THE NITROGEN ECONOMY OF LARCH : SPRUCE MIXTURES

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Declaration

I hereby declare that this thesis has been composed by me from the results of my own work, except where otherwise stated, and that no part has been presented for a higher degree.

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Abstract.

Foliar analysis has demonstrated a definite improvement in Sitka spruce (Picea sitchensis (Bong.) Carr) foliar nitrogen status in the presence of larch (Larix spp.), for stands growing on nitrogen deficient deep peats in the absence of nitrogen fertilizer. This improvement is reflected in increased height and diameter growth, while estimates of stand foliar nitrogen capital suggest a greater quantity of nitrogen in the mixture tree biomass.

Larch litterfall is an obvious nitrogen source for spruce in mixed stands. While larch foliar nitrogen levels may be high (1.82%), up to 74% is withdrawn or leached prior to abscission resulting in litter nitrogen levels of around 1%. Nitrogen cannot readily be leached from fallen larch litter (only 3.5%), although greater amounts of phosphorus (47.2%) and potassium (70.7%) are potentially leachable. A relatively greater quantity of nitrogen can be leached from larch foliage at a less advanced stage of senescence (15.9%). Throughfall fluxes for the period of abscission support these findings; larch foliage actually removes nitrogen from rainfall during senescence and does not become more leaky for this nutrient relative to Sitka spruce.

Despite these findings, larch litter appears to be a more available source of nitrogen for Sitka spruce seedlings than spruce litter. While incubation of 8 month old larch litter demonstrated considerable nitrification which was not apparent for equivalent spruce litter. However, the total nitrogen return in larch litter, 6.8 $kgNha^{-1}yr^{-1}$ in a mixed stand seems quantitatively unimportant.

Field and laboratory incubations of peat and litter from spruce and larch/spruce stands indicated an annual net mineralization of 28 and 60 $kgNha^{-1}yr^{-1}$ respectively. Differences do not relate to microclimate and are substantiated by estimates of nitrogen availability based on plant uptake and ion exchange resin bags. Differences in total soil nitrogen were not apparent while attempts to chemically fractionate organic nitrogen pools were inconclusive. Nitrogen fixation was not detected.

Findings suggest that the presence of larch enhances the mineralization of native organic nitrogen, perhaps through a stimulatory effect of larch litter and the associated microflora or the mycorrhizosphere.

INTRODUCTION

This study is concerned with the investigation of the apparent improvement in the growth and nitrogen (N) status of Sitka spruce (Picea sitchensis (Bong.) Carr.) when grown in mixture with Japanese (Larix kaempferi (Lambert) Carr.) or hybrid larch (L. X eurolepis Henry) on deep oligotrophic peat. To place the work in context the growth of Sitka spruce in its natural range is briefly discussed followed by a consideration of its growth and requirements in the United Kingdom. Finally, a statement of the reasoning behind the approach adopted is presented so that results given in later sections may be related to the problem as a whole.

1:1 The growth of Sitka spruce in North America

Sitka spruce is the largest member of its genus and occupies a narrow coastal range along the Pacific coast of North America; the species extends from northwestern California to southern Alaska, a distance of some 2900km (Fowells, 1965).

Climatically, the range is dominated by the Pacific Ocean; the area receives winter rainfall which extends down the west coast from British Columbia to southern California, but inland only as a narrow strip to the Cascades and Sierra Nevada. The amount of rainfall declines from north to south being 1050mmyr^{-1} at Vancouver but only 259mmyr^{-1} at San Diego (Walter, 1979). Rainfall is so high in the north that summer drought, if it developes, is short-lived. Further south the growth of hydrophilic species, such as Sitka spruce, occurs only because of a fog belt generated by cool ocean currents. Sitka spruce is adversely effected by high vapour pressure deficits and is therefore sensitive to atmospheric drought, exhibiting early stomatal closure in response to stress and reduced growth (Grace et al., 1975). In southern California Sitka spruce growth is restricted to within 1 or 2km of the coast, further north

in Oregon and Washington it occurs 50km inland, and in Alaska 200km inland. Locally, greater spread into the drier interior is restricted to river valley bottoms, at the southern extreme of its range growth only occurs along rivers and at river mouths.

Because of its coastal range, the species is restricted to low elevations; in southern Alaska commercial stands spread from 0 - 300m, further south in Alaska it may grow at 900m but growth is shrublike. In British Columbia growth seldom occurs above 300m.

Maximum stand development is reached on the Olympic peninsula and Queen Charlotte islands, this is associated with superhumid conditions, high rainfall (2000 $mmyr^{-1}$), 200 days cloud, and absence of extreme cold. Climatic variation over large parts of the range is slight due to the overriding influence of the Pacific. Best growth is associated with deep soils of moderate to high nutrient status, or sites continually flushed with nutrient rich water, which are always moist but well aerated. Both requirements are met by sites which are moderately well drained and receive inputs of aerated nutrient rich water, e.g. concave slopes.

For much of its range Sitka spruce occurs with Western hemlock (Tsuga heterophylla (Rafin.) Sargent); on moist sites (as described) spruce tends to dominate with Western hemlock and Western red cedar (Thuja plicata Donn) being secondary; on well drained sites hemlock becomes dominant with poorer spruce and cedar; wet sites are dominated by cedar with spruce and hemlock as associates, while on stagnant sites spruce is absent and cedar and lodgepole pine (Pinus contorta Dougl.) dominate with poorly developed hemlock. Sitka spruce tends to give way to these species on less fertile sites. In Oregon, Washington and British Columbia the species associates with Pacific silver fir (Abies amabilis (Dougl.) Forbes) on steep convex slopes at higher elevations. In Alaska Sitka spruce associates with mountain hemlock (Tsuga mertensiana (Bong.) Carr.) on shallow soils.

In its natural range Sitka spruce is therefore comparatively site intolerant giving way to more tolerant associated species

except on the better sites.

1:2 The growth of Sitka spruce in the United Kingdom

The United Kingdom occupies a similar latitude to the natural range of Sitka spruce; under British conditions the species performs well, especially at low elevations in the moist oceanic climate of the west, growing less well in the drier east and at higher elevations.

Early forest plantings this century, made use of a variety of coniferous species, with species requirements normally being matched to site conditions. However, the outstanding performance of Sitka spruce, and the developement of modern cultivation techniques, has led to this species being more widely planted than any other, over a wide range of site fertilities. While potentially high yielding, Sitka spruce is nutritionally demanding; the need to apply phosphorus (P) fertilizer on more infertile sites was identified in early trials (McIntosh, 1981). Later, as less fertile sites were afforested, and stands developed, the need for potassium (K) and N fertilizers became apparent (Zehetmayr, 1954).

Research into nutrient cycling indicates that a marked growth response to fertilizer is only likely in stands which have yet to close canopy; after closure is achieved a closed nutrient cycle is able to meet most growth demands (Miller, 1981) and economic rates of growth should be maintainable with less fertilizer input.

Table 1:1 indicates that fertilization may not be required on the most fertile sites, where a General Yield Class (GYC), $m^3 ha^{-1}$, of 16 - 20 may be obtained; on less fertile sites up to 3 applications of P or PK may be needed to ensure that at least GYC 14 is achieved (McIntosh, 1981). Problems of N deficiency are most common on deep oligotrophic (unflushed) peats and heathland podsols; on the former in particular, satisfactory growth is most unlikely in the absence of fertilizer. However, given the inputs listed in table 1:1 it is possible that GYC 16 - 20 can be achieved on these sites (McIntosh, 1981). Deficiency conditions develop on these soils due to low levels of available N, although total N levels may be high. This is almost certainly a consequence of low mineralization

rates, due to physical and chemical constraints on microbial activity.

TABLE 1:1

Fertilizer prescriptions for Sitka spruce in upland Britain (McIntosh, 1981).

Soil type	Year							
	At planting	4	6	8	9	12	15	16
Brown earth	(P)	Heather control if required		(P)				
Ironpan podsol	P	"		P				
Heathland podsol	P	"	N(P)		N	NP	N	
Deep unflushed peat	P(K)	"		PK	N	N	N	NPK

() indicates possible benefit

P at 50 $kgha^{-1}$ element applied as ground mineral phosphate

K at 100 $kgha^{-1}$ element applied as potassium cholride

N at 150 $kgha^{-1}$ element applied as ammonium nitrate or urea

A compounding factor which may affect any site, but which is normally restricted to the less fertile, is the presence of heather (Calluna vulgaris (L.) Hull). Where heather is a major component of the sward (50%) it has a deleterious influence on spruce growth and N status (Malcolm, 1975). There is evidence which suggests that the endophyte association of the heather root suppresses the ectotrophs of spruce, resulting in N deficiency and stunted growth (Handley, 1963; Robinson, 1972). On poor sites growth check due to heather is likely to occur 4 - 6 years from planting (McIntosh, 1983), however, the problem can be controlled by the use of herbicides (Biggin and McCavish, 1980; Mackenzie et al., 1976).

Prior to the development of modern herbicides heather was controlled silviculturally by the means of mixtures. Larch or pine (Pinus) species do not suffer from heather check and will suppress heather when planted either pure or in a mixture with Sitka spruce; once released from check, the greater growth potential of the spruce enables it to overtake the nurse species which is in turn suppressed leaving a pure spruce crop. On many sites, not ideally suited to the growth of spruce, this did not occur, requiring the nurse species to be selectively removed, complicating stand management. Consequently the use of mixtures was more or less abandoned in favour of herbicide treatments.

On the most deficient sites, even where heather is controlled or was not a problem, N deficiency is likely to develop after about 8 years. Deficiency does not develop immediately because tree demand is low, and because mineralization of native N appears to be stimulated by the application of P fertilizer, as ground mineral phosphate (Carey et al., 1981). With the onset of N deficiency there are 2 management options; 1) No treatment: where deficiency is not too severe, growth may be only slightly reduced and may be maintained at an acceptable level after canopy closure, but the rotation will be prolonged, 2) N fertilizer: as stated, it may be possible to achieve high rates of growth on poor sites if fertilizer is used. Tree response to N fertilizer is short-lived, 3 - 4 years (Dickson and Saville, 1974), and repeated inputs are required to maintain growth through to canopy closure (Table 1:1). Such an approach is expensive and N deficiency may return later in the rotation (Williams, 1983).

At present, there are few available options to prevent the onset of N deficiency and the need for remedial fertilization. Liming, to raise pH and improve conditions for mineralization, may be beneficial in the short-term only (Dickson and Saville, 1974), and high rates are required (McIntosh, 1983). Mixing of lime with the top layer of peat may prolong the response in some cases (Dickson, 1977), but practical problems exist. Both liming and fertilization increase nitrification (Mai and Fielder, 1978; Williams, 1972) which may lead to leaching

losses and associated environmental problems (Williams, 1983). Recent evidence suggests that high ammonium levels following fertilization may inhibit microbial enzyme systems and also increase the recalcitrance of organic N compounds (Berg et al., 1982a), reducing subsequent rates of N mineralization.

Observations of Sitka spruce growth in mixture with larch or pine, planted originally to control heather on heathland soils has indicated superior growth to that of pure spruce on the same sites (Weatherell, 1957; Zehetmayr, 1960). This effect appears to be separate from the suppression of heather and has been more recently noted on deep oligotrophic peat (O'Carroll, 1978), where it has been linked with the improved N status of spruce. It may be possible therefore to grow spruce on N deficient sites in the absence of N fertilizers, although P and K are still required.

The mechanisms involved in this nursing effect are unknown; clearly, the use of larch or pine spruce mixtures would be very attractive if the need for N fertilizer was removed, coupled with the advantages of self-thinning on unstable sites and heather control. However, the mechanisms responsible for this apparent effect need to be fully investigated if the best choice of nurse and spatial arrangement of mixtures is to be determined.

1:3 Research strategy and objectives

The initial objective of this study was to conclusively demonstrate improved growth and N status of Sitka spruce in mixture with larch, since many earlier observations do not adequately distinguish between a response due to the removal of heather check and the suggested secondary effect. This initial objective can be satisfied through foliar analysis of spruce in pure and mixed stands on peat sites where no N has been applied, and where heather was never a problem, or was controlled chemically soon after planting.

Improved foliar N levels would indicate a positive effect in terms of spruce N status, however such data alone cannot distinguish between 2 groups of causal mechanisms. Thus, 1) spruce foliar N levels may be higher but the N capital ($kgha^{-1}$) contained in the tree biomass may not differ between

pure spruce and mixed stands; 2) greater foliar N concentrations might be reflected in a greater N capital of the mixture tree biomass. To distinguish between these alternatives requires a strategy of biomass sampling.

If Case 1 applies then N uptake and therefore N supply must be similar and improved spruce growth and N status may be at the expense of larch. This would suggest what might be termed competition related mechanisms, i.e. spruce is a better competitor for available N than larch therefore a greater proportion of the available N can be exploited by an individual spruce in a mixture compared with a spruce stand. This could result from mycorrhizal differences, or differences in rooting morphology, rooting intensity and phenology, and phenological differences in N cycling and uptake.

For Case 2 to apply larch must be able to obtain N when spruce cannot and some of this N must become available to the spruce. Two questions require an answer in this case, 1) where and how does larch obtain N, and 2) how is N made available to the spruce?. These questions may or may not involve the same mechanism.

For young aggrading stands, nutrient cycling is relatively unimportant and virtually all N requirement must be met by the soil, atmospheric inputs and N fixation. Atmospheric inputs are unlikely to differ significantly between pure and mixed stands while N fixation, in the absence of symbiotic associations, is not important in temperate coniferous forest. This leaves the soil as the main supplier of N; larch must therefore obtain soil N which is unavailable to spruce. Possible mechanisms may involve, 1) greater rooting volume (more soil exploited), 2) effects related to rooting intensity, the rhizosphere and mycorrhizas (i.e. greater mobilization of N), 3) non-root related mobilization of soil N due to microclimate or priming effects, as a consequence of larch litter or throughfall.

N could be made available to spruce via root grafts, root exudates, mineralization of larch litter (root or leaf), throughfall or direct competition with larch. Clearly both a greater availability of N and transfer to spruce may be explained by the same mechanism, e.g. the rhizosphere of larch may

mobilize N unavailable to spruce, spruce obtains N by direct competition at the larch root surface. Mechanisms could, however, differ; larch may obtain more N as described above but spruce obtains N from increased mineralization associated with larch litter.

A subsidiary question which requires investigation is the duration of any positive effect. The actual mechanism may be transient but improved spruce growth maintained due to high N status, associated with rapid litter breakdown and N cycling. Alternatively, a mechanism may operate throughout the life of a mixture.

Following an initial demonstration of a mixture effect it was proposed to investigate experimentally some of the possible mechanisms outlined above. Since all of the suggested mechanisms relate to some aspect of the N cycle a synopsis of current views and understanding of N cycling in forest systems is presented in Section 2.

Nitrogen cycling in forested ecosystems.

2:1 Introduction

N is an essential nutrient which is a primary constituent of protein and therefore the protoplasm of plants, animals and microbes (Mengel and Kirby, 1982). As such its availability is central to ecosystem productivity, which it frequently limits (e.g. Gosz, 1981; Wollum and Davey, 1975).

The principal reservoir of potentially available N is the atmosphere. Geochemical theory (Stevenson, 1965) suggests that all atmospheric N was originally present as ammonium compounds and nitrides in the earth's matrix. Due to heating, N was driven off into the atmosphere where it existed mainly as ammonia. Atmospheric oxygen enrichment as a result of photosynthesis caused this to be oxidised to elemental N. Nearly 80% of atmospheric gas is N_2, but this accounts for only 2% of the earth's total N, virtually all the remainder being present in rocks, where the concentration is so low that it plays no part in cycling processes. Organically bound N represents a tiny fraction of the total.

Transfer of atmospheric N to living organisms is low, only a small quantity of the N used annually by undisturbed ecosystems comes directly from biological fixation or other atmospheric inputs (Melillo, 1981). Despite this, soils, in comparison with the original rocks, have been greatly enriched with N. 99% of this N is organically bound having accumulated as a result of fixation processes operating over long time scales. Thus N accumulation in a primary aggrading system depends largely on inputs which are atmospheric in origin (Reiners, 1981). As a succession develops the system's N capital increases until atmospheric contributions become unimportant relative to biologically mediated cycling within the ecosystem.

Plants obtain the bulk of their N from the soil solution, virtually all uptake being of inorganic N which may constitute less than 1% of the soil reserve. This available pool is maintained by the degradation of organic material by microbes, releasing N as exploitable inorganic forms. Inorganic N not utilized by plants or microbes is subject to leaching or gaseous loss, the latter returning N to the atmosphere and completing the cycle.

