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Nitrogen cycling in United Kingdom forests: the relevance of basic ecological research

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Following recent reviews on nutrient cycling in temperate and British forests, two aspects of N cycling are selected for examination because of their fundamental importance and their relevance to management–ecosystem research and mobilization of N during decomposition.

Despite the early work by J. D. Ovington and P. J. Rennie, only two major forest ecosystem studies have been developed in Britain. Summaries from these ecosystems show that they span the range of temperate forests in the N cycling characteristics. The *Pinus nigra* plantation on Culbin Sands is functioning on a low capital with low rates of transfer and shows N deficiency after 40 years. In contrast, the mixed deciduous Meathop Wood has a much larger capital of N and higher rates of transfer. The *Pinus* ecosystem retained a high proportion of added fertilizer N in the biomass and forest floor, and increased growth rates can be explained through N recycling within the trees.

Basic concepts of N mineralization are reviewed and it is shown that they need to be modified for application to forests. Uptake by saprophytic and mycorrhizal fungi from the pool of soluble organic N can short-circuit the ammonification pathway and N can be released from substrates with a high C:N ratio by lysis of microbial tissues and faunal feeding. Some examples of evidence of these processes are given, stressing the spatial and temporal mosaic of substrates acting as sinks and sources of N. Management practices can have a marked effect, not only on the quantity of N returned in residues, but on its availability as a result of variation in the associated carbon. However, growth experiments have shown that substrates with C:N ratios above 35 can release significant amounts of N to tree seedlings.

A final examination of the recycling processes in the four nutritional stages of a forest emphasizes the importance of the effects of management on the short- and long-term balance of mobilization processes in the forest soil.

1. Introduction

Current understanding of nutrient dynamics in relation to forest management in Britain has been reviewed in Ford *et al.* (eds) (1979), with a wider context of N cycling provided by some excellent papers in Clark & Rosswall (eds) (1981). As a further review is unnecessary, we will examine (i) some results from recent ecosystem studies in the U.K. and their relevance to forestry practice and (ii) the basic processes that are central to N mobilization in decomposing organic matter and their relation to uptake by trees. These aspects are selected because of their relevance to identified problems of nutrient cycling associated with site preparation, fertilization, felling and long-term site fertility (Miller 1979; Malcolm 1979*a*, *b*).

As a background, the state of forestry may be summarized as follows (C.A.S. 1980). The area of high forest in Great Britain is currently about 1.4 Mha conifers and 0.4 Mha broadleaved, with a further 0.3 Mha of coppice and scrub woodland. In recent years the rate of afforestation has been of the order of 20 kha annually, of which 80–85 % has been in Scotland. Forests will expand by about 30 kha annually, possibly more, over the next 20 years, predominantly in Scotland. Much of the planting will be on moorland, but the current rate of restocking, about 6 kha annually, will increase as mature forests are clear-felled.

Much of the earlier planting was on brown earth and gley soils, but future afforestation is likely to be concentrated on deep peats. Sitka spruce (*Picea sitchensis*) will be planted on reforested areas and on the better soils with lodgepole pine (*Pinus contorta*) on the poorer peats, although alternative species and mixtures may be introduced. Site preparation will probably increasingly use deep ploughing, but on reforestation stump planting or planting through branch waste will be used unless more suitable alternatives are found. Thinning may be restricted to minimize wind-throw. Fertilization will be mainly by aerial spraying of phosphates on the better soils and N on the peats, but rising costs may reduce fertilizer use. Clear-felling will continue to be the normal practice for cropping, probably with an increasing proportion of the crop removed from the site, and a reduced rotation time.

2. Forest ecosystems

Ecosystem research has been concerned with compiling energy and nutrient budgets, quantifying the inputs, the transfers within and between components, and outputs. Much of the research has been concentrated on relatively stable, climax ecosystems, with limited analysis of successions or of responses to perturbation because of the large effort required to examine a number of states. A further limitation to interpretation is the critical problem of assessing the accuracy of measurement of component processes individually and in combination. Possibly because of these problems, theory has outstripped the accumulation of hard data, although the reviews of Cole (1981), Cole & Rapp (1981), Gosz (1981), Melillo (1981), Van Cleve & Alexander (1981) and Vitousek (1981) show that a reasonably comprehensive range of forest information is now available, mainly through the International Biological Programme and the interest in watershed management.

In the U.K., despite the initial definition of the ecosystem concept by Tansley (1935), research has not been comprehensive. Early research by Rennie (1955) emphasized that forest-floor organic matter accumulates after moorland afforestation and indicated that the available and reserve nutrients in poor sites may be inadequate to meet the nutrient demand by the forest and the removal in crop. He warned that on such sites conventional forestry would inevitably result in soil degradation and reduced productivity unless adequate practices for soil amelioration were developed. Although much of Rennie's interpretation was based on data for calcium, potassium and phosphorus, he recognized the importance of N.

During the 1950s the intensive studies by Ovington, and his quantitative review of woodland ecosystems (Ovington 1962), provided estimates of the major nutrient characteristics of coniferous and deciduous forests. At that time information was lacking for two of our main commercial species, *Picea sitchensis* and *Pinus contorta*, and from plantations on our nutrient poor upland soils. Despite the strong case made by Rennie and Ovington for more comprehensive research on nutrient dynamics, in an ecosystem context, the only intensive study developed during the 1960s and 1970s to analyse the nutrient structure and function of forest ecosystems in relation to production and management was that on *Pinus nigra* var. *maritima* on the Culbin Sands (Miller *et al.* 1979). However, a second ecosystem study, Meathop Wood, concentrated on a mixed deciduous woodland on Carboniferous limestone in the Lake District and provides comparative information on nutrient dynamics, although not directly related to management (Satchell 1971; Burges 1976).

The summaries of the nitrogen cycles of *Pinus nigra* and Meathop Wood (table 1) mask a wealth of information but serve to raise a number of points.

