). We may dismiss out of hand other reports that simply assume contemporary soil properties to be due to contemporary vegetation, or extrapolate from short-term changes in humus layers or ground flora.

There is a further literature that may command attention at first glance, because it involves paired comparisons of soil beneath unlike vegetation within the same vicinity, or even side by side. Closer inspection shows that few of these comparisons are free of likelihood of sampling bias; few are replicated in location; and almost all simply assume antecedent similarity without examining sources of variation other than the present vegetation. The geologists' principle of 'multiple alternative hypotheses', which applies to many uncontrolled studies in nature, has gone ignored. To this category belongs Dudal's (1953) attribution of soil degradation to a 200-year monoculture of beech, as well as many more superficial studies. In some instances the changes reported as occurring within a few decades are simply physically impossible in terms of weathering rates, e.g. Duchaufour's (1954) account of the decalcification of a rendzina by a deciduous plantation only some decades in age. Thus, the conclusions of such reports must at best be regarded with reserve.

There remains a substantial body of evidence deserving serious attention, although not all of it is free of possible sampling bias. We can briefly summarize and illustrate this evidence under five headings: organic products, moisture relationships, soil porosity, chemical effects, and productivity.

Organic products

As already noted, species differ in foliage characteristics and in the extent to which decomposing organic matter accumulates on, rather than within the soil surface. The organic products from this decomposition, as well as from the foliage materials themselves, have attracted much attention in recent years (e.g. Malcolm & McCracken 1968). It seems not unlikely that such products, notably phenolics, influence nutrient availability and mineral weathering. Thus far, however, their comparative activity, other than as allelochemics, has not been demonstrated under field conditions.

No brief mention can do justice to the general topic of surface organic matter accumulation, which has commanded so much effort and led to such variety of views. It is sufficient here to acknowledge the concern that such accumulations serve as a 'sink' for nutrients, especially nitrogen, returned by the canopy. To the extent that such immobilization is real, it obviously increases annual withdrawal from circulation and may intensify the appearance of nitrogen deficiency on already marginal soils. Concern with possible differences among species in this respect has diminished somewhat as measurement substituted for impressions – often exaggerated – of accumulation, and as studies with fertilizer nitrogen emphasized the complexity of immobilization in both litter and mineral soil.

Moisture relationships

There is no difficulty today in understanding reports of increased soil wetness and the rise of water tables following clear cutting or other reduction of the forest canopy over large areas. In some moist climates continued opening allows excessive growth of mosses which further inhibit forest regeneration and may lead to 'swamping'. Vulnerable areas within a forest can be recognized from landscape position and soil profile characteristics. The problems engendered are not unique as to species, although in Europe at an earlier date they were wrongly identified with conifers because of the greater abundance of conifers on susceptible soils.

The present literature (Sopper & Lull 1967) also provides a rational view of how contrasting species affect the draft on soil water in semi-humid and humid climates. So far as our measures go, transpiration from the familiar deciduous species in full leaf appears to be about equal to that of conifers, provided that both have access to adequate moisture. The evergreen conifers transpire over a longer season than deciduous trees, and interception losses continue throughout the year. Thus, available soil moisture is often reduced earlier under evergreen forests and may average less throughout the growing season, requiring a longer period for recharge. One effect can be shorter duration of, and greater depth to perched ground water tables on ill-drained soils under evergreen than under deciduous species, as Levy (1969) has demonstrated by paired-plot comparisons. These results contradict earlier statements about greater soil saturation under conifers and imply that subsoil aeration should be more rather than less favourable for root development under them. The magnitudes of all of the foregoing differences and their effects are not absolute but depend on rainfall pattern and soil storage capacity. Moreover interception and transpiration are also altered by thinning practices to a degree that can override species differences.

Observations of rooting depth have long been confounded with penetrability of the soils on which different species occur. Thus the reputation of Norway spruce for excessively shallow rooting persists despite studies to the contrary (Kern, Moll & Braun, 1961; Levy 1968) and evidence of moisture uptake from depths greater than a metre (Blume, Munich & Zimmerman 1969).

Soil porosity

Inasmuch as conifers – Norway spruce in particular – are so often alleged to impair soil structure and porosity, it is worth examining evidence on this topic. Again, it will be found that many comparisons confound prior cultivation, erosion or differences in internal drainage with the tree species now present. But one evident difference among species in new afforestations of formerly open land must be acknowledged. Where earthworms are otherwise abundant, species with palatable litter more speedily develop a friable mineral surface that may have more macropore space than that beneath unpalatable species such as pine or spruce. Conceivably such differences may affect infiltration rates in plantations established on eroded surfaces or on those compacted by non-forest use. But this observation must not be generalized more widely: only the surface is markedly influenced; macropore space is already high in some soils being afforested; and an abundant literature demonstrates that surprisingly high macroporosity and infiltration rates characterize the surface layers of almost all native forests, regardless of species and humus type, except as impaired by grazing, fire or compaction. Paired comparisons of soil bulk density beneath spruce and beech (Nihlgård 1971), and of subsoil macroporosity beneath deciduous forests and first and second generations of spruce (Holmsgaard *et al.* 1961), give no support to assertions that spruce causes a 'clogging up' of pore space. Indeed, though the southern German investigators still refer to the surface soil acidity and structure found under spruce as 'degradation', the ill-drained pseudogley condition is now correctly seen as inherent rather than due to spruce (Werner 1964).