Since N cycling is a biological process it is influenced by a range of environmental variables and as a consequence considerable differences exist between cycling in different ecosystems.

Aspects of the N cycle are the subject of a multitude of research papers and numerous reviews, both general and specific, are available (e.g. Barthclomew and Clark, 1965; Clark and Rosswall, 1981; Nielsen and MacDonald, 1978; Svensson and Söderlund, 1976).

2:2 N distribution, uptake and use efficiency.

2:2:1 N distribution

An accounting approach which compartmentalises ecosystem N can be useful since it identifies the principal N pools. Pool size may not relate to rate of turnover or functional importance in the cycling process.

Ecosystem productivity and nutrient accumulation have been the subject of numerous research papers and much of this material has been presented in a number of review articles: for evergreen conifers and deciduous broadleaves, Cole (1981), Cole and Rapp (1981), Keeney (1980), Heal et al. (1982), Larcher (1975), Rodin and Bazilevich (1967); for evergreen conifers, Fogel (1980), Gosz (1981); for deciduous broadleaves, Melillo (1981).

Table 2:1 gives some general values for evergreen conifers and deciduous hardwoods. Despite considerable variation certain similarities are apparent. Most N is present in the soil, around 80%, while the tree biomass comprises approximately 10%, as does the forest floor. The root system is clearly important and accounts for 15 to 30% of tree biomass (Fogel, 1983; Persson, 1983), equal to 19 to 32% of tree N (Fogel, 1980:

Henderson and Harris, 1975; Wells and Jorgensen, 1975). Mycorrhizas may constitute 8% of tree biomass, mycorrhizal roots accounting for 25% of tree N and non-mycorrhizal roots 7% (Fogel, 1980).

TABLE 2:1

N values for compartments in coniferous and deciduous ecosystems $kgNha^{-1}$.
(From Cole and Rapp, 1981; Fogel, 1980; Melillo, 1981).

Coniferous[1]	Minimum	Mean	Maximum
Foliage	51	120	228
Branches	18	100	242
Bole	47	176	584
Total above ground	153	396	729
Roots	12	101	422
Total tree	165	470	900
Forest floor	85	613	2260
Soil (to rooting depth)	1753	4117	7100
Deciduous[2]			
Foliage	53	84	121
Branches	20	165	666
Bole	120	208	386
Total above ground	240	497	1071
Roots	57	169	434
Total tree	389	688	1260
Forest floor	44	399	1100
Soil (to rooting depth)	1380	6142	13800

1 Based on 21 sites.
2 Based on 20 sites.

2:2:2 Form of uptake.

This subject is dealt with extensively by Clarkson and Hanson (1980). Kirkby (1981), Mengel and Kirkby (1982). Novoa and Loomis (1981) and Nye and Tinker (1977).

Under acid conditions where the conversion of ammonium to nitrate is low, e.g. mor-humus soils, ammonium is the dominant inorganic species available to plants. Ammonium is normally present in the concentration range 0 to 5 ppm. (Bowen and Smith, 1981,) with solution concentrations up to 10^{-3}M (Nye and Tinker, 1977). At concentrations (μM rather than mM) and the pH (less than 9.25) usually found in soil, ammonium uptake is carrier mediated (Jennings, 1976). Ammonium is subject to cation exchange which can reduce its mobility: transfer to the root surface is by diffusion which is the rate limiting step in ion uptake, the absorbing capacity of the root/mycorrhizal complex only being a major determinant when ion transfer to the roots is rapid (Bowen, 1981). Consequently root abundance is of primary importance in uptake of ammonium, which is enhanced by the presence of ectomycorrhizas (Bledsoe and Zasoski, 1983; Bowen, 1981).

For undisturbed forest, nitrate appears to be of minor importance with the ratio of ammonium: nitrate being of the order of 10:1 (Cole, 1981). Since nitrate is an anion it is poorly held by the soil and therefore highly mobile. At high concentrations transport to roots is largely by convection and root absorbing capacity may influence rate of uptake (Bowen, 1981), under such conditions mycorrhizas have little effect on uptake. At low concentrations, however, diffusion becomes the major transport mechanism and under these conditions uptake is considerably enhanced by mycorrhizas (Bledsoe and Zasoski, 1983; Bowen, 1973).

Many vascular plants can utilise both nitrate and ammonium although one or other may be preferentially absorbed (Ho and Trappe, 1980; Van den Driessche, 1978). Preferential absorption of ammonium from a solution containing both inorganic forms is exhibited by most microbes (Paul and Juma, 1981). Of 27 ectomycorrhizal fungi studied by Lundberg (1970) most grew best with ammonium as their N source. Carrodus (1966) found

that excised beech mycorrhizas could utilise ammonium but not nitrate. More recent work has identified nitrate reductase activity in a range of mycorrhizas and forest tree roots (Bledsoe and Zasoski, 1983; Bowen, 1973; Buwalda et al., 1983; Ho and Trappe, 1980).

Bledsoe (1976) indicates that species which have evolved in a high ammonium and low nitrate environment have developed an uptake selectivity for ammonium, and vice versa. Considering that many forest ecosystems are N limited (e.g. Gosz, 1981; Keeney, 1980) it is strange to find a discrimination between the two forms of N, particularly when nitrate can act as a carrier for cation uptake. The uptake of nitrate does involve a reduction step not required for ammonium (Mengel and Kirkby, 1982) although it is unlikely that the energy demand of this reduction, 8 e^- per nitrate ion (Novoa and Loomis, 1981), would result in a selectivity for ammonium.

That many forest trees and their mycorrhizas do have a capacity to utilise nitrate should not be surprising; even though nitrate levels are low in most forest systems. The ability to use nitrate would be an advantage where N is limiting growth, and in reducing loss from the system (Ho and Trappe, 1980). Even where a selectivity is shown, uptake systems can probably respond to the presence of nitrate since nitrate reductase is a substrate inducible enzyme (Adams and Attiwill, 1982). Under forest conditions trees can probably utilise whatever N is available (Wollum and Davey, 1975).

Recent work (Alexander, 1982; Bowen, 1981; Bowen and Smith, 1981) has demonstrated the ability of mycorrhizas to exploit soluble organic N compounds, the uptake of which may be important (Heal et al., 1982).

2:2:3 Rates of N uptake.

Rates of N uptake vary with site conditions, species, stage of stand development, and rate of growth (Cole, 1981; Cole and Rapp, 1981; Gosz, 1981; Heal et al., 1982; Keeney, 1980; Melillo, 1981), consequently values of uptake, alone, have little meaning (Miller, 1979).

By comparison with intensively managed agricultural crops N uptake by forests seems minimal, being approximately one

half to two thirds of that required by a maize crop (Keeney, 1980). Cole and Rapp (1981) found a mean N uptake of 55 $kgha^{-1}yr^{-1}$ for 37 sites, ranging from 129 $kgha^{-1}yr^{-1}$ for red alder to 2.6 $kgha^{-1}yr^{-1}$ for black spruce. Generally N uptake by forests follows the pattern temperate $>$ boreal, deciduous broadleaved $>$ coniferous evergreen; with deciduous species taking up approximately twice as much N (Cole, 1981; Gosz, 1981). This difference in uptake does not appear to result from differences in production which are broadly similar for both types (Gosz, 1981), but may be associated with greater rates of mineralization under deciduous species. While natural forests may have very low rates of uptake managed stands have higher uptake values; the annual N uptake required to support maximum growth rate of Corsican pine was 69 $kgha^{-1}$; while Cole (1981) grew Douglas fir under conditions of theoretically unlimited N supply and obtained an uptake of 78 $kgha^{-1}yr^{-1}$, if ground flora were included total uptake was 215 $kgha^{-1}yr^{-1}$ (a value approaching those of agricultural crops).

N requirement differs from uptake, the latter (for a closed canopy system) being measured as N increment of woody components plus N loss from litterfall, crown leaching and root exudation. The former, N increment of woody components plus N required for current foliage production. Due to the simultaneous recycling of N, and the small amounts immobilized in stem wood, requirement may be only 8 to 38% of uptake (Miller, 1979). However, data from Cole and Rapp (1981) indicates that requirement can exceed 85% of uptake in temperate forests.

Rates of forest production and N uptake are highly correlated (Cole and Rapp, 1981), both being influenced by N availablity (Cole, 1981). For optimal growth the concentration of a nutrient in the soil solution should be maintained above a certain critical level below which yield is impaired (Mengel and Kirkby, 1982). This level is not fixed but is inversely related to the soils buffering capacity (Mengel and Busch, 1982). For ammonium this will depend on the soils cation exchange capacity and the rate of mineralization. Ingestad et al. (1981) have demonstrated that relative growth rate depends upon the relative

addition rate of N; it being possible to achieve a high relative growth rate, plus a stable internal N concentration, at low external N concentration, so long as the rate of addition is high (analagous to the buffering capacity mentioned above). The concept of a relative addition rate mimics the soil situation, where plant growth is initially exponential, being associated with an exponentially increasing N demand and N depletion at the root surface. Demand is partially satisfied by exponential exploitation of the soil by growing roots. Mineralization rate, relative root growth rate, root morphology and mycorrhizas all determine N status and growth by influencing the N flux available to the plant.

2:2:4 N use strategies and efficiency.

Differences in N uptake between coniferous evergreens and deciduous broadleaves can be partly explained by the former's longer foliage retention. Deciduous species adopt a stress avoidance mechanism during adverse environmental conditions by shedding their leaves; coniferous evergreens invest in stress resistance and possess needles which are morphologically and physiologically adapted to withstand periods of seasonal stress. Perennial leaf duration coupled with a high rate of photosynthesis and N retranslocation maximizes photosynthetic efficiency per unit of foliar N. Thus photosynthetic efficiency per unit of leaf N, is directly proportional to leaf longevity and photosynthetic rate, but inversely proportional to N concentration (Shaver, 1981; Small, 1972a, 1972b; Vitousek, 1982). Conifers have lower foliar N concentrations than broadleaves (Gosz, 1981) although the amount of N per unit of leaf area is actually greater due to a higher specific leaf weight. Conifers therefore invest greater carbon and mineral mass per unit leaf area but obtain an overall advantage through extended retention (Gosz, 1981). Additionally, conifers can concentrate N into a small area of photosynthetically active foliage maximizing photosynthate production per unit N (Schlesinger and Chabot, 1977).

The importance of needle retention is underlined by the observation that retention is longest for species adapted to poor sites, and increases in a given species in response to

low N availability (Cole, 1981). For managed stands the onset of N deficiency is often associated with the sacrificial abscission of older needles, as N is withdrawn to satisfy current demands (Miller, 1981), i.e. foliage longevity is reduced. These observations are not incompatible; natural stands are subject to comparatively stable levels of N availability, so growth rates and needle retention adjust accordingly. Also, the supply of other nutrients is likely to be in balance; managed stands are subject to greater fluctuations in N supply due to periodic fertilizer application, this may make it more difficult for relative growth rate to adjust to changes in N availability. In addition, other nutrients are commonly supplied as fertilizer in the absence of N, resulting in an imbalance of supply and the developement of N deficiency. This is associated with N withdrawal from older foliage with the resultant shedding of needles. Where a balanced nutrient supply is provided relative growth rate should respond to the rate of N supply and deficiency symptoms should not appear (Ingestad, 1982).

These adaptations enable conifers to produce 50% more dry matter per unit N for a given leaf area, or 100% per unit N for a given leaf weight, than deciduous species (Cole, 1981; Cole and Rapp, 1981; Gosz, 1981).

Efficiency of N use appears to be inversely related to N circulation in the ecosystem. Vitousek (1982), reviewing much of the recent literature, found that the amount of N in litterfall and nutrient use efficiency (expressed as the ratio of litter dry weight: weight of N in litter) were inversely proportional to N availability. For sites where N availability was high efficiency of N use was low, and vice versa. This may be explained in terms of species changes; conifers are more efficient than broadleaves and tend to be associated with sites where rates of N mineralization are low; or phenotypic change within a species. Turner (1977) showed that Douglas fir could adjust the portion of its N requirement obtained from N withdrawal from foliage, depending on soil N availability. However, Chapin (1980) found no evidence for increased N reabsorption on poor sites compared with good, while both absolute and relative N withdrawal may actually be greater in species with

high foliar N levels (Vitousek, 1982). This concurs with the findings of Cole and Rapp (1981) who found that N withdrawal was generally greater in broadleaves compared to conifers. It is probable that at least part of the increased use efficiency of N on poor sites results from greater reabsorption, which has been clearly demonstrated for some species (See Section 2:4:5).

Where N availability is low, conifers seem likely to dominate due to their lower N requirement. A change in species, or a change within a species, in response to low N availability, which results in greater N use efficiency may lead to a reduction in litter quality. This will reduce rates of mineralization, possibly resulting in a positive feedback which may maintain or even exacerbate N stress.

2:2:5 Changes in N uptake during stand development.

N uptake changes during ecosystem development (Attiwill, 1981; Kazimirov and Morozova, 1973; Miller, 1981; Turner, 1975). Initially, cycling is dominated by uptake which must continually increase to meet the demands of growth and development. At this stage leaf area and twig weight are continually increasing, each year foliage weight exceeds that of the previous years (or year in the case of deciduous species). Consequently virtually none of a tree's N requirement can be met through retranslocation.

The forest floor is just beginning to form, with annual release from litterfall being a function of tree size a year or more previously (Miller, 1981). Since crowns are still small, and do not fully occupy the site, capture of atmospheric inputs is minimal, while uptake by the tree biomass may be low due to limited root system development and a competing ground flora. Virtually all the trees uptake demand must be met by the soil. N concentration and replenishment of N in the soil solution is critical to stand development at this stage.

Maximum leaf area/biomass is achieved just before canopy closure whereafter it declines slightly and then stabilizes to remain more or less constant (Bray and Gorham, 1964; Rodin and Bazilevich, 1967; Vitousek, 1982). Leaf litterfall also becomes constant (Gessel and Turner, 1976) and the forest floor may attain a steady state, depending on the rate of decomposition.

Uptake remains fairly constant, since only N immobilization in woody components continues to increase, where the concentration of N is very low (Vitousek, 1982).

A large proportion of requirement can now be met by internal recycling, while increased capture of atmospheric sources can actually meet demand for certain nutrients, but not N or P. The soil is replaced by the forest floor as the main zone of uptake, associated with a shift in fine root abundance from the soil to the forest floor layers (Vogt et al., 1981). However, the soil must continue to supply some N (Miller, 1981).

Where N is especially limiting the increase in use efficiency, and decline in decomposition rate can lead to an accumulation of the forest floor, associated with N immobilization. This can lead to N deficiency, and progressive deterioration in mature stands (Williams, 1983).

N uptake will therefore increase progressively until canopy closure when it stabilizes slightly below its maximum value, as internal cycling mechanisms begin to operate. This situation may continue (Miller, 1981; Turner, 1975), or uptake may eventually decline as the stand becomes overmature (Grier et al., 1974; Gosz, 1981; Kazimirov and Morozova, 1973).

2:3 External N inputs into forest systems

2:3:1 Atmospheric N Additions

The transport of atmospheric N to vegetation surfaces and the soil occurs as a result of two distinct processes; dry deposition and wet deposition.

Wet deposition is mediated by precipitation, rain or snow, and measurements of N input by this mechanism exist for most geographical areas (Söderlund, 1981; Söderlund and Svensson, 1976). The quantity of N added by wet deposition depends on the amount of precipitation and the concentration of N compounds in the precipitation. Areas with low precipitation normally exhibit higher concentrations of N, although the total N added is lower than in high rainfall areas (Söderlund, 1981). Incorporation of N compounds into rain occurs within clouds or during drop descent. For Europe wet deposition returns 1 - 6 $kgha^{-1}$ nitrate and 1 - 5 $kgha^{-1}$ ammonium annually (Böttger et al., 1978). Maximum nitrate values occur in or

near industrial areas associated with high N oxide levels Henderson and Harris, 1975; Melillo, 1981), while high ammonium levels are associated with agricultural activity and particularly large numbers of livestock (Söderlund and Svensson, 1976).

Dry deposition is less clearly understood than wet deposition, consequently measurements of N inputs by this mechanism are less well established. Both particulate matter and gases are subject to dry deposition processes, which comprise: gravitational settling; eddy transfers; molecular diffusion and impaction by inertia (Miller, 1979; Söderlund, 1981).