TABLE 1. A SUMMARY OF THE N CHARACTERISTICS OF AN UNFERTILIZED *PINUS NIGRA* PLANTATION (CULBIN) AND A MIXED DECIDUOUS WOODLAND (MEATHOP WOOD)

(Estimates of compartments are in kilograms N per hectare and transfers in kilograms N per hectare annually. *P. nigra* results are from Miller *et al.* (1979); Meathop Wood results from E. J. White (personal communication).)

	Culbin	Meathop Wood†
input		
precipitation	5	6
N_2 fixation	?	40–100
compartments		
plant biomass	198	934
forest floor	183	165
mineral soil	722	5550
transfers		
plant uptake	21	169
plant recycling	22	67
plant increment	6	24
litter fall	12	97
soil increment	7	25
output		
drainage	0	13

† Note that the results for Meathop Wood supersede the preliminary results quoted in Cole & Rapp (1981).

1. The unfertilized *Pinus nigra* plantation, approximately 40 years after planting on bare sand, is functioning on a very low N capital which is accumulating. Although the amount of N in the original bare sand is unknown, the retained aerial input indicates an accumulation of 5 kg N ha^{-1} annually, and the current increments in tree biomass and forest floor indicate 13 kg N ha^{-1} annually. Growth of the stand was declining, apparently through N immobilization, but fertilizer additions were efficiently retained in the biomass and forest floor and mobilized to increase growth (Miller *et al.* 1979).

2. The mixed-aged stand of *Quercus*, *Fraxinus* and *Corylus* at Meathop Wood has a N capital about six times that at Culbin, and annual transfers are three to eight times higher.

3. The results from individual studies must be treated with caution because the errors attached to the estimates are usually unknown (Satchell *et al.* 1971), but are probably large owing to methodology and site variability. One aspect that is probably systematically underestimated is the N involved in fine roots. Recent studies indicate that the growth and death of fine roots (smaller than 5 mm) can provide a much greater input of N to the forest floor and soil than occurs through above-ground litter (Ågren *et al.* 1980; Melillo 1981; Persson 1980; Staaf & Berg 1977).

4. The estimates of N input, apart from rain, and output, apart from drainage, are very uncertain. Although the evidence for retention of N is strong, balancing of budgets is difficult because the input and output values are small in comparison with the components in the system, and redistribution of N within the system confuses the picture (Cole & Rapp 1981). However, analysis of successional changes indicates rates of accumulation in developing forests of about 5–50 kg N ha^{-1} annually. The reversion of the Broadbalk Wilderness from arable to deciduous woodland over 80 years resulted in a N accumulation of 65 kg ha^{-1} annually (Jenkinson 1971).

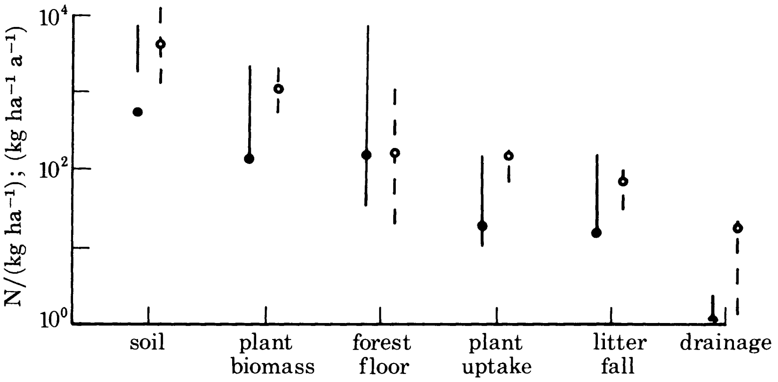

FIGURE 1. Some ecosystem parameters for N in temperate coniferous (—) and deciduous (- - -) forests (from Cole & Rapp 1981; Gosz 1981; Melillo 1981), showing the position of the Culbin (●) and Meathop Wood (○) ecosystems.

5. Much of the N uptake by vegetation in forests is from the decomposing organic matter of the forest floor (Cole 1981; Miller *et al.* 1979), but most of the ecosystem analyses of N dynamics do not show the extent and control of N turnover within the organic pool. Incubation techniques measure only net mineralization (Popovic 1980) and do no account for turnover of N within the microbial population (Paul & Juma 1981). Indirect estimates based on population dynamics of the microflora and fauna indicate that gross mobilization of N by decomposers is equal to or greater than estimated uptake by the vegetation. For example, in the mixed deciduous woodland at Coweeta, U.S.A., annual decomposer turnover accounts for 591 kg N ha^{-1}; compare this with plant uptake of 142 kg N ha^{-1} (Mitchell *et al.* 1975).

For Meathop Wood and Culbin, gross mineralization of N can be estimated from known annual loss of carbon in decomposition, the efficiency of microbial growth and N concentration in the microflora (Heal & MacLean 1975; Paul & Juma 1981). By using a range of N concentrations of 1–5% and two independent measures of decomposition, the estimated gross annual mineralization at Meathop is of the order of 65–458 kg N ha^{-1} by a microbial standing crop containing 1.5–7.5 kg N ha^{-1}. For Culbin an estimated 40–200 kg N ha^{-1} is mineralized annually. Thus microbial mobilization of N is much greater than plant uptake and may represent a turnover equivalent to 10–20% of the total soil N each year.

The ecosystem studies at Culbin and Meathop may appear as isolated examples, but comparison with other temperate coniferous and deciduous forests (figure 1) shows that Culbin has an exceptionally low N capital and low rate of biological transfers. In contrast, Meathop tends to be in the upper part of the range of N characteristics for deciduous forests. The two sites span much of the observed range of N dynamics in temperate forests, thus indicating the degree of variation that can be expected in other U.K. forests, with the implication that responses to management observed elsewhere can be applied, at least in general terms, to the U.K.