Chemical effects

Existing information allows some general forecasts of the direction of initial changes in chemistry of the surface soil when contrasting species are planted on the same soil. Differences in reaction, content of bases and nitrogen, and surface accumulation of organic debris have been reported many times and usually relate in obvious ways to leaf composition, cellulose–lignin ratio and palatability to large soil fauna. Extrapolation of initial trends is hazardous for a number of reasons, not the least of which is the changing canopy density with time, and stabilization of litter accumulations (Page 1968). As already emphasized, differences in percentage composition do not indicate mass transfers. Moreover, it is not unreasonable to view the changes in mineral nutrient composition of soil through the first generation as chiefly positional, an argument put forward by Petch (1965). That is, elements are withdrawn throughout the rooting depth; those not retained in the biomass are returned to the surface layers. Concentration there presumably facilitates reabsorption by trees as well as by shallow-rooted understory vegetation. Microbial processes are presumably influenced also, possibly including nitrogen fixation. But evidence on this point as well as on differential rates of nutrient solubilization, leaching or atmospheric capture is lacking. Without such evidence there is no basis for characterizing one species as more or less 'enriching' than another, except in a figurative sense. So far as we know, both merely retain some fraction of the absorbed nutrients and redistribute the remainder, without altering the total within the rooting profile.

The difficulties in establishing real differences (other than symbiotic nitrogen fixation) among species is illustrated by Nihlgård's (1971) painstaking comparison of the soil beneath 55-year-old spruce, *Picea abies*, and adjacent older beech, *Fagus sylvatica*, forest presumed identical with the starting condition of the spruce. Total and exchangeable contents in metric tons per ha to a depth of 65 cm were calculated:

	N	K		Ca		Mg	
	total	total	exchang.	total	exchang.	total	exchang.
Beech	7.8	120	0.056	112	0.17	23	0.038
Spruce	6.9	130	0.065	136	0.15	23	0.031

(Nihlgård 1971.)

None of the differences can be significant in view of the few profiles and numerous separate analyses involved. The total quantities of bases in only the upper 65 cm are so large that any differences due to half a century of spruce cannot be discerned. On the other hand, the currently exchangeable amounts are far too small to account for the amounts which have been withdrawn into the biomass. Here, as elsewhere, soil analyses tell much more about changes in nutrient concentration, organic matter and reaction in the surface layers than they do about any cumulative change in nutrient availability throughout the exploitable volume.

Since most comparisons only extend over a century or much less, Alban's (1969) observations of soils beneath individual trees of western hemlock, *Tsuga heterophylla*, and western red cedar, *Thuja plicata*, in virgin forests of eastern Washington and Idaho have particular interest. These two species differ in calcium content by a factor of 2.5–4. The hemlock was 4–5 centuries in age and up to 1.5 m d.b.h., whereas the western red cedar ranged to 10 centuries and 2.5 m d.b.h. Only a few profiles were examined (table 1), and at location I at least these were selected to demonstrate maximum differences between the two species. Some of the results from his three locations are shown in table 1.

At the two lower rainfall regimes, calcium content, base saturation and reaction of the upper mineral soil were markedly affected by species. These differences all but disappeared with the high leaching under 230 cm annual precipitation. It is noteworthy that the maximum effect of contrasting species acting uninterruptedly for a minimum of four centuries extended to a depth of about 30 cm. A leached A_2 horizon either developed or persisted despite the high calcium content and only moderate acidity (pH 5.0–5.3) of the cedar organic layer at locations I and II.

Table 1. Differences in exchangeable calcium status and A_2 horizon associated with individual trees of western red cedar and western hemlock (Alban 1969)

	location		
	I	I	III
location and profile characteristics			
precipitation/cm	115	80–100	230–250
A_2, hemlock	strong	weak, sporadic	very strong
A_2, cedar	moderate sporadic	very weak, sporadic	very strong
differences in exchangeable Ca, cedar–hemlock, mmol/100 g			
depth/cm			
0	34	21	0.7
10	10	6	0.4
20	8	4	0.0
30	5	4	−0.3
50	2	1	—

Nitrogen availability is a major factor limiting growth in the many present-day European forests. Hence efforts have been made to stimulate mineralization of acid organic layers by thinning, liming or introduction of species with rapidly decomposing litter, in addition to direct additions by fertilizers or nitrogen-fixing plants. An opposing influence, leaching of bases and soil acidification resulting from leaching of nitrate in excess of plant uptake, has gone unconsidered. Such consequences are revealed by paired comparisons of soils beneath 30- to 40-year-old stands of red alder, *Alnus rubra*, and conifer, largely *Pseudotsuga menziesii*, in coastal Oregon (Franklin *et al.* 1968). In this instance exchangeable soil calcium is lower under alder, although its litter has a higher content than the Douglas fir.