Factors influencing rates of deposition are: 1) Physical/ chemical nature of the surface. This influences surface resistance which in turn largely depends on aerodynamic roughness; it is influenced at one level by surface micro-properties, e.g. cuticular waxes, stomatal pores and leaf hairs, and at another by gross canopy features such as height and foliage density (Gorham et al., 1979). The presence of a vegetation canopy normally increases dry deposition (Melillo, 1981) being greater for forests than other vegetation types or bare soil (Chamberlain, 1975). 2) Particle size: N compounds occur as both small ($< 2\mu m$) and large ($> 2\mu m$) particles, ammonium being more commonly associated with the smaller size (Brosset, 1978). For large particles deposition is largely a result of gravitational settling with surface factors being of little importance, re-suspension can occur easily (decreasing net deposition). Fog and mist behave as large particles (Söderlund, 1981). Small particles depend largely on surface criteria and eddy transfers (therefore windspeed): once impacted, resuspension is unlikely to occur due to strong electrostatic binding. 3) Solubility of gases: most N gases present in the atmosphere are highly soluble in water, solubility being reduced above pH 9 for certain compounds. Gases can therefore be rapidly absorbed onto wet surfaces, under such conditions surface resistance will be of little importance. Surface moisture may partially explain ammonia absorption by soils (Paul, 1976) and acid moss flora (Tamm, 1953). 4) Wind velocity: high wind velocities increase the probability of turbulent processes, these are more efficient than molecular diffusion which occurs when air flow is laminar.

5) Concentrations of N compounds in the atmosphere; deposition is normally expressed as a deposition velocity, which is proportional to the compound's atmospheric concentration (Miller, 1979).

Of these variables N concentration in the atmosphere, is most rate determining, with windspeed being of secondary importance, after which vegetation characteristics assume local significance (Melillo, 1981). As with wet deposition, inputs are greatest near industrial areas or where there is a high density of livestock.

Amounts of N contributed by dry deposition are uncertain but are probably less than wet deposition, e.g. Mayer and Ulrich (1974) found an input of 5.8 $kgNha^{-1}yr^{-1}$ by dry deposition compared with 22.6 $kgNha^{-1}yr^{-1}$ in bulk precipitation for beech forest. Nilhgard (1970) found 0.7 $kgNha^{-1}yr^{-1}$ compared to 8.2 $kgNha^{-1}yr^{-1}$, again for beech. Bulk precipitation inputs for Europe range around 5 $kgNha^{-1}yr^{-1}$, e.g. Heal et al. (1982) 6 $kgNha^{-1}yr^{-1}$, Miller (1979) 5 $kgNha^{-1}yr^{-1}$ and Tamm (1982) 4 $kgNha^{-1}yr^{-1}$. For thirty-six I.B.P. sites the mean N input in bulk precipitation was 9.8 $kgNha^{-1}yr^{-1}$, the range being 1 - 22.8 $kgha^{-1}yr^{-1}$ (Cole and Rapp. 1981).

Evidence suggests that conifers are considerably more efficient than broadleaves at trapping aerosols. Conifers generally have a greater leaf area resulting in greater interception, 3 - 6 mm of rain being needed to wet conifer foliage compared with 0.5 - 2 mm for broadleaves (Larcher, 1975). This high interception is accompanied by greater dry and wet deposition (Mayer and Ulrich, 1978; Schlesinger and Reiners, 1974). These factors, coupled with autumnal foliage loss by many broadleaves, may result in significantly greater atmospheric input into coniferous evergreen systems; an important consideration for poor sites (Gosz, 1981).

2:3:2 Biological N fixation.

Biological N fixation is another source of N input into forest systems. Development of the acetylene reduction assay, a rapid technique for assessing N fixation (e.g. Hardy et al., 1973; McNab and Geist, 1979), has led to considerable research interest in N fixation in a range of natural and managed

systems. For forests much of this material has been reviewed by Granhall (1981); Granhall and Lindberg (1978, 1980); Jones (1978) and Waughman et al. (1981). In addition, biochemical aspects of N fixation have been dealt with by Hardy and Burns (1968); Hardy et al. (1973) and Stewart (1982), who also consider the biochemical basis of the acetylene reduction assay.

Apart from certain symbiotic associations, e.g. legumes, casuarina, podocarpus and Alnus (Nutman, 1976; Smittle, 1979), where fixation may be high, over 200 $kgNha^{-1}yr^{-1}$ (Cole and Rapp, 1981), N fixation in forests is due largely to heterotrophic organisms and autotrophic blue-green algae (Granhall and Lindberg, 1978). The heterotrophs are free living and include actinomycetes, fungi and bacterial genera (both aerobic and anaerobic). Blue-green algae may be free living, e.g. crust forming species in some Swedish forests (Waughman et al., 1981), associated with mosses (Granhall and Selander, 1973; Weber and Van Cleve, 1981) or in symbiotic associations with lichens (Alexander et al., 1978). Blue-green algae are important N fixers in tundra and boreal systems while heterotrophic fixation dominates in temperate forests (Granhall, 1981).

A range of environmental factors influence free living N fixers. 1) Oxygen. N fixation is a reductive process and the enzymes responsible are inhibited by high oxygen levels, however the influence of oxygen varies since many species possess effective enzyme protection systems. 2) Moisture. Fixation is stimulated by increasing soil moisture levels and inhibited by dry conditions (Jaeger and Werner, 1981). 3) Temperature. Nitrogenase activity of heterotrophic microbes is highly temperature sensitive (Waughman and Bellamy, 1980) with a Q_{10} of 3-6 (Stewart et al., 1978). Most N fixers are mesophiles with a temperature optimum around 30°C (Granhall, 1981), fixation being inhibited by very cold conditions (Jordan et al., 1978). 4) Soil pH. Up to 34% of the variability in nitrogenase activity can be explained by pH (Waughman and Bellamy, 1980). Most N fixers have a pH optimum of around 7 but certain bacteria and blue-green algae can fix down to pH 4 (Granhall and Lindburg, 1978; Granhall and Selander, 1973). Bulk pH measurements may not reflect the importance of microsites. 5) Inorganic

compounds. Nitrogenase activity is correlated with calcium and potassium levels in peatland ecosystems (Waughman and Bellamy, 1980). molybdenum levels can be important as can concentrations of aluminium (Granhall and Lindberg, 1978). High ammonium levels are detrimental (Hardy et al., 1973). 6) Energy. The availability of carbohydrate material is probably the main control on fixation in forest ecosystems (Granhall, 1981), an increase in fixation commonly occurring on the addition of available carbohydrate (Waughman et al., 1981). Mycorrhizas may depress fixation through competition (Gadgil and Gadgil, 1978). Rhizosphere fixation may be a consequence of carbon rich exudates (Barber and Lynch, 1977).

N fixation can be detected in most components of forest ecosystems (Melillo, 1981). Phyllosphere fixation has been detected by a number of workers (Jones, 1978; Richards and Voigt, 1965; Sucoff, 1979). Results obtained by Jones suggested important levels of canopy fixation but later revision of these estimates (Sucoff, 1979) and the findings of other researchers suggest that inputs are low (e.g. Granhall and Lindberg, 1978). For 51 woody species the maximum level of canopy fixation was 0.2 $kgNha^{-1}yr^{-1}$ (Sucoff, 1979), and it seems unlikely that values exceed the revised values of Jones (2.4 $kgNha^{-1}yr^{-1}$).

Fixation is associated with living and dead woody material, particularly stems (e.g. Granhall and Lindberg, 1978; Spano et al., 1982; Waughman et al., 1981). Amounts are invariably low but may be important where woody litter constitutes the bulk of the forest floor (e.g. Graham and Cromack, 1982). Forest floor fixation is particularly associated with the F layer (Waughman et al., 1981) which, in relative terms, is an important site for N fixation (O'Connell et al., 1979) as is the surface soil (Jones, 1978).

Stimulation of N fixation in the rhizosphere seems well known; Barber and Lynch (1977); Dobereiner (1974); Rambelli (1973); Richards (1973). Richards and Voigt (1964, 1965) suggest that N fixation associated with pine mycorrhizas is due to microbes present in the rhizosphere; Jurgensen and Davey (1971) give conflicting results but suggest that rhizosphere N fixation may occur only in the presence of fungal exudates. Silvester

and Bennet (1973) found nitrogenase activity on the short roots of native New Zealand conifers.

Total quantities of N fixed by biological means vary but are probably in the range 1 - 12 (28) $kgNha^{-1}yr^{-1}$(Granhall, 1981; Granhall and Lindberg, 1980; Jones, 1978), with many forest systems fixing less than 10 $kgNha^{-1}yr^{-1}$ (Tamm, 1982: Waughman et al., 1981). Though absolute amounts are small they can represent 5 - 10% of the N annually cycled through vegetation (Paul, 1978); even small additions will be significant for systems where N is limiting.

The importance of biologically fixed N may outweigh the actual amounts, such N is released as diverse organic compounds which may stimulate other microbial processes. In particular, the decomposition of woody litter with very high C:N ratios is linked with N fixing bacteria which provide an N source for basidiomycetes attacking the N poor substrate (Silvester et al., 1982; Spano et al., 1982; Sunderström and Huss, 1975).

2:3:3 Geological N inputs

Weathering of primary geological deposits is unimportant as an N input to forest ecosystems, however, the weathering of certain organic rich secondary deposits can be important in a few restricted localities (Reiners, 1981; Woodmansee et al., 1979).

2:3:4 N losses and N budgets

Mechanisms of N loss from forested ecosystems are discussed in Sections 2:5:3 and 2:5:6. For undisturbed systems losses are controlled by a number of self regulating mechanisms, perhaps the most important of which is plant uptake (Cronan, 1980b; Vitousek et al., 1982). Additionally, the soil retains N in the form of ammonium ions, while high rates of nitrification are prevented in many forests. Significant N loss normally only occurs where nitrate levels are high in the absence of effective plant uptake (Bormann et al., 1974).

Due to N conserving mechanisms, losses determined for a variety of forest ecosystems have been found to be low; Cronan (1980a); Feller (1977); Keeney (1980); Miller et al., (1979); Rapp et al., (1979); Sollins and McCorison (1981); Sollins et al., (1980). Reported values ranging from 0.1 to around 4

$kgNha^{-1}yr^{-1}$ (Cole and Rapp, 1981; Gosz, 1981), although higher values do occur (e.g. Melillo, 1981). A large number of budgetary studies indicate that N inputs exceed N losses, often by a factor of 2 (Gorham et al., 1979; Gosz, 1981; Melillo, 1981; Reiners, 1981; Tamm, 1982). For 36 I.B.P. sites (Cole and Rapp, 1981) the net balance of N was an increment of 4.5 $kgNha^{-1}yr^{-1}$, with only one stand showing an N deficit.

2:4 Internal N cycles.

2:4:1 Introduction

External inputs and losses of N have already been considered, the internal cycling of N will be dealt with here. Within an ecosystem N moves between three compartments, the vegetation, the forest floor plus organic soil layers, and the sub-soil. Trees take up inorganic N from the forest floor and soil releasing N through litterfall, throughfall, root death and exudation. Release of organically bound N occurs via decomposition and mineralization in the forest floor.

2:4:2 Throughfall

Throughfall and stemflow are the subject of a comprehensive review by Parker (1983).

As rain passes through a canopy its chemical nature is altered due to foliar leaching and adsorption (Feller, 1977; Olson et al., 1981; Tukey, 1970, 1980); enrichment from accumulated deposition including fog and cloud droplets (Parker, 1983; Söderlund, 1981); cation exchange (Eaton et al., 1973); and nutrient uptake and release by epiphytes and the phylloplane microflora (Lang et al., 1976; Parker, 1983; Ruinen, 1974). Because of differences in these variables throughfall characteristics vary with season, quantity and nature of precipitation, foliar element concentrations and tree species (Miller, 1979).

Work conducted by Carroll (1979) identified several factors influencing throughfall; 1) an increase in the cation concentration of incident precipitation increased nutrient adsorption (or decreased leaching); 2) leaching losses declined with increasing exposure to rain, i.e. in autumn and winter; 3) high solution losses of N followed dry periods while high particulate losses followed wet periods; 4) leaching losses were greater

from older foliage than younger; 5) for an individual rain event there was an initial flux of N mainly as particulate matter which rapidly declined to remain at a low level. He concluded that for rain events of long duration canopies were ultimately N sinks.

The cycling of N as throughfall seems relatively unimportant in terms of quantity, most studies indicate a decrease in the amount of N (as ammonium, nitrate, and total N) or a slight increase, relative to rainfall, (e.g. Luxmoore et al., 1981 ; Olson et al., 1981; Ostman and Weaver, 1982; Ryan and Bormann, 1982; Zimka and Stachurski, 1979). However N concentrations increase due to evaporation (Parker, 1983). The quality of rain is markedly changed by contact with the canopy. Most obvious is the increase in organic N compounds (Nykvist, 1963; Olson et al., 1981; Verry and Timmons, 1977) due to foliar leaching and exudates or decomposition products from epiphytic microbes (Mahendrappa and Ogden, 1973). The presence of organic N compounds may act as a growth stimulus for saprophytic organisms in the forest floor (Clarholm and Rosswall 1980).

A portion of the rain intercepted by a canopy may be directed towards the stem and become stemflow, amounts will clearly be influenced by crown structure and bark characteristics (Ford and Deans, 1978), being greater for smooth barked species (Parker, 1983). Stemflow transports smaller amounts of material to the forest floor than throughfall, 1 - 20% (mean 12%) of the throughfall flux (Parker, 1983), with absolute amounts of N probably being less than in rainfall (Olson et al., 1981). However, element concentrations tend to exceed those of throughfall by an order of magnitude while pH is invariably lower (Parker, 1983). Of potential importance is the redistribution of rainfall as throughfall and stemflow (Ford and Deans, 1978) which may lead to spatial differences in a number of forest floor, soil and plant growth processes.

2:4:3 Root exudation

Assessing the importance of root exudates in the cycling of N is extremely difficult, both composition and quantity are influenced by the age, nutritional status, light, temperature,

moisture and rhizosphere microbes (Bowen and Theodorou, 1973; Rambelli, 1973). In addition, the presence of mycorrhizas seems to increase root exudation (Reid et al., 1983). Exudates cannot be readily collected without altering the root environment and therefore exudation (e.g. Smith, 1970). consequently it is difficult to extrapolate such data to the field.

Root exudates contain N mainly as amino acids (e.g. Smith, 1976) and this may amount to 0.8 - 4 $kgNha^{-1}yr^{-1}$ (Harris et al., 1979; Smith, 1976). Although amounts are small such N is highly labile and the stimulating effect of specific amino acids on the rhizosphere or soil microflora may be important (Barber and Lynch, 1977).

2:4:4 Litter inputs

a. Introduction

The formation of litter is a first step in the recycling of N to plants. In forests it is the dominant pathway for supplying carbon and N to the soil system. Reviews by Bray and Gorham (1964) and Rodin and Bazilevich (1967) cover most of the earlier literature while much of the recent material is included in a synopsis by Staaf and Berg (1981). In addition Cole and Rapp (1981) present a synthesis of I.B.P. data.

b. Above ground inputs

Input rates

Rates of litter production and N return are broadly proportional to primary productivity (Bray and Gorham, 1964; Miller, 1979; Rodin and Bazilevich, 1967; Staaf and Berg, 1981) with leaf fall accounting for most of the N returned through litterfall (Gosz, 1981; Melillo, 1981). Up to 83% of the N returned annually to the forest floor is through litterfall (Cole and Rapp, 1981). Primary production is similar for conifers and broadleaves with litterfall being slightly higher under the former, however N return is greater under deciduous broadleaves due to the higher N concentrations in the litter (Table 2:2).

TABLE 2:2

Litterfall and litter N beneath coniferous and broadleaved forest (from Gosz, 1981).

	Coniferous		Broadleaved
Total litterfall ($t\,ha^{-1}yr^{-1}$)	2-7	$\geqslant$	5-7
Litterfall N ($kgha^{-1}yr^{-1}$)	10-90	$\leqslant$	45-90
Leaf litterfall ($t\,ha^{-1}yr^{-1}$)	0.3-6	$\geqslant$	1-5
Leaf litter N (%)	0.4-1.3	$<$	0.5-1.8

For temperate deciduous broadleaves 60 $kgNha^{-1}yr^{-1}$ is returned as litterfall while 36 $kgNha^{-1}yr^{-1}$ is returned under temperate conifers (Cole and Rapp. 1981).