(*a*) *Application to management*

Despite the limited ecosystem research on N cycling in forests in the U.K., the results provide a framework for discussion of the relevance of such basic research to forest management. The research of *P. nigra* (Miller *et al.* 1979), which has now been sustained for nearly 20 years, was concentrated on the crop response to varying levels of N fertilization, applied in 1964–6 when the crop was showing N deficiency. Detailed analysis has shown that retention of N in the ecosystem declined with increasing fertilizer rates, reaching 45% at the highest rate (504 kg N ha^{-1} annually). When there was high retention, approximately equal amounts were accumulated in the trees and in the forest floor. Internal recycling has been identified as a key mechanism that sustains growth after fertilization, with marked changes in the needle area and net assimilation rate (Miller & Miller 1976). The efficiency of growth, in terms of kilograms production per kilogram of N taken up, decreased from 533 in the unfertilized crop to 142 at a fertilizer addition of 168 kg N ha^{-1} annually. This probably reflects storage of N that is used in subsequent production. Despite this, the fertilized *P. nigra* is still more efficient than the deciduous woodland at Meathop (47 kg kg^{-1} N).

Thus the mechanisms of plant response to fertilizers at Culbin have been identified and explored to determine the N fluxes necessary to sustain growth. In contrast, the fate and consequences of N retained in the forest floor at Culbin and elsewhere is uncertain (Heal 1979; Malcolm 1979*a*, *b*; Miller 1979). Accumulation by retention of fertilizers or other inputs to the floor may be regarded as capital for later mobilization and compensation for subsequent losses. Alternatively, accumulation may represent effective removal from availability to the crop, with possible development of nutrient deficiency. Although mechanisms of mobilization of N in the forest floor have been identified, the understanding of the complex interactions does not yet allow translation into management. However, the development of models to determine fertilizer régimes (see comments by H. G. Miller in the discussion), based on current ecosystem information, should help to improve on the necessarily pragmatic assessment of input and growth response (Atterson 1979; Davies 1979).

A recurrent concern at the ecosystem level is that nutrient removal through harvesting, and in some areas by burning of slash, will deplete the nutrient capital of the site and hence reduce future production. Input in rain, aerosols, fixation and fertilizers may compensate for losses. The concern is increased by the development of whole-tree harvesting and by reductions in the length of rotations. In Britain, since the question was raised by Rennie (1955), the debate has centred on nutrient budgets (see, for example, Carey (1980), Miller (1979) and Miller *et al.* (1980)).

Conventional clear-felling or whole tree harvesting may remove 50–700 kg N ha^{-1}, depending on the tree species, nutrient status, time and type of cropping. Annual losses are generally equivalent to 1–5 kg N ha^{-1}, although complete tree removal and short rotations can give higher values. Simple budget analysis indicates that net accumulation during forest development will compensate for direct and indirect losses at all but the highest rates of crop removal. However, the margin of error on estimates of input and losses is large. Where the soil nutrient capital is small, implying a small annual net increment, the general conclusion is that N losses in crop removal could reduce the growth of subsequent crops but could be compensated for by fertilizer addition.

The analysis by Miller *et al.* (1980) is the most complete study so far in the U.K. Based on *P. nigra* they estimated crop removals of 1.6–13.5 kg N ha^{-1} annually for various yield classes and harvesting régimes. By comparison with probable inputs and losses, they suggested that only very intensive harvesting of fast-grown trees is likely to remove more than the expected input of N. As in some previous studies, removal of phosphorus was of greater potential importance to long-term growth.

In the uplands of the U.K. the N capital of the soils ranges from 3 t ha^{-1} in the rooting zone in peats with low bulk density, to 10–20 t ha^{-1} on the rough grazings (see papers by Batey and Newbould, this symposium). Thus loss of capital in tree removal is unlikely to become a significant problem. Further corroborative evidence comes from analysis of N transfers in an upland blanket peat at Moor House in the north Pennines (Rawes & Heal 1978). Here a *Calluna–Eriophorum–Sphagnum* community has a sustained annual uptake of about 30 kg N ha^{-1}. Annual losses in run-off, sheep and grouse crops, burning, and accumulation below the rooting zone are of the order of 2.9, less than 1, 2.5 and 6 kg N ha^{-1} respectively. Thus ecosystems of the type which undergo afforestation can sustain N circulation, at high altitudes, of the order required for tree growth despite recurrent losses equivalent to those in upland forests, including crop removal.

Ecosystem research provides a quantitative framework for analysis of management practices and it is necessary to retain a view of the main pattern of inputs, turnover and losses. However, the research has emphasized that the response of the forest ecosystem depends on a series of internal responses. The research at Culbin has shown the type of information necessary to assess the internal responses of the trees to management, but the dynamics of nutrient release from organic matter in relation to crop demand remains a critical area for research, an area considered in the next section.

3. Mobilization of N during decomposition

(*a*) *Basic features*

The importance of the pool of organic N within the litter and soil derives not only from the large proportion of the N capital that it represents (table 1 and figure 1), but also because the mobilization of this N is essential for the functioning of the ecosystem. Plant production depends on the availability of N, which is largely determined by the processes of mineralization of plant litter and soil humus, mediated by the decomposer organisms. Furthermore, the response of the nitrogen cycle to various aspects of management is, to a large extent, determined by the capacity of the litter and soil to retain or release N.

In most concepts and models of the nitrogen cycle there is implicit recognition of the importance of mineralization processes but little explicit recognition of the complexity of these processes, which regulate N flux between litter–soil and plant root (Frissel & Van Veen, this symposium). In agricultural soils it has been possible to predict much of the behaviour of N in soils on the basis of a few simple hypotheses. Predominant among these is the C:N theory.