Productivity

An alternative to soil analyses is to examine what if any changes in productivity occur when one species or another is grown for a long period. The question that has troubled European foresters most is whether yields of planted conifers decrease in the second and third generations, apart from obvious factors of root disease or overt nutrient depletion. Assumption and assertion based on past writings remain abundant; unequivocal evidence is difficult to obtain and meager. Nevertheless several modern studies agree in their primary conclusion:

In Holland, Van Goor (1954) examined a series of Scots pine plantations on acid brown podzolic soils previously occupied by poor oak coppice. Yields of second- and third-generation pine stands were lower wherever the soil had been cultivated by deep spading after clearing the oak. In contrast, they were maintained undiminished when the soil had been planted without prior tillage. The decreased yields coincided with reduced total contents of organic matter, nitrogen, and phosphorus in the upper 50 cm of soil. These reductions presumably resulted from accelerated decomposition of organic matter following tillage. A later study of Douglas fir on humus podzols (van Goor 1967) indicated that production of second- and later-generations were somewhat higher than that of the first, except on the driest soils. The improvement was thought to be due to better nitrogen availability.

The most thorough-going analysis of growth in first- and second-generation spruce stands is that by Holmsgaard *et al.* (1961) in Denmark, where spruce is not native. Annual height growth patterns varied markedly with climate, but without consistent differences between generations. The first-generation stands were sited on soils of slightly greater available moisture holding capacity and when allowance was made for this fact volume production by the two generations was almost identical.

Hausser (1964) in southern Germany reached somewhat similar conclusions; growth of second-generation spruce was actually greater than that of the first generation on the few plots for which detailed records were available. He emphasized that the widespread opinion of poorer yields in successive generations of spruce was due not to species but to the cumulative effects of exploitive use, including litter gathering, grazing and intermediate agricultural use. Gennsler's (1959) thoroughgoing studies in the northwest German 'Mittelgebirge' reveal greater acidity and lower base saturation of humus layers under spruce, as expected, but no evidence of declining yields.

Prospect

What conclusions does this sceptical summary suggest about eventual differences in soil productivity arising from the kinds of forests we chose to grow on the lands available?

We need not recapitulate the many changes that occur when arable soils or those under other vegetation are first occupied by any kind of forest. The early rates of change and the initial impact upon the soil surface are clearly species dependent but superficial. Beyond this period, the consequences of choice of species are far less certain, less well documented, and in many ways much less profound than often believed. Concepts of nutrient cycling are more elaborate, more quantified than ever before, but this improvement makes more apparent our ignorance about sources and transfers in the soils, and diminishes the importance that can be attached to surface concentrations alone.

But most of the evidence on which this discussion is based is in a sense obsolete. It assumes that forests are still planted and tended only with minimal physical inputs, as they generally were in the past, and that soils change only through humus layer formation, nutrient cycling, and the alchemy of the selected species. To the extent that real changes due to species can be separated from myth, they prove to be slow or limited in effect (always excepting symbiotic nitrogen-fixation).

In contrast, the impacts of present-day forest management upon the soil are often abrupt, profound, and sometimes brutal: to an ever-increasing degree soils are prepared for planting by drainage, mixing, shaping, herbicide treatments and fertility adjustments that obliterate many previously significant differences in surface properties. Sometimes in the process they are also inadvertently compacted by heavy machinery or laid open to erosion. Such preparation also widens the choice of economic species. Later, the developing stands are subject to spacing and thinning regimes that increase radiation, temperature and moisture at the soil surface more rapidly than in the past, thus hastening decomposition rates. Again, nutrients may be added if warranted by expected responses. Still later, the forest is harvested by a technology that has been undergoing very rapid change. Heavy equipment now reduces labour demand but carries a potential for physical damage to soils and watersheds. Greater removals of small wood – possibly even the entire above-ground crop – increase useful yields but may easily double or treble nutrient losses. Areas on which recreational rather than timber management goals predominate are not immune because decade-long human traffic likewise has a capacity to destroy vegetation and to compact or erode soils. And one can only speculate about how already-troublesome root diseases will respond to these new influences.

Thus our present needs are, first to understand the potential of these new treatments to enhance or degrade soil stability and productivity, and second, to modify or control their application accordingly. To meet these needs requires a more realistic model of the soil system under modern forest management than that presented in most nutrient cycle diagrams.

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Discussion

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I was impressed by your figures for the amount of nutrient returned to the soil from dying roots. With this as a background, do you have any comment on the wisdom of removing whole trees, including roots, in an effort to increase the availability of wood fibre?

E. L. Stone

As a first approach, one could compare the value from greater fibre yield, or lower area harvested, with whatever costs were required to maintain productivity, as through fertilizer additions. Extraction of root systems on a commercial scale, by using heavy equipment in all kinds of weather is another matter. Obviously, it could cause unacceptable soil damage in many situations.