Patterns of input.

Deciduous species exhibit a marked temporal input prior to the onset of cold or dry seasonal conditions while evergreen conifers from temperate and boreal regions also exhibit seasonal variation of leaf litter input, with maximum amounts and lowest N concentrations before the start of adverse seasonal conditions (Bares and Wali, 1979; Lee and Correll. 1978). Reproductive structures also exhibit seasonality and may have high N concentrations (Melillo, 1981); the input of pollen in early summer when conditions are suitable for active decay may be a useful source of N in temperate coniferous forest (Stark, 1972).

The input of large woody components does not follow a seasonal phenology, although the quantity and proportion of woody litter increases erratically throughout the life of a stand (Gessel and Turner, 1976), but relates to damaging events such as high wind or heavy snow (Staaf and Berg, 1981). During periods when the proportion of woody litter is high total N returns are greater due to the larger mass, although the litter's mean N concentration is considerably reduced (Gessel and Turner, 1976). There is considerable spatial variation in the input of large woody components (Foster and Lang, 1982; Graham and Cromack, 1982).

c. Below ground input rates.

Early studies (such as those reviewed by Rodin and Bazilevich, 1967) appear to have drastically underestimated the importance of below ground litter inputs. Fine root biomass ranges from 1 to 12.6 Tha^{-1} with turnover accounting for 63 to 77%, of primary production (Ågren et al., 1980; Fogel, 1983; Harris et al., 1979). Turnover of fine roots is frequently 90% of the standing crop (Fogel, 1980) resulting in an organic matter input of 2 to 5 times that from above ground litterfall (Fogel, 1980; Persson, 1978), equivalent to an N return 2 times greater (Henderson and Harris, 1975; Wells and Jorgensen, 1975).

Most research seems to indicate that fine root growth and death occurs independently of shoot growth, temporal variation being largely a result of environmental changes. Growth seems to take place where and when soil moisture and temperature conditions are favourable. Poor growth and death of fine roots are commonly associated with soil moisture stress and low temperatures (Deans, 1979; Nambiar, 1983; Persson, 1980).

d. Short circuits.

Primary consumption, particularly of foliage, can influence litter formation by altering the timing of input, influencing the general condition of the plant, and removing N to the primary consumer food chain (Staaf and Berg, 1981).

Recently it has been suggested that the feeding activities of defoliating insects can have ecosystem level consequences as a factor regulating biogeochemistry in certain systems (Swank et al., 1981). Defoliation results in an input of frass and foliage debris, plus leaching of elements from the damaged canopy, which may stimulate decomposition processes and enhance nutrient availability (Kitchell et al., 1979; Mattson and Addy, 1975). In a system where litter inputs are low in N, and forest floor accumulation and nutrient immobilization occur (Williams, 1983), defoliation could stimulate turnover and production. Swank et al. (1981) have reported increased nitrate loss from hardwood ecosystems suffering chronic defoliation associated with increased soil respiration, mineralization, and above ground net primary production.

2:4:5 Cycles within the tree.

In addition to cycling between plants and the soil, cycling also occurs between plant parts. This is best documented for foliage (Viro, 1955), involving the mobilization and translocation of N from older foliage to younger foliage, stem, branches and roots in the case of evergreen species; while deciduous trees can only translocate to perennial organs. Trees may also withdraw N from xylem during heartwood formation, preventing long term immobilization (Merril and Cowling, 1966; Miller, 1981).

Translocation of N from ageing or abscissing tissue gives the tree an energy advantage if the N withdrawn is stored in the organic form (Staaf and Berg, 1981), while reducing loss through leaching, volatilization or immobilization. Also, translocation conveys a level of nutritional independence from the soil when new growth commences in spring, at a time when mineralization and N availability may be low. N withdrawal is associated with the simultaneous translocation of carbohydrate and other elements (Chapin and Kedrowski, 1983: Staaf and Berg, 1981). On breakdown the mobile fraction can be withdrawn and stored in perennial organs, in evergreen species the main site for storage is the foliage (Miller, 1981).

Deciduous species translocate significant quantities of N prior to foliage abscission, e.g. 78% for chestnut oak (Ostman and Weaver, 1982), 90% for tamarack (Cole, 1981), 33 to 36% for northern hardwoods (Ryan and Bormann, 1982) and 70% for eastern deciduous forest (Luxmoore, et al., 1981). Coniferous evergreens also exhibit a marked withdrawal of N, e.g. 39% for loblolly pine (Switzer and Nelson, 1972), 76.6% for Scots pine (Stachurski and Zimka, 1975), 85% for Scots pine (Viro, 1955). There is some evidence to suggest that conifers as a group translocate less N than deciduous species, which may depend more on internal cycling than conifers (Attiwill, 1981; Cole, 1981). Cole and Rapp (1981) indicate that some 30% of broadleaved N requirement is met by translocation from senescing leaves while there is little or no translocation for conifers, where uptake is generally equal to requirement. Luxmoore et al. (1981) found less translocation from conifer foliage, com-

pared to hardwood, for the same site. These findings disagree with those presented above and with Miller (1981) who indicates that 50% of the N requirement of Corsican pine may be met by translocation.

Differences may in part result from tree response to differing site conditions. There is evidence that translocation (i.e. cycle tightness) increases on poorer sites (Gosz, 1981; Vitousek, 1982). Stachurski and Zimka (1975) demonstrated that on an N rich older site oak and hornbeam trees withdrew only 14% of foliar N while 68% was withdrawn by the same species growing on a poorer site in association with pine. Lamb (1975) showed that N withdrawal from needles of Pinus radiata was more marked on poor than fertile sites. One would therefore expect low N concentrations in the litter of trees growing on infertile sites, which appears to be the case (Florence and Chuong, 1974; Lamb and Florence, 1975; Mahendrappa and Weetman, 1973; Miller and Miller, 1976). However, in a recent review of the available literature Chapin and Kedrowski (1983) found both an absolutely and a proportionally greater reabsorption of N in species with more N in foliage. They proposed that low N levels in the litter of species from poor sites merely reflects low foliar N concentrations, not greater withdrawal.

In evergreen species most retranslocation is not associated with tissue death but represents N accumulation during dormant periods and susequent mobilization for use during active growth (Miller, 1979). N is stored mainly as protein which undergoes hydrolysis to amino acids which can be moved around the tree (Chapin and Kedrowski, 1983). Translocation between organs follows a seasonal pattern, which combined with uptake should normally meet tree N requirements. Should requirement exceed these first level sources (Miller et al., 1979), due to low soil availability or heavy demand, the tree can utilize N accumulated from previous growing seasons. This mobilization from second level sources (Miller et al., 1979) is at the expense of proper functioning, or even existence, of organs. Second level sources represent N stored in excess of requirement.

2:4:6 Internal cycling and ecosystem development

Differences in internal cycling may have an important influence on the overall form of cycling within an ecosystem. Stachurski and Zimka (1981) identified two cycling extremes associated with poor and fertile sites, typified in their study by pine forest and mixed alder/deciduous forest. The alder site had a large N capital and high foliar N concentrations, virtually all N was recycled through litterfall with only 7% being re-translocated. This resulted in litter with a high N concentration which supported considerable saprophytic activity, resulting in rapid decomposition and N release (half life for N release was 1 month). The N capital at the pine site was only half that of the alder, and foliar N levels were low. Up to 78% of this N was withdrawn before abscission giving litter with a very high C:N ratio, resulting in low saprophytic activity and slow N release (half life for N release was 2.5 years, 30 times that at the alder site).

The form of cycling described for the alder site tends to dominate in rainforest on fertile soils, where foliar N concentrations are high and very little N is withdrawn (Nye, 1961). On poorer soils, however, rainforests translocate greater amounts of N (Grubb, 1977). Rainforest may be a special case with growth being more constant and less seasonal than in temperate latitudes. Conditions give rise to rapid rates of decomposition which exceed rates of input so that there is little litter accumulation (Witkamp and Ausmus, 1976). Leaching losses are minimized due to a well developed network of fine roots and mycorrhizas which make cycling unusually efficient (Stark, 1977; Stark and Jordan, 1978; Went and Stark, 1968).

Data from Cole and Rapp (1981) suggests that many ecosystems lie between the two extremes, depending on both withdrawal and litterfall as a means of recycling N. Since individual species exhibit considerable plasticity in cycling as a response to N availability one cannot generalise about the form of cycling adopted by a species or species group.

Individual species seem capable of responding to differing environmental conditions by modifying their use and cycling of N. This implies an ability to modify physiological processes

(Vitousek, 1982) including polyphenol levels, N withdrawal, and foliage retention. A high internal redistribution of N on deficient sites would result in litter of high C:N ratios which would be slow to decompose (e.g. Alexander, 1977; Heal et al., 1982). An accumulation of N in slowly decomposing litter is an effective loss from the system, at least in the short term. Such accumulation can occur as a stand enters middle age, the formation of a mor humus layer commonly being associated with a progressive decline in tree growth following the onset of N deficiency (Miller, 1981; Ovington and Madgwick, 1959; Williams, 1972).

Changes in N availability can cause alteration of tissue quality; most important is the production of polyphenols, which are commonly produced by plants subjected to environmental stress (Dell and McComb, 1978; Puritch, 1977). Plant polyphenols are complex organic molecules which can have a tanning effect on plant proteins and microbial enzymes, resulting in complexes highly resistant to microbial degredation. The degree of tanning undergone by leaf proteins during senescence determines their subsequent rate of decay (Davies et al., 1964). Polyphenols may act as precursors of aromatic and carboxylic components of humic and fulvic acids which are major constituents of humus (Davies, 1971). In living leaves polyphenols occur in vacuoles, separate from cytoplasmic protein with which they mix when autolysis occurs during senescence.

Many workers (Coulson et al., 1960; Davies, 1971; Davies et al., 1964) have reported a greater quantity and diversity of polyphenolic substances in the leaves of species growing on nutrient deficient sites (associated with mor humus formation), compared with the same species on fertile sites. Davies (1971) found leaf polyphenol content to be inversely proportional to soil nutrient status, which for young soils closely reflects the nutrient status of the parent material.

The level of available calcium has an important modifying effect on polyphenols, stimulating polymerization to a point at which they become insoluble (Davies, 1971; Coulsen et al., 1960). Thus the absolute polyphenol level is less important than the extent of polymerization and consequently polyphenols

are more stable on acid sites where calcium levels are generally low. It is likely that certain species produce a high proportion of stable polyphenols which tends to encourage mor humus formation (Gosz, 1981).

Fine roots are undoubtably important in humus formation, with several studies (e.g. Fogel, 1983; Kimmins and Hawks, 1978; Vogt et al., 1981) indicating that fine root systems occur mainly in the humus layer on mor sites. Recent work indicates that the major litter input into forest systems may be from roots and mycorrhizal fungi (Fogel, 1983). Unfortunately no data exists on polyphenol levels in these organs, although they may be of dominant importance.

The supply of N and species plasticity in cycling can lead to mor and mull humus formation under the same species. It also accounts for the reversability of the process following an increase in N availability, e.g. fertilization, or factors leading to increased rates of decomposition (Gosz, 1981).

2:5 Ammonium and nitrate; dynamics and behaviour in the soil.

2:5:1 Ammonium and the soil.

Ammonium is a cation and as such can be adsorbed by the soil cation exchange complexes. The cation exchange capacity (c.e.c.) of most soils is large compared with their ability to adsorb anions, being 0.1 to 40 milliequivalents per 100 g. of soil. In general, c.e.c. increases with the clay and/or organic matter content of a soil, being low in sandy soils or soils with little organic matter. A portion of c.e.c. results from pH dependent charge on the soil colloids, increasing with a fall in pH due to dissociation of hydrogen from the hydroxyl groups of clay minerals or the functional groups of organic molecules.

Exchangeable ammonium is freely available to plants and rapidly equilibriates with free ammonium in the soil solution, together these readily available forms comprise less that 2% of the total N in soils with only a little occurring in the ionic form in the soil solution ($<$ 2 ppm (Cole, 1981)). See Brady (1974), Jenny (1980), Pritchett (1978) and Russell (1973).

In addition, some non-exchangeable ammonium is present in most soils where it occurs in; 1, crystalline compounds

formed from constituents in the soil solution; 2, primary silicate minerals such as micas and feldspars, where it occupies sites normally occupied by potassium; 3, interlayer positions in minerals such as vermiculite and illite, which may also be occupied by potassium. For surface soils, non-exchangeable ammonium may represent 1 - 25% of the total soil N (Kudeyarov, 1981). Of these non-exchangeable forms only the third is reasonably available to plants and microbes (Nõmmik, 1981); some 30 - 60% of fixed ammonium can be exploited by the biota (Kudeyarov, 1981).

Due to exchange and fixation processes ammonium mobility through the soil is an order of magnitude below that of nitrate (Bowen, 1973). In addition, ammonium is rapidly taken up by plants (Cronan, 1980b) and is central to the mineralization/immobilization process (Jansson, 1958; Paul and Juma, 1981; Winsor, 1958). These factors combine to give low solution concentrations of the ion, with very low leaching losses from undisturbed ecosystems (e.g. Herbauts, 1980; Sollins and McCorison, 1981; Sollins et al., 1980).

2:5:2 Ammonification

This is the first, and often final, stage of mineralization in which organically bound N is transformed to the inorganic forms, ammonium then nitrate, by microbial action. Strictly, ammonification is the reduction of amino N to ammonium, the initial breakdown of organic material to yield amino N being proteolysis (Mengel and Kirkby, 1982). In both cases the reaction is carried out by heterotrophic microbes which derive energy from the transformations.

A very wide range of heterotrophic microbes are involved in ammonification, including both anaerobic and aerobic organisms, possessing considerable biochemical diversity (Heal, 1979). It is this biochemical heterogeneity which determines the influence of environmental factors on ammonification. Because of this diversity ammonification is never eliminated but the rate may be markedly affected by environment. In this respect it differs from nitrification which is mediated by a more restricted group of organisms and is, as a result, readily influenced by changes in the environment.

The general relationships between environmental factors and ammonification have been known for a long time (e.g. Harmsen and Van Schreven, 1955; Waksman and Gerretsen, 1931 ; Witkamp, 1966). Since ammonifying populations contain aerobes and anaerobes ammonification proceeds over a wide range of oxygen and moisture levels. Under anaerobic conditions more ammonium may accumulate since less is required for microbial growth (Williams et al., 1979), a fact exploited by anaerobic incubation techniques to assess potentially mineralizable N (Waring and Bremner, 1964). The transformation is inhibited by excessively dry conditions approaching wilting point (Alexander, 1977; Hopmans et al., 1980), although certain systems appear able to function under unusually dry conditions (Nagy and Macauley, 1982). Clarholm et al. (1981) found a positive relation between inorganic N levels and moisture content over the range 20 - 100% of the water holding capacity of a pine forest podsol. For a wide range of soils optimum moisture levels for ammonification are between 50 - 75% of the water holding capacity (Alexander, 1977).

Ammonification is enhanced by cycles of drying and wetting (Birch, 1964), inorganic N release generally increasing with the duration of the dry phase (McColl, 1972; 1973). This response is in part a result of physical changes, due to organic material being made available for degradation which was previously inaccessible to microbial attack. The main explanation, however, is probably a partial sterilization effect on the biomass, killed cells undergoing lysis or rapid breakdown by the remaining biomass resulting in a carbon dioxide and nutrient flux. These fluxes have been shown to be proportional to the size of the initial biomass and the effect has been used to assess the size and nutrient content of the soil biomass pool (e.g. Anderson and Domsch, 1978; Brookes et al., 1982; Jenkinson and Powlson, 1976). Similar fluxes occur after any soil disturbance which results in death of some fraction of the biomass e.g. freezing and thawing (Birch, 1964; Witkamp, 1969) or grinding (Powlson, 1980).

Temperature influences ammonification by acting on microbial respiration and enzyme systems; respiration rate is directly

related to mineralization of physiologically active plant nutrients (Witkamp, 1966; Wollum and Davey, 1975). Respiration increases with temperature, with maximum rates of ammonification occurring between 40 - 60°C, thermophiles dominating at these temperatures. Many workers have demonstrated the importance of temperature (e.g. Buldgen, 1982; Kai et al., 1969) which can be the major limiting factor under cold conditions (e.g. Moore, 1981; Van Cleve et al., 1981). Temperature and moisture show considerable interaction in their influence on respiration and ammonification (e.g. Bunnell et al., 1977); thus respiration is maximal at high temperatures and high moisture levels, with the response to temperature declining at low moisture levels and vice versa. Meentemeyer (1978) demonstrates the importance of this interaction, showing that litter decomposition is highly correlated with actual evapotranspiration, on a macroclimatic scale, which is effectively an index of energy (temperature) and moisture.