Since the 1920s various workers have shown that when organic resources are incorporated into the soil the amount of inorganic N increases if the N in the initial resource is greater than about 2% (C:N = 25), decreases if the initial concentration is below about 1.4% (C:N = 35), and is unaffected by intermediate concentrations. The reason for this pattern is the demand for N in microbial growth as carbon is utilized. The resource provides the N when its concentration is high, and N in excess of microbial demand is released to the inorganic pool by deamination processes given the general term 'ammonification':

$$RCH(NH_2)COOH + \tfrac{1}{2}O_2 \rightarrow RCOCOOH + NH_3.$$

The reverse occurs when the organic N of the resource is low.

As plant litter decomposes, carbon is released by respiration, N is retained by the microorganisms and the N concentration rises. This process continues until C:N reaches 25–35, when the concentration levels off as net mineralization releases inorganic N. An initial increase in the absolute amount of N in the resource is often observed as a result of N_2 fixation, immigration by organisms or input of leachates. In organic matter with a low initial C:N ratio, loss of N occurs at an early stage as a result of leaching or plant uptake of soluble N in excess of microbial demand. In all cases the amount of organic N in the initial resource will decrease with time as it is converted (immobilized) into microbial organic N or secondary organic products (Swift *et al.* 1979).

Thus the supply of N to the root is pictured as being regulated by the opposing processes of mineralization and immobilization, with inorganic nitrogen being available when the critical C:N ratio is reached and net mineralization occurs. There is good empirical evidence to support this concept in agricultural soils (see, for example, Alexander (1977) and Paul & Juma (1981)), where organic matter input tends to be high in N and is associated with relatively homogeneous, mineral soil with high rates of bacterial activity. However, there are good reasons for supposing that the general concepts may be inadequate to explain N dynamics in forest soils where there are major inputs with low N concentration, in a markedly heterogeneous environment that tends to be peaty, acid, waterlogged and dominated by fungi.

Three features of particular importance in the nitrogen dynamics in forest soils are as follows.

1. Within the diverse microbial community, the fungi possess a wide range of biological and biochemical mechanisms whereby they may compete for N. They have the capacity within and between species to utilize a variety of N sources and to function with a wide range of cellular N concentration. The ability to immobilize N in biomass is offset by recycling through lysis of microbial tissue and faunal feeding, resulting in turnover of extracellular pools of N even when N concentrations are low (C:N high).

2. After depolymerization of larger organic molecules, saprophytic fungi have the capacity to absorb soluble organic N, which is deaminated within the cell, thus short-circuiting the process of ammonification leading to extracellular pools of inorganic N. The ability of ectomycorrhizal fungi also to utilize soluble organic N (Bowen & Smith 1981; Alexander 1982) provides a mechanism of N uptake by trees that does not involve the inorganic pool and may also be an important mechanism of competition between saprophytic and mycorrhizal fungi: an extension of the concept of competitive saprophytic ability (Garrett 1956, 1978).

3. Humus formation during decomposition also represents a potential immobilization process for N. Nitrogen, mainly in the form of amino-N, is bound to the humus molecules in a manner analogous to the tanning of protein. The formation of humus fractions, partly or mainly through microbial synthesis, occurs throughout the decomposition process, with lignin as a major contributor of carbon and aromatic compounds influencing the rate of formation. Thus, in forest soils the input of organic matter rich in lignin and aromatics may significantly increase the proportion of N incorporated into humus. Despite its high concentration, mobilization of humus N by the microflora is slow, although the large pool of humus may compensate for the slow turnover in contributing N to plants.

The basic features of mobilization of N in forest soils emphasize the presence of a series of sinks and sources in both space and time (figure 2). Potential mechanisms exist by which N is circulated by the microflora and taken up by plants at substrate concentrations at which it is often considered that N is immobilized.

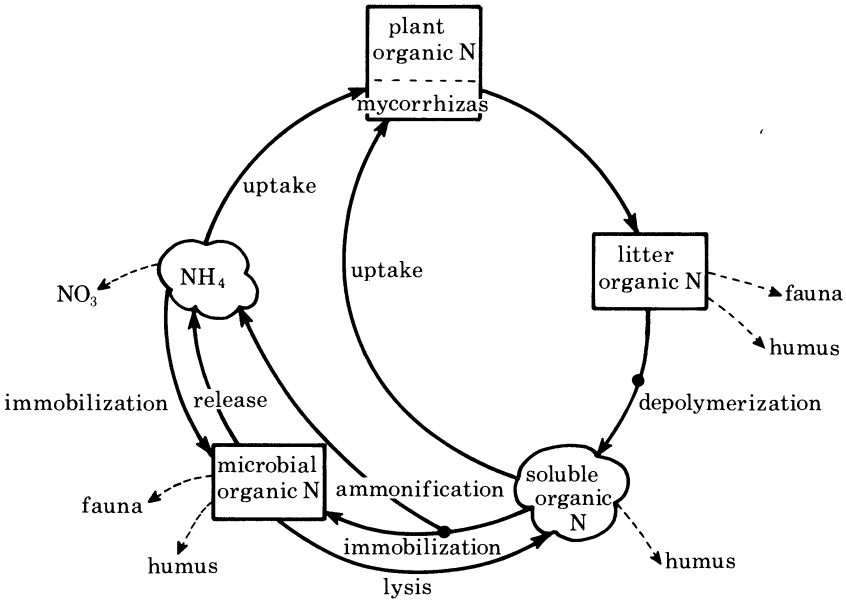

Figure 2. Nitrogen mobilization processes in forest soils, emphasizing the stage of a soluble organic N pool that can be absorbed directly by the microflora and trees. The primary cycle initiates a cascade of secondary cycles as organic N compounds are reformed and become new substrates for mobilization (– – –).

(b) *Mobilization in forests: evidence and implications*

The previous section examined briefly some of the fundamental features of N mobilization in forests. Some examples of field and laboratory evidence amplify these features and indicate their relevance to management.

(i) *Soluble organic* N

Information on the size and turnover of the pool of soluble organic N is sparse, but Van Cleve & White (1980) have determined the main pathways of N transformation in the forest floor of a 60 years old stand of *Betula papyrifera* in Alaska (table 2). The pool of soluble organic N, determined by chemical analysis, of about 40 kg ha^{-1}, composed nearly 10% of the total N and was much larger than the inorganic pools. ^{15}N labelling of the nitrate and ammonium pools and subsequent isotope dilution analysis showed that turnover of soluble organic N constituted the major pathway. The results indicate that a considerable proportion of the mobilized N does not pass through the inorganic fractions. While it is tempting to suggest that the results reflect uptake of amino acids, amino sugars, uric acid and other organic N compounds by the saprophytic and mycorrhizal flora, there is no further evidence to test the hypothesis. The results do not have direct implications for management, but they indicate the need for research on the dynamics of soluble organic N and its significance in microbial and tree nutrition.

TABLE 2. THE SIZE AND TURNOVER OF N POOLS IN A TAIGA BIRCH FOREST FLOOR, ESTIMATED BY LOW-LEVEL ADDITIONS OF $K^{15}NO_3$ AND $^{15}NH_4Cl$ (CALCULATED FROM VAN CLEVE & WHITE 1980)

pool	nitrogen content (±s.e.) mg m^{-2}	turnover time days	daily flux mg N m^{-2}
nitrate	105±5	147	0.7
ammonium-N	560±245	235	2.38
soluble organic N	3940±509	54–94	42–73

(ii) *Mobilization of* N *in microbial biomass*

Nitrogen incorporated in the microbial biomass may be temporarily immobilized, i.e. not available to plants, particularly if the biomass is increasing. However, there may be considerable turnover of the microflora, with recycling of N, although there is no detectable change in the biomass. Measurement of net mineralization by incubation techniques does not reflect the turnover of the nitrogen but ^{15}N studies, e.g. by Paul & Juma (1981), confirm a large turnover of N associated with negligible biomass change.

One of the mechanisms of turnover is grazing by fauna, involving in forest soils, microfauna, such as protozoans and nematodes, and arthropods (Anderson *et al.* 1981; Anderson & Ineson 1982). The mobilization of microbial N into a form available for plant uptake can occur when the C:N ratio is high, as shown in a microcosm experiment with macroarthropods feeding on oak leaf litter. With varying numbers of animals, release of ammonium was increased by up to six times that in controls without animals (figure 3), although other elements were not affected (Anderson & Ineson 1982). The mechanism involved seems to be through qualitative and quantitative changes in the microflora, and limitation of carbon sources probably prevents full utilization of released N by proliferating bacteria. Faunal biomass in coniferous forest soils may be small but, because management practices can markedly influence population size and

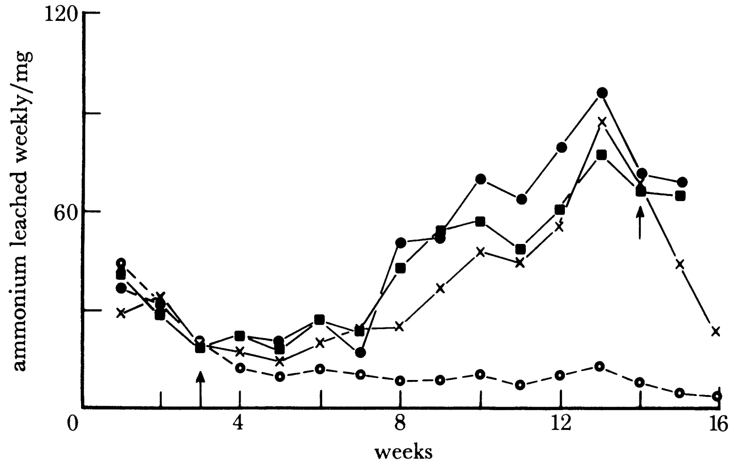

FIGURE 3. Release of ammonium in leachate as a function of *Glomeris* feeding on decomposing oak leaves in microcosms. Animals were added after 3 weeks (two (×) four (●) and eight (■) per microcosm), except in controls (o). Animals were removed from microcosms containing two animals at 14 weeks. (From Anderson & Ineson (1982).)

structure (Bååth *et al.* 1980; Lundkvist 1977; Tamm 1976), fauna can modify the pattern of N availability within a forest floor.

(iii) *Decomposition of stumps*

Tree stumps remaining after felling are indicative of the mosaic of nutrient sinks and sources within a forest, their rate of decomposition being slow compared with other organic inputs in the forest. During decomposition the low initial N concentration increases through carbon loss in respiration from the fungal colonizers. An increase in the absolute amount of N, characteristic of most litters, may not occur until the late stages of decomposition (figure 4), the stump acting as a N sink for possibly 20 years after felling. The stage at which net mineralization occurs is unknown, but it is probable that, at least in the early stages of decomposition, N is immobilized in the enlarging fungal biomass until most of the N from the tree tissues has been converted into fungal mycelium. The immobilization phase is followed by release, associated with invasion by fauna (Swift 1977). Nitrogen fixation in decomposing stumps is known (Granhall 1981), but in the stumps of *Picea sitchensis* (figure 4) parallel increases in other nutrients were recorded, indicating translocation by fungi, immigration by fauna, or throughfall as the mechanism of accumulation.