Ammonification is generally enhanced in neutral environments and depressed by acid conditions, being higher in soils with mull humus than those with moder, mor or peat (De Laune et al., 1981; Lodhi, 1982; Witkamp and Van der Drift, 1961). Many workers have indicated an increase in ammonification following the application of lime to acid soils, although this may be short-lived (e.g. Carey et al., 1981; Keeney, 1980; Nõmmik, 1978; Robertson, 1982).

The presence of inorganic and organic metabolites influences microbial growth and ammonification. Thus ammonification can be enhanced in the rhizosphere in the presence of plant/microbial exudates (Rambelli, 1973). Clarholm and Rosswall (1980) found that spring and autumn peaks in the number of fungi and bacteria were associated with rainfall when moisture was non-limiting. They concluded that this was a result of inorganic and organic material 1) present in the rain, and 2) leached from foliage.

Resource quality is of major importance in influencing the rate and timing of ammonification, this will be discussed in Section 2:6 with reference to litter decomposition.

The afforementioned factors are variables of macroclimate expressed through microclimatic and soil conditions, as such one would expect considerable variability within and between ecosystems.

2:5:3 Ammonia volatilization

Apart from loss through leaching, negligible for ammonium, ammonium can be subject to gaseous loss on conversion to ammonia, although this is unlikely to be a significant N loss mechanism in unfertilized forests (Keeney, 1980).

Since ammonia is a gas under normal environmental conditions, and as the partial pressure in the atmosphere is low, it is readily volatilized under certain conditions, this being influenced by physical, chemical and biological factors (Freney et al., 1981).

For volatilization to occur there must be an ammonia source this can result from the decomposition of organic N in natural systems, or from fertilizers applied to managed systems (especially urea). Where large quantities of organic matter decompose localised areas of high pH can occur (Freney et al., 1981) which may act as sites for volatilization even when the bulk soil is acid. The decomposition process results in ammonium ions rather than ammonia, therefore conversion to ammonia controls the rate of loss. This depends to a large extent on pH with the ammonia:ammonium ratio increasing with pH; in poorly buffered soils the production of hydrogen ions on the conversion of ammonium to ammonia leads to acidification of the soil solution with a resultant decrease in ammonia loss. At high pH and high initial ammonium levels the main control on volatilization is the soil buffering capacity (Freney et al., 1981).

For a given pH volatilization is positively correlated with temperature, since more ammonium is converted to ammonia at high temperatures. Any factors leading to low ammonium levels will clearly reduce loss, such factors act in most undisturbed forest ecosystems (See previous sections).

Thus while substantial loss may occur from urea treated soils (Keeney, 1980; Morrison and Foster, 1977; Wollum and Davey, 1975), volatilization is unlikely to be important in unfertilized forest or forest treated with acid forming fertilizer,

e.g. ammonium sulphate. Loss from decomposing organic residue can occur but at the pH of most forest soils this will be low; at pH 6 and below only 0.1% of ammonium + ammonia occurs in the ammonia form (Wollum and Davey, 1975).

2:5:4 Nitrate and the soil

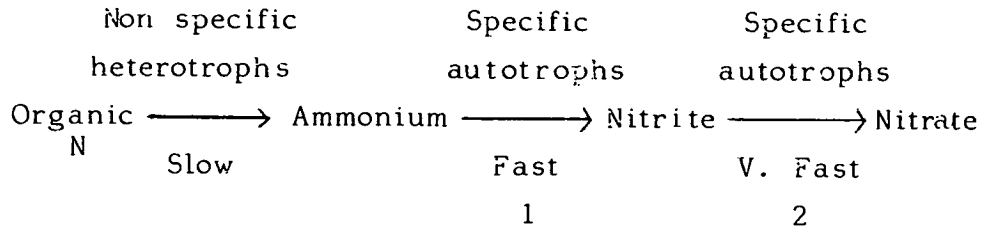
Nitrate is an anion and as such is highly mobile under most soil conditions, rendering it susceptible to both solution and gaseous loss. The anion adsorption capacity of most soils is low in comparison with their cation exchange capacity (e.g. Brady, 1974). Certain minerals and amorphous soil colloids can adsorb anions very strongly, e.g. hydrous iron and aluminium oxides (particularly as surface deposits on other minerals),1:1 and 2:1 clay minerals, iron and aluminium organic complexes and calcium carbonate (e.g. Jenny, 1980; Russell, 1973). Two main forms of anion adsorption occur; ligand exchange (e.g. phosphorus with metallic hydrous oxides) and adsorption by protonated groups, the former being a chemically specific reaction while the latter is purely electrostatic and non specific in nature. Both forms of adsorption are pH dependent and increase with increasing hydrogen ion concentrations. Anion adsorption is therefore highest in acid soils rich in iron and aluminium oxides and/or clay minerals.

Nitrate does not undergo ligand exchange and is only weakly adsorbed, consequently it moves freely in the soil solution and is readily leached (Khanna, 1981). Once formed nitrate does not enter into the immobilization/mineralization process, except via plant uptake (heterotrophic microbes show a preference for ammonium as an N source, Jones and Richards, 1977). Reduction to ammonium by contact with highly reducing soil conditions is unlikely. Loss of nitrate in downward percolating water is associated with the loss of balancing cations (Robertson, 1982).

2:5:5 Nitrification

Extensive reviews have been published regarding nitrification, biochemical aspects (Focht and Verstrate, 1977), ecological aspects (Verstrate, 1981), microbial aspects (Alexander, 1977), and in forest ecosystems (Robertson, 1982).

The initial product of mineralization of organic N is ammonium. Depending on the environmental conditions this may be the end product, or it may be oxidised by microbes to produce nitrate, e.g.



The initial step of ammonification is carried out by a vast range of heterotrophic microbes. Oxidation of ammonium and subsequent further oxidation to nitrate is mediated largely by obligately aerobic autotrophic bacteria. These can collectively gain up to 440 KJ of energy per mole of ammonium oxidised when nitrate is the end product (Robertson, 1982).

Step 1 is known to be carried out by the genera Nitrosomanas, Nitrosococcus, Nitrospira and Nitrosolubus (Focht and Verstrate, 1977), while step 2 is carried out by the genus Nitrobacter (Alexander, 1977). Only Nitrosomanas and Nitrobacter occur commonly in soils. Since nitrite does not occur above trace levels in terrestrial ecosystems there is strong evidence that ammonium and nitrite oxidisers normally occur together. Certain methane oxidising bacteria have been associated with ammonium oxidation, these organisms can occur under more acid conditions than can be tolerated by the groups mentioned above, although their significance is uncertain (Verstrate, 1981). A wide range of heterotrophic bacteria and actinomycetes can oxidise ammonium to nitrite, but only in trace amounts. Further, this normally occurs only in the presence of excess substrate and when active growth has ceased. At least two fungal genera have been shown to oxidise nitrite therefore an entirely heterotrophic pathway is possible in a mixed microbial population (Alexander, 1977).

Rates of nitrification can vary markedly between different ecosystems; for natural systems a low level of nitrification is central to N preservation (Likens et al., 1969; Vitousek

et al., 1979; Vitousek et al., 1982). Where ammonium oxidation is low mineral N remains in the relatively immobile ammonium form (see Section 2:5:1). Where oxidation is rapid ammonium is rapidly converted to nitrate which is subject to loss (see Section 2:5:6). Hydrogen ion production during nitrification can exacerbate ion loss by increasing the level of base cations in solution as a result of cation exchange.

Factors influencing nitrification in both undisturbed and disturbed systems have received considerable recent attention (e.g. Adams and Attiwill, 1982; Jones and Richard, 1977; Khanna, 1981; Lohdi and Killingbeck, 1980; Matson and Vitousek, 1981; Sollins and McCorison, 1981). Six major environmental factors have been identified as influencing autotrophic nitrification in well drained soils (nitrification will not occur in poorly aerated soils since the autotrophs responsible are obligate aerobes); temperature; moisture; pH, substrate availability; the supply of essential nutrients; alleochemicals (Robertson, 1982). The size of the nitrifying population is commonly included in this list but is really an expression of the other factors.

Increasing moisture and temperature stimulates nitrification to a point beyond which rates are reduced. Substrate availability is particularly important; in most forests, litters of high C:N ratio, coupled with readily oxidisable carbon and an active heterotrophic microflora, results in rapid ammonium immobilization, and therefore low levels of nitrification. Mycorrhizal fungi also compete very effectively for low levels of nutrients and may be able to suppress other microflora (Gadgil and Gadgil, 1978). Autotrophic nitrifiers are generally considered poor competitors for ammonium in the presence of heterotrophs (Jones and Richards, 1977). Several workers consider low ammonium availability (due to low levels of gross mineralization or rapid immobilization) to be dominant in the control of nitrification (e.g. Adams and Attiwill, 1982; Vitousek et al., 1982) which is in agreement with the classic work of Jansson (1958).

Soil pH has long been considered the most important environmental factor influencing nitrification (Alexander, 1977; Keeney, 1980). Observations, largely the result of incubations and

laboratory studies, suggest that autotrophic nitrification is severely inhibited below pH 6. However, nitrate is commonly detected in systems of much lower pH, down to pH 4.5 (Robertson, 1982). This could be a result of methylotrophic or heterotrophic nitrification but there is little direct evidence to support this theory (Verstrate, 1981). Bulk pH measurements are probably inadequate and disregard the presence of microsites of higher pH which could act as centres for nitrification. Also, autotrophic nitrifiers exhibit considerably greater ecological flexibility and phenotypic diversity than previously supposed (Verstrate, 1981; Robertson, 1982). Thus nitrifiers exhibit widely differing K_s values (200 X), tolerance to maximum substrate levels, tolerance to maximum levels of end product, inorganic salts, heavy metals and temperature. Robertson (1982) found little correlation between levels of relative nitrification ([nitrate]:[ammonium]) and pH or C:N ratio, he concluded that nitrifiers can adapt to conditions in situ, so that the inability of a population from a neutral environment to nitrify under acid conditions may not reflect the ability of a population which has developed under acid conditions. Therefore in most forests, nitrification per se may be relatively unaffected by conditions e.g. pH.

In agriculture, nitrification is commonly associated with general nutrient availability and levels of fertility. P seems to be of particular importance to autotrophic nitrifiers (Verstrate, 1981), as such, mycorrhizas with their pronounced affinity for phosphorus could exert further control on nitrification.

Alleopathic controls have been frequently suggested (Lodhi and Killingbeck, 1980; Rice and Pancholy, 1974) but doubt has been cast concerning many of the techniques used to demonstrate alleopathy, which possess fundamental flaws (Robertson, 1982).

That nitrification is minimized in many forest systems is demonstrated by the low rates of loss measured by many workers (e.g. Feller, 1977; Sollins and McCorrison, 1981; Sollins et al., 1980). Where nitrification occurs readily losses can be high (Melillo et al., 1981).

2:5:6 Denitrification

This has been the subject of several recent and comprehensive review articles; Focht and Verstrate (1977); Knowles (1981, 1982).

Denitrification is the dissimilatory reduction of one or both of the ionic N oxides (i.e. NO_3^- nitrate and NO_2^- nitrite) to gaseous N oxides (NO, nitric oxide and NO_2, nitrous oxide) which in turn may undergo reduction to gaseous N_2 (Knowles, 1982). All gaseous forms are subject to loss to the atmosphere. The denitrification reaction can be represented as;

$$\underset{\text{solution}}{NO_3^-} \xrightarrow{NR_1} \underset{\text{solution}}{NO_2^-} \xrightarrow{NR_2} \underset{\text{gas}}{NO} \xrightarrow{NR_3} \underset{\text{gas}}{N_2O} \xrightarrow{NR_4} \underset{\text{gas}}{N_2}$$

each of the steps being catalysed by a different N oxide reductase (NR_x). A large range of microbes can carry out some part of the denitrifying reaction where N oxides act as a terminal electron acceptor in the absence of oxygen. The genera involved are biochemically and taxonomically diverse, all are bacteria of which most are heterotrophs and aerobic (Knowles, 1981).

Five environmental factors control denitrification, both in terms of rate and the proportion of products (due to the differential response of the four reductases). These factors are; oxygen, organic carbon, substrate level, pH and temperature. N oxide reductases are depressed by oxygen consequently denitrification occurs only under anaerobic conditions, as a result it commonly occurs during periods of high soil moisture content. However, denitrification can occur in apparently aerobic soils following low levels of rainfall as a result of anaerobic microsites in soil aggregates (Smith, 1980). The most abundant denitrifiers are heterotrophic therefore denitrification is well correlated with organic carbon levels, which are high in most forest soils (e.g. Cole and Rapp, 1981). Denitrification is positively correlated with pH, being maximum at pH 7 to 8, but still occurring with N_2O as the product at pH 4.0 (Nømmik, 1956). Denitrification shows strong temperature dependence in the range 10 - 35°C, being maximum at 60 - 75°C but

still detectable at 0 - 5°C (Focht and Verstrate, 1977). The presence of nitrate is essential as a substrate for denitrification, therefore where conditions result in low nitrate levels denitrification will be insignificant or absent.

One would expect rapid denitrification in anoxic, warm, neutral soils high in organic matter (Keeney, 1980). Little information exists on denitrification in forests but it is likely to occur, at least at low levels (Wollum and Davey, 1975). Forests could provide excellent conditions for denitrification due to the high levels of soluble organic matter in the forest floor. However, pH in most forests is well below the optimum while anaerobic conditions are unlikely to develop in the well aerated forest floor, although nitrate could be leached to anaerobic zones at greater depth. The low level of nitrate in most forest ecosystems should also restrict denitrification.

Despite these factors several workers e.g. Melillo (1981) have detected significant levels of denitrification; Bormann and Likens (1979) found that 19% of N entering a northern hardwood forest was lost through denitrification; Melillo et al. (1981) found that 27 $kgNha^{-1}yr^{-1}$ underwent gaseous loss in a deciduous forest.

2:6 Litter decomposition and N release

N release from litter is a basic process in the cycling of N within an ecosystem. Litter quality, soil organisms and environment regulate decomposition and therefore nutrient release (Berg and Ekbohm, 1983; Berg and Staaf, 1980, 1981; Heal, 1979; Heal et al., 1982; Staaf and Berg, 1981).

The influence of specific environmental factors has already been discussed: litter quality refers to those physico-chemical characteristics which influence decomposition. These include the nature of the carbon source, nutrient sources, modifying compounds and physical properties. Litter quality varies between and within species, depending also on the site conditions (Berg and Ekbohm, 1983) and age (McGill et al., 1981), it also varies between components of the same plant (Heal, 1979). Physical properties which influence decomposition are surface toughness, particle size (surface area) and, in particular, moisture uptake. The latter is influenced by the degree of

physical contact with the soil and therefore particle size (Kääarik, 1974). Conifer needles have a hydrophobic surface and small surface area, as a result they may be slow to take up moisture but are effective at retaining it. They retain their surface integrity for longer than broadleaved leaf litter, which is readily wetted but does not retain moisture to the same extent (Heal, 1979).

A wide range of organic compounds act as carbon and energy sources for microbes, the ease with which a given substrate can be decomposed depending heavily on the properties of its organic constituents (e.g. Minderman, 1968). Water and acetone soluble components such as sugars, amino acids, steryl esters and triglycerides decompose first, disappearing almost completely within the first year. These are followed by celluloses and hemicelluloses then lignin (Berg, 1978; Berg and Staaf, 1981; Berg et al., 1982a, 1982b; Reber and Schara, 1971). Polyphenols and phenols may take even longer to decompose (Minderman, 1968; Reber and Schara, 1971) although polyphenol content may decrease during the first year with an initially rapid fall (Hayes, 1965). The recalcitrance of polyphenols may result from their apparent inhibition of fungal growth (Berg et al., 1982b, 1980).

Although many substances are involved, the rate of decomposition (assessed as CO_2 flux or weight loss) of carbonaceous material is strongly influenced by lignin (Aber and Melillo, 1980; Berg et al., 1982b; Fogel and Cromack, 1977; Meenteymeyer, 1978; Melillo et al., 1982; Parkinson, 1979) which decomposes 5 to 10 times slower than other more soluble compounds. Bunnell et al. (1977) accurately modelled weight loss from decomposing litter by use of a double exponential model to express both rapid and slow rates of decomposition, a similar approach being used to model weight loss by other workers (e.g. McGill et al., 1981).