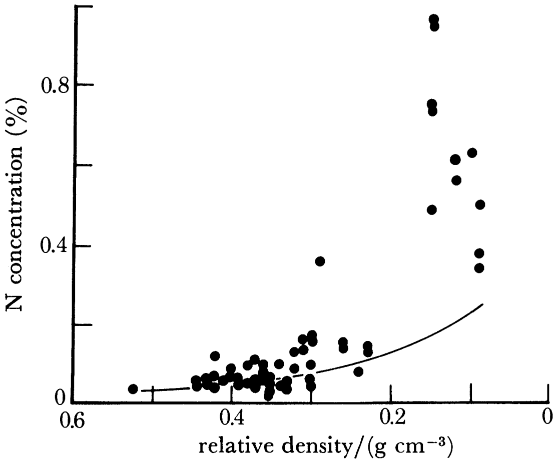

FIGURE 4. Accumulation of N in decomposing stumps of *Picea sitchensis*. The relative density is a measure of the stage of decomposition, freshly cut stumps being 0.4–0.5 g cm^{-3}; thus a relative density of 0.1 represents a mass loss of 75–80 %, reached 10–20 years after felling. The line represents the change in concentration resulting from decomposition if there was no addition or loss of the initial N content (K. Newell & O. W. Heal, unpublished).

The current practice of planting the second rotation crop against stumps is providing successful establishment, but the long-term effect of an adjacent stump is unknown. Seedling establishment beside stumps may result from microclimatic factors, including improved draining along root channels in waterlogged sites, and nutrient accumulation at the stump base from needle decomposition and stemflow before felling. The stump may become a nutrient source for the tree at a much later stage. Alternative patterns of mobilization are under the control of forest management, e.g. the distribution or burning of brash, the modification of ground vegetation, the ploughing in of organic residues and the redistribution of organic matter from mineral horizons, but information on their short- and long-term effects on the mosaic of N supply to the crop are sadly lacking.

(iv) *Input of crop residues after felling*

One feature of management that has not been widely recognized is the effect of variation in crop residues left on the site. Not only does the amount of N vary with cropping régime, but so does the form of the associated carbon resulting in variation in the subsequent rate of decomposition and mobilization of N from residues.

TABLE 3. INPUTS OF N IN CROP RESIDUES OF DIFFERENT QUALITY AS A RESULT OF THREE CROPPING RÉGIMES: (1) REMOVAL OF STEM WOOD, (2) REMOVAL OF STEM WOOD PLUS BARK AND BRANCHES, (3) REMOVAL OF ALL ABOVE GROUND BIOMASS

(The C:N ratio is used to distinguish quality of different fractions, and the input is expressed as the percentage of the total input of N in each quality class (recalculated from Nihlgard 1972; Miller *et al.* 1980).)

	Fagus sylvatica†			*Picea abies*‡			*Pinus nigra*§		
C:N of resource	1	2	3	1	2	3	1	2	3
< 50	10	39	0	39	75	0	35	60	0
50–100	79	16	27	36	6	22	0	0	0
100–200	4	16	27	17	6	22	58	28	71
200–500	7	27	47	0	0	0	0	0	0
> 500	0	0	0	7	14	56	7	12	29
total N/(kg ha^{-1})	990	257	150	690	360	90	267	156	62

† 60–120 years old. ‡ 55 years old. § 50 years old, yield class 12.

Calculations from the dry mass and N concentration in different residue fractions of beech, Norway spruce and Corsican pine show that with conventional removal of stem wood most of the N returned to the soil has a fairly low C:N ratio and can be expected to decompose within a few years (table 3). Additional removal of bark and branches, while greatly increasing N loss, leaves much of the residue in a more rapidly decomposing form. Further removal of foliage results in most of the low input of N being in residues with very high C:N ratios and slow rates of decomposition. Reduction in short-term N supply to trees by the addition of residues that increase the C:N ratio of the forest floor has been shown by Turner (1977). The N associated with wood as stumps and roots forms a high proportion of residues when foliage is removed and, as emphasized earlier (§3*a*), is more likely to become incorporated into humus fractions. Although these calculations are crude, they show the potential effects of management on the balance between residues with fast and slow rates of N mobilization and hence on the timing of supply in relation to tree demand.

(v) *Effect of resource composition on* N *uptake by trees*

The argument given earlier, that the relation of mineralization to resource C:N ratio developed for agricultural systems may be inapplicable to forests, can be tested directly in seedling growth experiments. For example, Youngberg (1978) and K. Van Cleve (personal communication) have grown seedlings of Douglas fir (*Pseudotsuga menziesii*) and paper birch (*Betula papyrifera*), respectively, on forest floor organic matter from a range of sites. In both cases seedling growth was negatively correlated with the C:N ratio of the organic matter (figure 5) but there was significant uptake of N at ratios well above 35, the organic matter tested by Youngberg (1978) ranging from 41 to 66. Thus tree seedlings have the capacity to compete with the saprophytic microflora for N, under conditions when immobilization would be expected, and there is no indication of a critical point at which inorganic N becomes available to the plants.

As indicated from the field responses of *Pinus nigra* to fertilization (Miller *et al.* 1979), the tree physiology is altered by varying levels of N. In the laboratory experiments with paper birch, the N concentration in seedling leaves was negatively related to the C:N ratio of the decomposing organic matter, ranging from 2.0 to 1.2 %. Preliminary examination of the results also indicates that the efficiency of growth (dry matter production per unit of nitrogen taken up) was greatest at intermediate C:N levels, declining at both high and low levels of N supply. With decreased N supply, the seedling also sacrifices stem growth before growth of leaves and roots (Van Cleve, personal communication). The varying growth response of the tree (and ground flora) to N supply is one of the mechanisms by which there is a feedback effect on decomposition and nutrient release, through varying quality of litter.

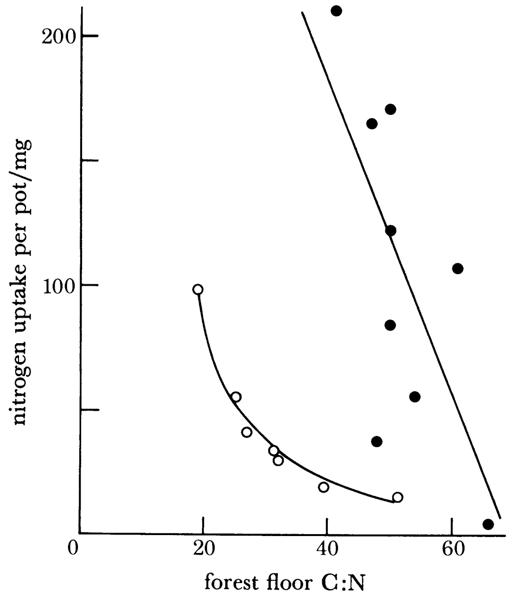

FIGURE 5. Nitrogen uptake by seedlings of *Pseudotsuga menziesii* (●) and *Betula papyrifera* (○) grown on forest floor organic matter with different C:N ratios. The regression for *P. menziesii* is $y = 427–6.17x$, $R^2 = 0.47$, and for *B. papyrifera* is $y = 22800x^{-1.88}$, $R^2 = 0.96$. (From Youngberg (1978) and K. Van Cleve (personal communiction).)

4. SYNTHESIS

Given the complexities of N cycling in forests it is necessary to concentrate our understanding to clarify the major patterns of variation and responses to management. Miller (1981), based on studies of pine, recognizes three distinct nutritional stages. In stage I, from establishment to canopy closure, growth is determined by supply from the soil. Although the trees do not fully occupy the site, the initial ground flora demand is high and, in the early years, there is only a small return of nutrients from the trees in litter fall. During this stage a positive crop response to fertilizers can be expected. Stage II, after canopy closure, is characterized by high interception of input of atmospheric nutrients, by reduced rates of accumulation in the crop through dominance of wood increment and by recycling within the ecosystem and within the tree. Accumulation within the tree is replaced by accumulation in the forest floor, but management such as thinning and fertilizing can retard the change. Accumulation (immobilization) of N in biomass and humus as trees age can lead to late rotation N deficiency characteristic of stage III. The development of deficiency is influenced by the nutrient capital of the site and the reduction in tree demand with age, so the length of stage II and the onset of stage III are variable.

The general concepts outlined by Miller (1981) provide guidelines for fertilizer management. Response to fertilizer is through increased growth rate, which shortens the rotation time. The enhanced growth rate will eventually revert to the growth rate appropriate to the nutrient supply characteristic of the site and, in general terms, this baseline supply is linked to the N capital and its turnover. It is recognized that the rate of mineralization varies with age of the crop and N status of the site but, in the absence of suitable data, a constant rate has proved adequate to describe short-term nutrient availability in the pine model (Miller 1981). Miller argues that 'only when the amount of fertilizer nutrient retained is large in relation to the original capital of the site can any measurable long-term effect be expected'. Recognizing the simplicity of the assumptions, he shows that with the addition of 200 kg N ha^{-1} and a continued rate of mineralization of 4%, availability only increases from 60 to 63 kg N ha^{-1} annually at Culbin. However, a small shift in the rate of mineralization, from 4 to 4.5%, would increase availability to 71 kg N ha^{-1} annually, a difference roughly equivalent to the rate of immobilization that is apparently causing deficiency in the crop. Thus a shift in the rate of mineralization, rather than in the amount of N in accumulated humus, could significantly modify short- and long-term supply to the crop.

In terms of general management guidelines, factors that increase the rate of decomposition, and therefore decrease the C:N ratio, will increase the site supply of N to the crop. Relevant management practices obviously include, for example, fertilizing and liming, although the effect on decomposition may be delayed for a number of years (Adams *et al.* 1978), but less obvious manipulation of mixtures of species, and of the ground flora, may produce similar effects. Conversely, management practices that reduce the rate of decomposition and increase the C:N ratio (e.g. table 3) will reduce N supply to the crop, recognizing again the feedback effect that reduced N supply has on litter quality.

To Miller's three nutritional stages may be added a fourth. Immediately after felling, input of crop residues, removal of tree uptake and, initially, a small uptake by ground flora allows decomposition processes totally to dominate the site. At this stage nutrient retention in the site is minimal through lack of plant uptake and increased run-off. Vitousek (1981) summarizes the main patterns of processes and it seems likely that in the uplands of Britain the felling of conifers will usually result in a small increase in nitrate levels in water. The high C:N ratio of crop residues, low temperature, wet and clay-rich soils will result in slow decomposition, microbial immobilization, limited nitrification, and adsorption of ammonium. The existing low nitrate levels in upland streams may be increased locally, possibly for up to 10 years after felling, but unless a large proportion of a catchment is felled, or the site is particularly fertile and well drained, general large increases in nitrate are unlikely.

As to the long-term effects of harvesting at varying intensity and rotation length, the results of Swank & Waide (1980), Aber *et al.* (1979) and others indicate that the conclusions given earlier in this paper, derived from simple budget models, may be too optimistic. When the dynamic processes of mobilization in the soil were included in compartment models, simulation of harvesting over a number of rotations showed a decline in crop yield. A reduction in yield of up to 30% was associated with decreased soil N and, although there was a significant loss of N in crop removal, increases in denitrification were apparently a critical factor (Swank & Waide 1980), emphasizing yet again the importance of the response of mobilization to management.

5. SUMMARY AND CONCLUSIONS

From this selective and brief examination of some of the basic concepts and recent research on N dynamics and their relation to forest management the following conclusions are drawn.

1. Despite the initiating work of Rennie and Ovington, ecosystem studies on forests in the U.K. have been very limited. The two studies discussed (Culbin and Meathop Wood), although not directly relevant to our upland forestry, provide useful comparative information. International information shows the two forests to be at the lower and upper ends of the range of variation in N dynamics in coniferous and deciduous forests respectively.