The reasons for lignins recalcitrance are discussed in detail in a review by Zeikus (1981). Since lignin is one of the last substances to start to decompose its concentration increases relative to those substances which exhibit rapid weight loss. For needle litters no lignin loss may occur until 40 to 45%

of initial needle weight has been lost, i.e. until the lignin concentration has reached around 30% (Fogel and Cromack, 1977). Even after lignin has begun to decompose it does so more slowly than other organic fractions, consequently its concentration still continues to rise (Berg and Staaf, 1980, 1981; Berg et al., 1982b; Melillo et al., 1982). Lignin can also reduce the decomposition rates of more labile compounds which it may structurally enclose, rendering them resistant to microbial attack (Nilsson, 1973; Zeikus, 1981). Because of its recalcitrance lignin decomposition is rate determining for the weight loss of a large fraction of litter (Berg et al., 1982b; Melillo et al., 1982; Parkinson, 1979). High lignin levels or lignin: N ratios being associated with low decomposition rates (Aber and Melillo, 1980). Highly lignified material such as bark and wood decomposes very slowly (Foster and Lang, 1982; Heal et al., 1982) therefore most soil organic matter reflects their unique isotopic carbon ratios (Waring, 1980). In vascular plants lignin may account for 25% of dry weight with lignaceous litterfall accounting for 80% of primary production in some forests (Zeikus, 1981).

N levels have long been correlated with rates of decomposition, weight loss occurring more rapidly for litters with a high N content (Berg and Staaf, 1981; Heal, 1979; Melin, 1930; Witkamp, 1966). However other workers have found the lignin level to be more rate determining (Fogel and Cromack, 1977; Melillo et al., 1982). Hermann et al. (1977) found that weight loss was more highly correlated with the lignin : carbohydrate ratio than it was with the C:N ratio. Initial weight loss (up to 30% of initial weight) is strongly correlated with N (and other nutrient) concentrations, this is largely the decomposition of soluble compounds, cellulose and hemicellulose. Once lignin starts to decompose the weight loss enhancing effect of N appears to be smothered by the slow decomposition of lignin. Recent work (Berg et al., 1982a) indicates that lignin decomposition is actually depressed in litters which had a high initial N concentration. There appears to be an inhibitory effect of ammonium on the ligninolytic enzyme systems of microbes (Keyser et al., 1978) with the rate of decomposition

being shown to decrease following ammonium application (Bengtsman, 1936; Titus, personal communication). Lignaceous material can also fix ammonium leading to the formation of heterocyclic ring compounds which are highly resistant to microbial degradation. Such fixation is indicated by Berg and Staaf (1981) who found that the increase in litter N concentration during decomposition was linearly correlated with an increase in lignin N. Melillo et al. (1982) found that more N was immobilized, per unit of carbon respired, the higher the initial lignin concentration. Thus while initial weight loss may be well correlated with N level (Aber and Melillo, 1980), except where external N sources are high (Melillo et al., 1982), the situation becomes reversed once the decomposition of lignin has started.

N release from decomposing litter is essentially regulated by the same factors as decomposition, but is modified by immobilization process. The pattern of N release from litter follows three phases, although not all need occur under a given set of conditions (Berg and Staaf, 1981). Prior to and during litterfall epidermis integrity may be reduced by the phylloplane microflora, with very early weight loss and N release resulting from the physical leaching of soluble compounds (Nykvist, 1963). The quantity of leachable N appears to be 2 to 4% of the total N, irrespective of the amount (Berg and Staaf, 1981). Since this leachable fraction has a very rapid turnover (Berg, 1978) it is likely that some is decomposed within the litter, particularly in the case of conifer needles (Nykvist, 1963). Early release of N as a consequence of leaching is normally associated with high N levels in the litter, however Berg and Staaf (1980) report leaching loss at a litter N concentration of 0.58%.

Most litters undergo a phase of N accumulation (immobilization) when N concentrations progressively increase. This is a well known phenomenom (Bocock, 1963; Gosz et al., 1973) which can occur whether there is a release of N or not (Berg and Staaf, 1981), and results from a loss of carbon through respiration while N is retained by microbes. Accumulation starts early during decomposition and tends to continue up to approximately 35% weight loss (Berg and Staaf, 1981; Howard and Howard, 1974). For Scots pine needles the period of N

accumulation is associated with the invasion of fungal hyphae (Berg and Staaf, 1979). Under certain conditions an absolute increase in the quantity of N occurs, postulated sources for this N are, N fixation, absorption of atmospheric ammonia, throughfall, dust, insect frass, green litter and fungal translocation/immobilization (Howard and Howard, 1974; Melillo et al., 1982). While the N concentration and absolute N content of the substrate plus microbial biomass may increase the quantity of N in the substrate itself will decrease with time as it is immobilised into microbial N or secondary organic products (Heal et al., 1982; Swift et al., 1979).

The initial N content of litter definitely influences whether immobilisation does or does not occur, however a critical N value above which accumulation does not occur (e.g. Mulder et al., 1969) does not seem generally applicable to the forest situation. The use of C:N ratios to predict patterns of immobilisation/mineralisation in agricultural soils appears to work well (Jansson, 1958; Paul and Juma, 1981), with mineralization occurring below C:N 25 and immobilization above C:N 35, being relatively unaffected by intermediate values (Heal et al., 1982). These patterns result from microbial demand for N during growth as carbon is used, the substrate provides N when the concentration is high, and N in excess of microbial requirements is released by deamination (more generally termed ammonification). Immobilization occurs when the organic N of the substrate is low (Alexander, 1977). Material with C:N ratios above 35 increase in N concentration until a critical value (C:N. 25-35) is reached when N release occurs. This classical model does not adequately describe N behaviour in forests (Berg and Staaf, 1981; Heal et al., 1982) where accumulation occurs at initial N concentrations ranging from 0.3 to 1.4%. 1.4% appearing to be an upper limit (Berg and Staaf, 1981).

Accumulation is related to microbial processes and has been shown to be linearly correlated with weight loss (Berg and Staaf, 1981), i.e. microbial activity, additionally, accumulation increases at high lignin levels (Melillo et al., 1982). The influence of environment seems especially important; Anderson (1973) found that N accumulation in beech leaves incubated

on soil was twice that of those incubated in air; Dowding (1974) found that barley straw accumulated N up to 170 and 230% of its original N content at two tundra sites while no accumulation occurred on a third; Berg and Ekbohm (1983) found that the C:N ratio above which net immobilization and below which net mineralization take place differed between a clear-felled (C:N, 63) and forested (C:N, 109) site.

Accumulation is followed by N release, although N concentrations can continue to rise after a net release has occurred. The N level at which release occurs varies markedly between forest types but can occur at concentrations as low as 0.7 to 0.8% (Berg and Staaf, 1981). Once N release has started it is linearly correlated with weight loss. As with accumulation the critical level for N release depends on site, increasing with the rate of first year weight loss (Berg and Staaf, 1981). This is probably a conservation mechanism to prevent N loss on sites where decomposition is rapid.

From what has been said it is clear that a high litter input, low in N but high in lignin, and containing a large proportion of wood, will give low rates of decomposition and N release. Under such conditions considerable litter accumulation may occur (Witkamp and Ausmus, 1976). The contribution of large woody components is often underestimated (Graham and Cromack, 1982; Richards, 1981) but their contribution in terms of biomass and N returned to the forest floor can be large, increasing as the stand matures (Gessel and Turner, 1976). Such woody materials may be exceptionally low in N, combined with organic recalcitrance, resulting in very low rates of decomposition and prolonged N immobilization (Vitousek, 1982). Fungi dominate in the decomposition of woody substrates, and all substrate N may have to be converted to mycelium before release can occur (Heal et al., 1982; Käärik, 1974; Richards, 1981), a process which may take 20 years, during which time the material can act as a sink for mineralized N (Graham and Cromack, 1982).

There is comparatively little information on the decomposition of fine roots, although it is assumed that this is controlled by the same factors influencing the decomposition of above

ground litter (Gosz, 1981). N concentrations in fine roots and mycorrhizas have been reviewed by Fogel (1980) and Kimmins and Hawkes (1978), these range from 0.33 to 2.03%, thus one might expect rapid release or slow release of N depending where in this range a sample lay. It is not known whether fine roots undergo physiological changes associated with abscission in an analagous manner to foliage (Fogel, 1983), if they do this would obviously influence their rate of decomposition.

Ford and Deans (1977) report rapid disappearence of dead fine roots, while Popović (1980) associates them with slow decomposition and N mineralization. Berg et al., (1982c) found first year weight loss of root litter to be very similar to leaf litter (32%). Such differences probably reflect stand N status in much the same way that this influences leaf litter decomposition. Decomposition of fine roots may account for 42% of carbon release being 2 to 2.8 times that released by above ground litter (Edwards and Harris, 1977). N release during the decomposition of fine roots may be 1.4 to 2 times that from above ground sources (Henderson and Harris, 1975; Wells and Jorgensen, 1975), while Fogel (1983) found mycorrhizas and fine roots accounted for 43% of N release in a Douglas fir stand.

2:7 N mineralization, the importance of the microflora

The importance of the microflora in the cycling of nutrients in soil systems has been comprehensively reviewed by Coleman et al. (1983). Measured rates of N mineralization in forest ecosystems range from 30 to 50 $kgha^{-1}yr^{-1}$ for conifers and 100-300 $kgha^{-1}yr^{-1}$ for deciduous broadleaves (Gosz, 1981). Sites where temperature or moisture are limiting may have lower rates e.g. 3.9 to 1.6 $kgha^{-1}yr^{-1}$ (Popović, 1980) or 11.5 $kgha^{-1}yr^{-1}$ (Rapp et al., 1979). Such values are based on incubation techniques which only measure net mineralization, N released in excess of microbial requirement, and do not account for turnover of N within the microbial biomass (Heal et al., 1982; Paul and Juma, 1981).

N incorporated into the microbial biomass is temporarily immobilized, immobilization normally being associated with an actively increasing biomass (Clarholm et al., 1981). Fungal

tissue may be 2.2 - 19.6% N and can account for 160 - 1430 $kgha^{-1}$ of soil N (Bååth and Soderström, 1979). Frequently. sequential measurements of the microbial standing crop show little change in pool size, however, tracer techniques. (Paul and Juma, 1981) and observation of respiration rates (Clarholm et al., 1981) indicate rapid turnover (Anderson et al., 1981). The reason for this rapid turnover is grazing by the soil fauna, thus the actively proliferating microflora is maintained as a relatively small standing crop with a very rapid turnover (Anderson and Ineson, 1982; Parkinson, 1979). The soil fauna excrete N rich substances and increase the homogeneity of decomposer distribution, thus maximising substrate utilization and increasing N availability (Anderson et al., 1981).

N turnover between the substrate, microbial biomass and soil fauna considerably exceeds net mineralization e.g. estimates of gross mineralization may be as high has 591 $kgha^{-1}yr^{-1}$ (Heal et al., 1982), far in excess of plant requirements (Cole and Rapp, 1981). This N is potentially available to plants through competition with soil saprophytes.

Fungi are nutritionally extremely diverse and dominate in acid forest situations (Bååth and Soderström, 1982; Richards, 1981). Many are able to decompose materials with extremely low N concentrations, perhaps by transferring N from N rich substrates (Berg and Staaf, 1981). N immobilized in fungal tissue is released by lysis and faunal grazing, causing the release of N even when C:N ratios are high ($>$ C:N 35). Many fungi are able to utilize soluble organic N following the initial breakdown of large molecules, deamination then occurring within the mycelium. Thus N turnover can be accomplished without the need for an inorganic pool. Mycorrhizas can also utilize low molecular weight organic N (Alexander, 1982; Bowen, 1981; Bowen and Smith, 1981) enabling plants to compete with saprophageous fungi for a soluble organic N pool. Recent work (Van Cleve and White, 1980) indicates that this pool may be appreciable, 40 $kgha^{-1}$, representing nearly 10% of total system N. Their work has indicated that much of this organic N does not pass through the inorganic pool, suggesting uptake of organic N by saprophytic and

mycorrhizal fungi (Heal et al., 1982).

It has been suggested that the rhizosphere of certain tree species can mineralize or somehow make available some fraction of soil organic N resistant to microbial breakdown under previous vegetation. The magnitude of this rhizosphere effect varies with species, but seems most developed for pioneers such as larch and pine, and less developed for spruce (Fisher and Eastburn, 1974; Gosz, 1981; Jones and Richards, 1977, 1978; Skinner and Attiwill, 1981; Stone and Fisher, 1969; Yeates et al., 1981). Since mycorrhizas can exploit very little humus bound N (Lundberg, 1970) it seems likely that rhizosphere microbes are primarily responsible for N mineralization.

A Comparison of Sitka spruce foliar nutrient levels in pure and mixed stands

3:1 Introduction

As outlined in Section 1, an objective of this study was to determine conclusively whether the presence of larch species exerts a positive influence on the growth and nutrient status, particularly N, of Sitka spruce.

Foliar analysis of Sitka spruce, in pure stands and in mixture with larch, was carried out at two Forestry Commission experiments (Mabie 7 and Inchnacardoch 164) to assess spruce nutrient status under the two regimes. The use of foliar analysis in assessing tree nutrient status is widespread, being a useful means for comparing treatments or identifying deficiencies provided the limitations of the method are appreciated (McIntosh, 1983).

Plant nutrient status is commonly determined by tissue analysis, results being expressed as a nutrient concentration for the entire plant or, as in the case of forest trees, some sampled component (recently Dighton and Harrison (1983) have drawn attention to an alternative method which does not depend on tissue analysis). Results from such analyses are frequently compared with values which are considered optimal for the growth of the species in question, these values are normally based on a large number of analyses for trees exhibiting a range of growth rates (Everard, 1973). The concept of an optimal concentration for growth is attractive but its use is limited in practice; 1) optimal values are not fixed but vary with age and the developmental status of the stand (Miller, 1981; Miller et al., 1981), 2) the optimum depends on the growth parameter chosen (Miller et al., 1981), 3) optimum levels may never be achieved under field conditions. Consequently it is more useful to consider a critical level, below which growth is severely impaired and deficiency symptoms are manifested, when a response to fertilization would be expected.

For forest trees the organ most frequently sampled is the leaf, although other metabolically active tissue can also reflect nutritional status, e.g. twigs and roots (Van den Driessche and Weber, 1977) or inner bark (Olsson, 1978). Whatever the organ chosen it is essential that the temporal and spatial variations in its mineral content be appreciated. Seasonal variation in foliar nutrient levels is well documented (Chapin and Kedrowski, 1983; Maclean and Robertson, 1981; Ostman and Weaver, 1982; Schueller, 1978; Smith et al., 1981). For both conifer and broadleaved species foliar N, P and K decline during the growing season while calcium increases and magnesium fluctuates with no consistent trend. Concentrations stabilize during dormency in late autumn and early winter, which are generally considered the best times for sampling (Everard, 1973; Maclean and Robertson, 1981). For deciduous species, sampling must obviously be undertaken prior to leaf abscission, although opinion varies as to precisely when.

Spatial variation of foliar concentrations within the tree crown is also important. These generally decrease down the crown for N, P and K, although an increase can occur at the base of the live crown (Maclean and Robertson, 1981; White, 1954). For conifers, sampling is normally restricted to the topmost whorl (Everard, 1973) which has the advantage of being a physiologically defineable position (Miller, 1982. Unpublished).

Due to the translocation of nutrients within the tree to metabolically active areas (Fagerström and Lohm, 1977; Miller, 1981) it can be argued that top whorl nutrient concentrations, maintained at the expense of older foliage, may not truly reflect tree nutrient status. Thus Smith et al. (1970) suggest that sampling should include older (more stressed) foliage, Stachurski and Zimka, (1975) propose that nutrient levels in both old and new foliage should be determined to give a gradient over several age classes, an approach adopted by Maclean and Robertson (1981) and by Florence and Chuong (1974). Lamb (1975) has demonstrated that nutrient withdrawal from older needles is more marked on poorer sites. Because of this some workers (Lea and Ballard, 1982; Mahendrappa

and Weetman, 1973; Miller and Miller, 1976) have suggested the use of nutrient concentrations in needle litter as an indicator of nutritional status.