2. Ecosystem studies have provided a quantitative framework and have focused attention on the internal dynamics of N. Studies such as those of Miller *et al.* (1979) and Miller (1981) on *Pinus nigra* have shown the importance of the internal crop responses to N input and uptake, and provide management guidelines, but the links with mobilization pathways within the soil remain unquantified and require basic research.

3. Research in other countries indicates that effects of felling on water quality are unlikely to be important in Britain, except where a large proportion of a catchment is felled or the site is particularly fertile and well drained. However, the long-term consequences of conventional and alternative felling practices are less certain. Budget models of N removal in crops indicate that long-term effects on fertility will not be significant, except where soil capital is small and crop removal large. More detailed analyses, which include assessment of internal dynamics, indicate that even where the soil N capital is large, intensive cropping and reduced rotation length could reduce subsequent yields.

4. The principles of N mineralization, mobilization and availability to plants have been developed mainly through research on agriculture, lowland mineral soils and bacteria. These principles need to be adjusted for application to forests, organic upland soils and fungi.

5. Mobilization of N in organic residues results in a large turnover of N, which passes through a pool of soluble organic N. The soluble organic N may be absorbed by saprophytic and mycorrhizal fungi, thereby short-circuiting the ammonification pathway. It is suggested that the ability of mycorrhizal fungi to compete with saprophytes is one mechanism by which N uptake by plants occurs when the C:N ratio is higher than the conventionally accepted value of 25–35.

6. The importance of the mosaic of rates of mobilization, in space and time, to the availability of N to the tree crop is emphasized. The effects of variation in the quality of organic matter input resulting from management are likely to be as important to mobilization as the amount of N.

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Discussion

H. G. MILLER (*Macaulay Institute for Soil Research, Aberdeen, U.K.*). Mr J. N. R. Jeffers, as chairman, expressed the hope that integrated studies of the nitrogen cycle in forests should lead to models that may be of direct value in forest management. This, indeed, was the long-term objective of the studies carried out by the Macaulay Institute at Cublin forest, to which the authors refer in their paper. We have now reached the stage in this work where we could be said to be producing such models (papers are to appear later in 1981 in *Forestry* and in *Canadian Journal of Forest Research*) and, are about to construct a model to stimulate the N control of growth throughout the rotation, from planting to clear-felling, in pine.

Our experience to date suggests that detailed ecosystem studies and modelling can give an understanding of the system that has direct implications for management. For example, our models of the cycle of N within the tree show that although a tree of age 40 requires 57 kg N ha^{-1} to supply its annual foliage production, as against 27 kg for a 10 years old tree, the extent of retranslocation in the older tree means that the net demand made by the trees on the soil is the same at both ages, i.e. 18 kg N ha^{-1}. When this is coupled with the enhanced cycle through the tree–soil system and the greater interception of atomospheric nutrients, it is shown that demand on the soil capital in fact declines after canopy closure. However, the slow nitrogen immobilization in the humus may mean that, on sites of low nitrogen capital, the trees become nitrogen-deficient at a late age (H. G. Miller & J. M. Cooper (1973) *Forestry* **46**, 157–190; H. G. Miller *et al.* (1979) *Can. J. For. Res.* **9**, 19–26). Thus, we can now advise the forest manager that N fertilizers should only be applied before canopy closure or late in the rotation. During the intervening period a response should not be expected unless the cycle is interrupted, as might happen if the crown reserves are depleted by a thinning or insect attack.

The extent to which trees become independent of soil supplies after canopy closure is more marked for the metallic cations than for N and is very dependent on both the enhanced interception of atmospheric nutrients and the cycle within the tree. Indeed, we have had to invoke changes in sink–source relations to explain an observed shift in optimum foliar nitrogen concentration as trees age. This shift, incidentally, is, at least until canopy closure, very similar to the decline in N in crop plants referred to by Dr Greenwood in his paper.

There is much more that could be said, but may I simply reiterate our belief that detailed ecosystem analysis leading to simulation models helps to provide the understanding that is essential if the forest manager is to be able to rationalize and extrapolate the results of empirical experiments to particular crops under his jurisdiction.

M. J. **Swift**. Dr Miller has illustrated again the value of models as management tools when they are based on falsifiable observations. We should like to reiterate the view of Frissel & Van Veen (this symposium) that models may also play an important or indeed vital role in the development of our conceptual appreciation of ecological problems. For the particular problem of N cycling in forests it is our view that the elucidation of the pathways of N flux in the litter–soil–root systems is an area demanding particular analysis. It is of interest, for instance, to compare the low level of resolution that we have in soil models with the much higher levels demonstrated in Stewart's models (this symposium) for freshwaters.

A. J. **Holding** (*Department of Agricultural and Food Bacteriology, The Queen's University of Belfast, U.K.*). The authors presented data that showed ammonium production from decomposing leaves (C:N ratio 100:1) after the addition of *Glomeris* spp. Normally it would be expected that the decomposition of organic matter with a high C:N ratio would result in the net immobilization of nitrogen compounds. Are the authors able to offer an explanation for this very interesting observation?

J. M. **Anderson**. The overall C:N ratio of decomposing leaf litter obviously gives no indication of the location or availability of N because within a short period after the onset of decay most of the N is immobilized in fungal tissues. The feeding activities of saprophagous and mycophagous invertebrates reduce fungal biomass and activity, but extensive bacterial growth occurs during the passage of food through the animal gut. The faeces of soil animals contain a large bacterial biomass, irrespective of soil pH, and high concentrations of ammonium. The ammonium is derived from fungal cytoplasm and excretory products of the animals through the activity of ammonifying and uricolytic bacteria in the gut. We believe that bacterial immobilization of ammonium (and by fast-growing microfungi) is limited by available carbon and energy resources, and hence free ammonium is available for root or mycorrhizal uptake. Bacteriophagous nematodes and protozoa are involved in the release of N from bacterial biomass in the soil. These processes result in N mineralization at C:N ratios where N immobilization is theoretically occurring.