Once determined, nutrient concentrations are normally expressed on a percentage dry weight basis which, under certain circumstances, may be misleading since major changes in carbohydrate (i.e. weight) content could confound interpretation. Smith et al. (1981) have shown variation in needle weights on a seasonal basis and for stands with different silvicultural treatments while Bradbury and Malcolm (1978) demonstrated an increase in the dry weight of Sitka spruce needles during the dormant season. These problems can be largely overcome if mineral concentrations are expressed on a weight per unit leaf area basis (Gholz, 1978; Smith et al., 1981; Stachurski and Zimka, 1975).

In the present study top whorl material was taken for analysis and the concentrations expressed on a dry weight basis. This approach, the norm in the United Kingdom (Everard, 1973), permitted comparison with the published values of other workers and with the critical nutrient levels accepted for Sitka spruce.

3:2 Site descriptions

3:2:1 Experiment Mabie 7.

The experiment is located in the Lochar Moss Section of Mabie Forest (Compartment S46), Dumfriesshire (National Grid Reference: NY 046686). Lochar Moss is an extensive raised bog of uniformly deep peat, at least 4m in depth overall (Malcolm, 1972), with a virtually level surface. Elevation is 13m a.s.l. with moderate exposure in all directions, the site receives 1016 mm of precipitation per year. The peat is oligotrophic in nature and fits grouping 10a, lowland sphagnum bog, in bog group D, oligotrophic basin or raised bog, of the Forestry Commission's peat classification (Pyatt et al., 1979). The underlying geology consists of permian sandstone. Prior to afforestation the area was sporadically used for extensive sheep grazing, the dominant vegetation including Trichophorum caespitosum L. Hartman, heather, Eriophorum vaginatum L., and E. angustifolium Honck. together with sphagna, resulting in a

mainly fibrous peat structure.

Cultivation and drainage were carried out in May 1966 by single mould board plough giving a mean furrow spacing of 2m and a depth of 50-70 cm. Deep drains, 1m wide and 75cm deep, were ploughed at 10 furrow intervals. Planting was with Sitka spruce transplants (1+1) and hybrid larch seedlings (1+0) at a 1.4m spacing in February 1967. The mixture pattern being 3:1, alternate triplets of Sitka spruce in alternate rows, i.e. 25% Sitka spruce. Treatment plots are 0.09 ha with a 0.04 ha assessment plot, the pure spruce plots being designated OW and the spruce-larch mixtures H. Each treatment has 3 replicates arranged in a randomized block design. All treatments received P at planting and a top dressing of K the following year, fertilizer inputs are displayed in Table 3:1. In addition, the OW treatments received a 2,4-D ester weed control in 1969 which completely eliminated heather. No weed control was undertaken in the H treatments. After afforestation heather can become a problem on peats of this group where it may become dominant and provide severe competition for the spruce (Handley 1963), this competition does not seem to influence the growth of pines or larch which eventually suppress heather growth completely.

TABLE 3:1

Fertilizer input and weed control for the Mabie 7 treatments ($kgha^{-1}$ element).

Treatment	1967	1968	1969	1973	1980
OW	27P	95K	2,4-D	50P.95K	50P.95K
H	27P	95K	-	50P.95K	50P.95K

P applied as ground mineral phosphate
K applied as potassium chloride.

3:2:2 Experiment Inchnacardoch 164.

The experiment is located in Inchnacardoch Forest (compartments 499 and 508) near Fort Augustus, Invernessshire (National Grid reference NH 332081). The experimental site lies on an extensive area of blanket bog with a variable small scale topography due to glacial drift deposits, resulting in peat of varying depth, 0.35 - 2.20m (mean 1.05m). Elevation is 295m a.s.l. and the site receives 1270mm of precipitation annually.

The peat is oligotrophic in nature and fits bog group C, oligotrophic slope bogs (hill peat), peat type 11 of the Forestry Commission's peat classification (Pyatt et al., 1979). The underlying geology consists of Moine Schists and associated pre-Cambrian granites with surface deposits of glacial drift material. Prior to afforestation the area was managed as deer forest, the dominant vegetation including heather, Molinia caerulea (L.) Moench, E. vaginatum, E. angustifolium and T. caespitosum.

Cultivation and drainage were carried out in 1965 by single mould board plough giving a mean furrow spacing of 1.8m and a depth of 50-70 cm. Deep drains were ploughed across the experiment at irregular intervals. Planting was with Sitka spruce and Japanese larch transplants (1+1) at a 1.2m spacing. The mixture pattern is alternate triplets of spruce in alternate rows giving 25% Sitka spruce, the mixture treatment being designated JL/SS and the pure spruce treatment SS. The original treatment plots were split in 1973 and one half randomly assigned an N treatment giving plots with (+N) and without (-N) an N input. Treatment plots are 0.04 ha with a 0.02 ha assessment plot. Fertilizer inputs are displayed in Table 3:2 (N.B. the SS-N treatment received 168 $kgha^{-1}$ N element in 1967 while the JL/SS-N treatment has received no N input). Heather has never been a problem on the site and no weed control has been considered necessary. Each treatment has 5 replicates in a randomized block design.

TABLE 3:2

Fertilizer input for the Inchnacardoch 164 treatments ($kgha^{-1}$ element)

Application date	Treatment SS-N	SS+N	JL/SS-N	JL/SS+N
1965	50P	50P	50P	50P
1967	168N	168N	-	-
1970	50P.100K	50P.100K	50P.100K	50P.100K
1973	-	168N	-	168N
1976	50P	50P.150N	50P	50P.150N
1979	-	160N	-	160N
1980	100K	100K	100K	100K

P applied as ground mineral phosphate

K applied as potassium chloride

N applied as urea.

3:3 Methods

3:3:1 Field sampling procedure

Sampling was carried out at Mabie 7 during November 1980, 20 spruce trees were randomly selected from each of the 3 OW and H plots. At Inchnacardoch sampling was carried out in December 1980, with 10 spruce trees being randomly selected from each of the 5, SS-N, SS+N, JL/SS-N, and JL/SS+N plots.

For each tree a fully illuminated side shoot was removed from the topmost whorl for foliar analysis. Shoots were stored in polythene bags at 2-3°C for 18 hours prior to oven drying.

3:3:2 Chemical analysis.

Shoots were oven dried to a constant weight at 85°C after which needles were separated from the shoots and retained for analysis. For each shoot the weight of 50 needles was determined, needles were then ground in a ball mill to approximately 0.5mm mesh size.

Total N, P and K contents of the needles were determined using a modified micro-kjeldahl digest (Allen et al., 1974). 0.1g of sample was accurately weighed into a pyrex digest tube to which was added 2ml of 36N H_2SO_4 and 1ml (dropwise) of 30% (100 volumes) H_2O_2. Tubes were placed in a heating block at 340°C for 5 hours, after which all organic material had been destroyed and the solutions had cleared. Samples

were cooled, transferred to 50 ml volumetric flasks and made up to 50 ml with distilled water. Reagent blanks were run with each set of digested samples, 1 sample in 10 being duplicated to provide a check on reproduceability.

Total N (as ammonium) was determined in solution using an automated colorimetric method employing the salicylate-dichloroisocyanurate reaction in the presence of nitroprusside (Crooke and Simpson, 1971). Total P (as phosphate) was determined in solution using an automated colorimetric method employing the molybate blue complex, ascorbic acid being used as the reducing agent in the molybdenum system (Murphy and Riley, 1962). Total K in the digested solution was determined directly by atomic emission using a Pye Unicam Sp 9 atomic absorption/emission spectrophotometer.

3:4 Results

The randomized block designs of both experiments allowed results to be analysed by a 2-way analysis of variance (Snedecor and Cochran, 1967). Prior to statistical analysis all data were checked for normality while an F test was conducted to ensure that variances were equal.

At Mabie 7 needle dry weights and concentrations of N, P and K are significantly greater in the H treatment (Table 3:3): exceeding the OW treatment by 27%, 44%, 21% and 32% respectively. Expressing the results as a nutrient weight per 50 needles accentuates treatment differences (Table 3:4), indicating that H treatment foliage contains 83% more N, 55% more P and 68% more K than that of the OW.

At Inchnacardoch 164 needle dry weight, %N, %P and %K in the SS-N treatment are all significantly lower than the equivalent values in the SS+N, JL/SS-N and JL/SS+N treatments (Table 3:5 and 3:6). Values for the SS+N treatment do not differ significantly from those in the JL/SS-N treatment, except in the case of %K which is significantly lower in the former. SS+N values are all significantly lower than JL/SS+N values, the same holds for a comparison of the JL/SS+N and JL/SS-N treatments except for needle weights, which do not differ significantly, and %K, which is significantly higher in the -N mixture.

Using data for needle dry weight and nutrient concentrations to give a nutrient content per 50 needles (Table 3:7) accentuates the differences between treatments indicating that JL/SS-N needles contain 246% more N, 253% more P and 205% more K than the SS-N treatment.

TABLE 3:3

Needle weight (g) and nutrient concentrations for the OW and H treatments. Mean values (n=60) and 95% confidence limits.

	Treatment		
	OW	H	Significance
ODW	0.353(0.0232)	0.449(0.0222)	**
%N	0.98 (0.045)	1.41 (0.038)	**
%P	0.28 (0.019)	0.34 (0.017)	**
%K	1.04 (0.055)	1.37 (0.039)	**

ODW = Oven dry weight of 50 needles

** = Means significantly different at P = 0.01 in a 2-way analysis of variance. Actual values of F are displayed in Appendix 1A.

TABLE 3:4

Nutrient content (mg) of 50 needles for the OW and H treatments.

	Treatment	
	OW	H
N	3.46	6.33
P	0.99	1.53
K	3.67	6.15

TABLE 3:5

Needle weight (g) and nutrient concentrations for the Inch-nacardoch 164 treatments. Mean values (n=50) and 95% confidence limits .

	Treatment			
	SS-N	SS+N	JL/SS-N	JL/SS+N
ODW	0.250	0.438	0.467	0.492
	(0.0244)	(0.0235)	(0.0286)	(0.0292)
%N	0.80	1.53	1.48	1.79
	(0.032)	(0.089)	(0.076)	(0.063)
%P	0.18	0.33	0.34	0.40
	(0.012)	(0.023)	(0.024)	(0.027)
%K	0.77	0.98	1.26	1.07
	(0.048)	(0.075)	(0.055)	(0.055)

ODW = Oven dry weight of 50 needles.

TABLE 3:6

Significance of differences between Inchnacardoch treatment means in a 2-way analysis of variance.

ODW	SS-N	SS+N	JL/SS-N	JL/SS+N
SS-N	-	**	**	**
SS+N	-	-	NS	**
JL/SS-N	-	-	-	NS
JL/SS+N	-	-	-	-
%N				
SS-N	-	**	**	**
SS+N	-	-	NS	**
JL/SS-N	-	-	-	**
JL/SS+N	-	-	-	-
%P				
SS-N	-	**	**	**
SS+N	-	-	NS	**
JL/SS-N	-	-	-	**
JL/SS+N	-	-	-	-
%K				
SS-N	-	**	**	**
SS+N	-	-	**	**
JL/SS-N	-	-	-	**
JL/SS+N	-	-	-	-

ODW = Oven dry weight of 50 needles

** = Means significantly different at P = 0.01

NS = Means not significantly different at P = 0.05

Actual values of F are displayed in Appendix 1B.

TABLE 3:7

Nutrient content (mg) of 50 needles for the Inchnacardoch 164 treatments.

Treatment	N	P	K
SS-N	2.00	0.45	1.93
SS+N	6.70	1.45	4.29
JL/SS-N	6.91	1.59	5.88
JL/SS+N	8.81	1.97	5.26

3:5 Discussion

3:5:1 Experiment Mabie 7.

In the absence of N fertilizer the presence of larch in the H treatment would appear to have resulted in a marked increase in spruce needle weight and foliar concentrations of N, P and K, compared with spruce in the OW treatment.

N concentrations in the OW spruce lie in the range (less than 1%) which is associated with deficiency symptoms and poor growth (Everard, 1973), this is consistent with visual observations of the foliage at the time of sampling which exhibited a general soft chlorosis. P and K concentrations, however, are at a level (above 0.18% and 0.5% respectively) sufficient for good growth in the absence of N deficiency. N concentrations in the H spruce fall in the upper part of the range 1-1.5% where growth may be marginal to good. They exceed the 1.2% quoted by McIntosh (1983) above which growth is seldom impaired and fertilizer treatment is normally unnecessary. P and K concentrations are well above those required for good growth and are significantly greater than those in the OW treatment.

On the basis of foliar analysis, the OW spruce are clearly N deficient and should respond to N fertilizer while no such response (or a very limited one) would be expected from the H treatment where N levels appear adequate.

It is interesting to note that the improvement in spruce foliar properties in the H treatment has occurred despite the continued presence of heather in the ground flora. Heather was completely removed from the OW treatment in 1969 following the application of 2,4-D. Herbicide treatment should have benefited the OW treatment as a result of reduced competition, removal of the heather root/endophyte complex, and release of nutrients from killed vegetation.

Data collected by the Forestry Commission's Research Branch is presented in Figures 3:1 - 3:4. These data have been collected periodically during the life of the experiment and permit growth differences to be followed from planting to the present. Foliar N levels were initially higher in the OW treatment (Figure 3:1a) probably as a consequence of the 2,4-D

FIGURE 3:1. FOLIAR NUTRIENT CONCENTRATIONS IN OW AND H TREATMENTS FOR THE PERIOD 1970-1982. ARROWS INDICATE APPLICATION OF PK FERTILIZER.

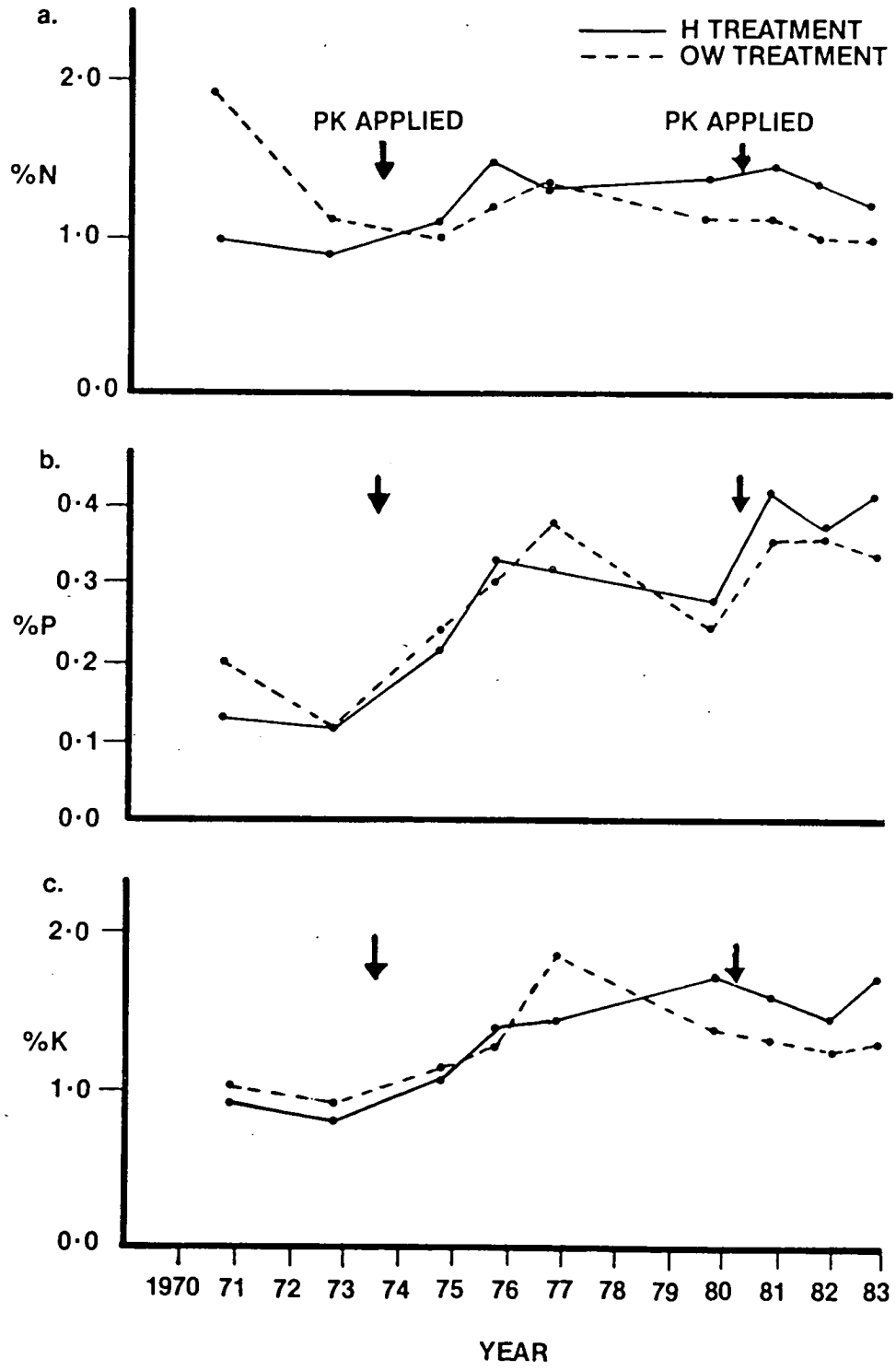
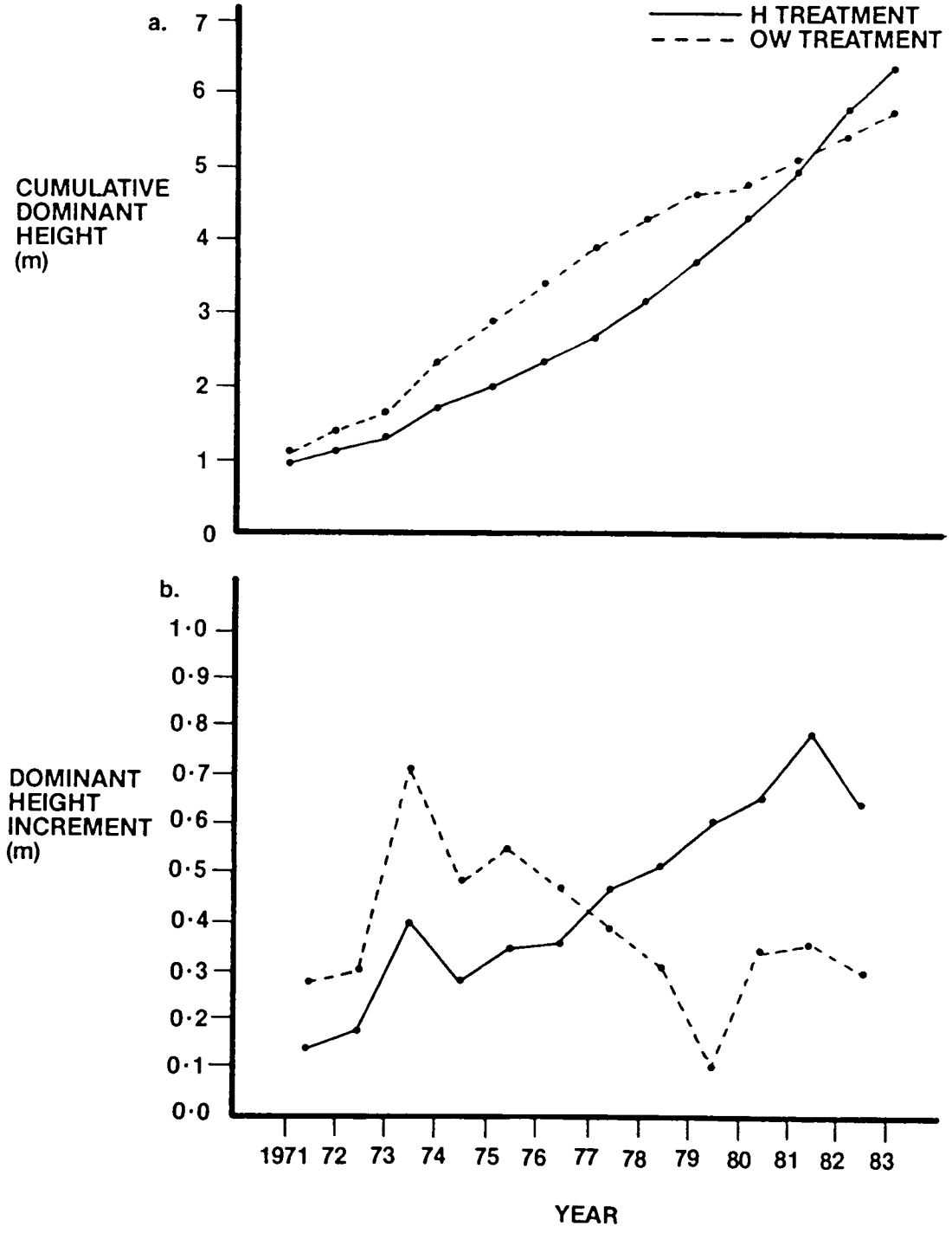


FIGURE 3:2. CUMULATIVE HEIGHT GROWTH AND HEIGHT INCREMENT OF DOMINANT TREES IN THE OW AND H TREATMENTS FOR THE PERIOD 1971-1983.



application in 1969 and heather competition in the untreated H plots. However, OW N levels fall progressively until overtaken by those in the H treatment in 1974 which have remained at a higher level since then. Peaks in foliar N levels may be a response to the application of PK fertilizer in 1973 and 1980. It has been noted (Carey et al., 1981) that the application of ground mineral phosphate enhances mineralization of native organic N.

Foliar P levels exhibit the same trend for both treatments (Figure 3:1b) with a general increase since planting with concentrations peaking then declining following each P fertilization. P concentrations in the H treatment have exceeded those in the OW since 1979. Foliar K levels show a similar response to fertilization but with a reduced amplitude (Figure 3:1c), they have also been higher in the H treatment since 1979.

Height growth of the dominant trees is shown in figure 3:2a, the H treatment remaining below the OW until 1981 when it overtakes it. Height increment values (Figure 3:2b) are greater in the OW treatment until 1977 when they decline below increment in the H treatment. Height increment for the H spruce has increased consistently since planting, peaking after each P/K application. That in the OW spruce increased until 1973 then declined (with similar peaking following P/K fertilization). This decline in height increment is associated with a general fall in foliar N concentrations (Figure 3:1a) however there is no clear correlation between the two. In conclusion, foliar nutrient levels and height increment were initially greater in the OW spruce, probably due to the benefits of weed control. However, this benefit has been short lived and the OW spruce have become N deficient with an associated decline in height increment. In contrast, the H spruce have increased then maintained their foliar N levels and consistently increased their height increment since measurement began in 1970.

3:5:2 Experiment Inchnacardoch 164.

Comparing the pure spruce and mixture treatments it appears that the presence of larch enhances spruce needle weight and foliar concentrations of N, P and K. In the absence of N (SS-

N and JL/SS-N treatments) this difference is dramatic with needle weight increasing by 87%, N by 85%, P by 89% and K by 64%. Even with the application of N fertilizer (SS+N and JL/SS+N treatments) the presence of larch seems to enhance spruce foliar quantities, with needle weight increasing by 12%, N by 17%, P by 21% and K by 9%. Clearly the effect of the presence of larch is depressed when N availability is increased.

The SS-N treatment is N deficient with foliar N levels within the range (less than 1%) quoted by Everard (1973) as being characteristic of N deficiency. In fact, a level of 0.8% is indicative of extreme N deficiency (McIntosh, 1983). Foliar P levels are in a range considered marginal for growth while foliar K is adequate. Consequently there is a marked response to N fertilization in the SS+N treatment with needle weight increasing by 75%, N by 91%, P by 83% and K by 27%. SS+N foliar values are all at a level which should support good growth.

The JL/SS-N treatment is not N deficient with foliar N levels well above the 1.2% below which a response to N fertilizer might be expected (McIntosh, 1983). Foliar P and K are also in the range where growth should be good. That this treatment is not N deficient is underlined by the lack of response to N fertilizer in the JL/SS+N treatment where needle weight does not increase significantly. However there is an increase in foliar N and P concentrations, but this is considerable less than that in the pure spruce treatment.

It is interesting to note that in terms of foliar quantities the SS+N and JL/SS-N treatments are very similar, differences being non significant, except in the case of K. This suggests that the presence of larch primarily influences spruce N status rather than P or K, since all treatments received identical quantities of PK fertilizer. It is tempting to suggest that the larch nurse in the JL/SS-N treatment is equivalent to the 646 $kgha^{-1}$ N received by the SS+N treatment. However, it is invalid to do this on the basis of foliar nutrient concentrations alone since these give no indication of standing biomass.

Data collected by the Forestry Commission's Research Branch is presented in Figures 3:3 and 3:4. For the first six years

FIGURE 3:3. CUMULATIVE HEIGHT GROWTH AND HEIGHT INCREMENT OF DOMINANT TREES IN THE INCHNACARDOCH 164 EXPERIMENT FOR THE PERIOD 1968-1983.

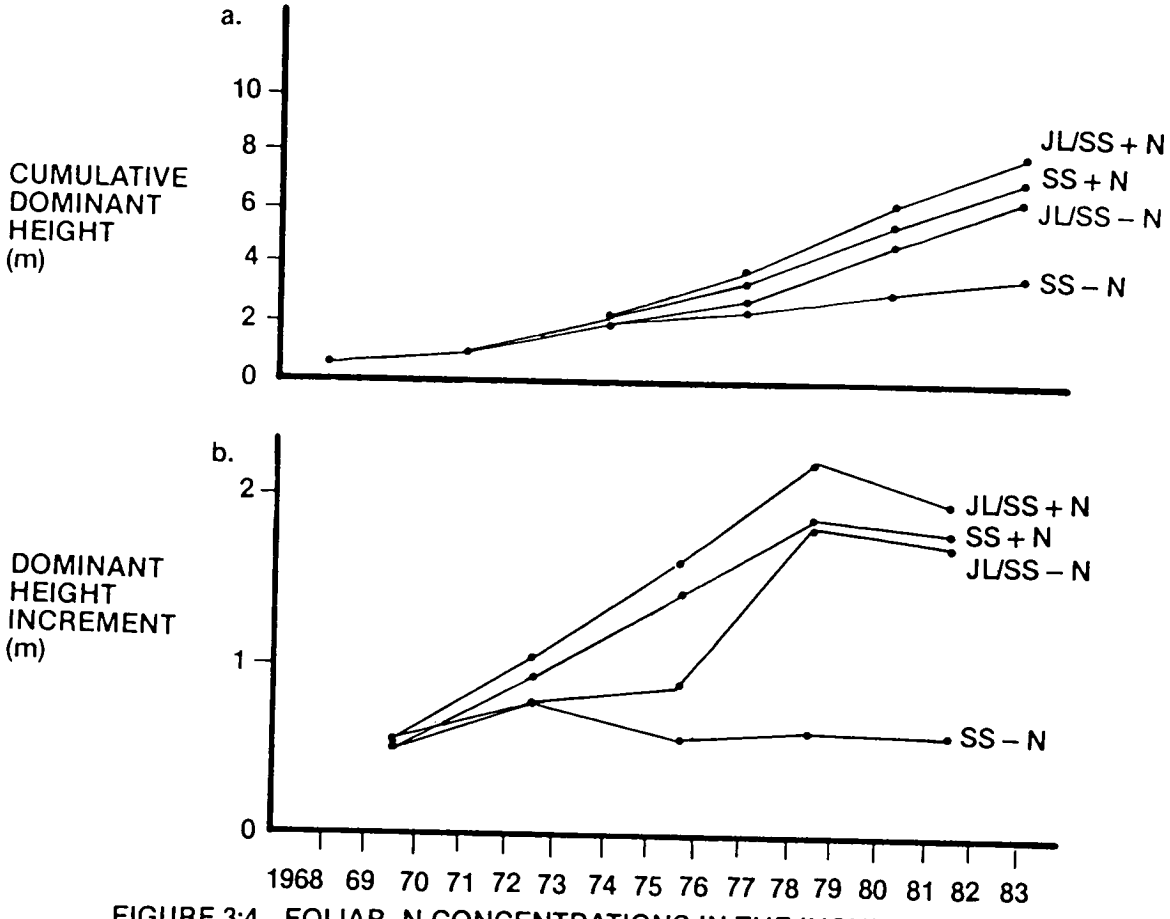
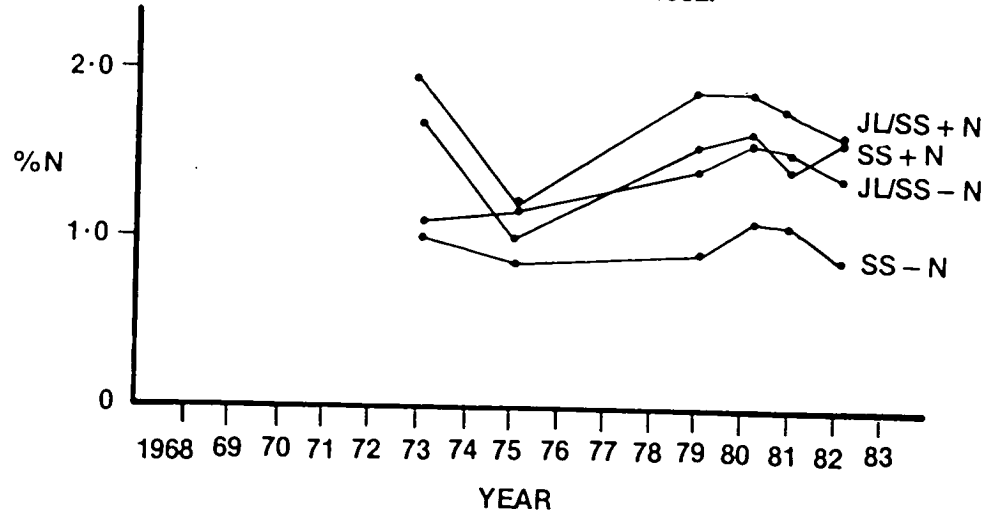


FIGURE 3:4. FOLIAR N CONCENTRATIONS IN THE INCHNACARDOCH 164 EXPERIMENT FOR THE PERIOD 1973-1982.



of measurement height was similar for all treatments (Figure 3:3a), subsequently the mixture and +N treatments have achieved considerably greater height growth than that in the SS-N. As in the case of foliar quantities the presence of larch has resulted in increased height growth both with and without N fertilizer. Height growth is similar in the SS+N and JL/SS-N treatments which further underlines the parity between these treatments. Height increment (Figure 3:3b) fell off early in the SS-N treatment and is consistent with the decline in foliar N (Figure 3:4). Increment in the JL/SS-N treatment was initially similar to that in the SS-N but instead of declining it increased dramatically between 1972 and 1978 and has remained at a level comparable to the SS+N treatment.

The presence of larch appears to enhance spruce nutrient status and height growth, and is similar to the response achieved in pure spruce following the application of N fertilizer.

3:6 Conclusions

At 2 experimental sites spruce, in the presence of larch, exhibits markedly improved foliar nutrient levels and greater needle weight, these are associated with increased height growth. Results, particularly from the Inchnacardoch 164 experiment, indicate that this response is the result of an improvement in spruce N status which can be reproduced in the absence of larch by the application of N fertilizer.

As outlined in section 1:3, the improved N status of mixture spruce may or may not be associated with a greater N capital in the mixture tree biomass, relative to pure spruce.

A Comparison of basal area, derived values for foliage weight and the weight of foliar N ($kgha^{-1}$) between pure and mixed stands.

4:1 Introduction

It has been demonstrated, Section 3, that Sitka spruce in the presence of larch exhibits increased needle weight, foliar concentrations of N, P and K and increased height growth. On the basis of this information alone it cannot be assumed that the mixture treatments contain more N ($kgha^{-1}$) since no account has been taken of N contained in the larch and therefore in the stand biomass. An expression was required for the above ground N capital in pure and mixture treatments.

Usually such quantities are determined by a strategy of biomass sampling based on a regression technique such as that described by Young and Carpenter (1976). Such techniques exploit an allometric relationship between an easily measured independent variable, frequently diameter or basal area, and a dependent variable such as stem weight or foliage weight, which is less readily determined.

A sample plot is laid out in the study area and a number of trees, selected randomly or systematically, are destructively sampled. The relationship between the quantities it is desired to determine (dependent variables) and one or more tree dimensions (independent variables) is calculated. Knowing the relevant linear dimensions of all trees within the sample plot the value of the dependent variables for each tree, and thus for the plot as a whole, can be readily determined.

In this case due to constraints of time and the limited size of the experimental plots (destructive sampling of the intensity required would have significantly altered the experiments) it was not possible to derive specific regression equations for the two experimental sites. In the absence of specific equations it was necessary to use pre-existing regress-

ions developed by other workers for the same species growing under similar conditions. This decision increases the error likely to be attached to any derived quantities but does permit the identification of probable differences between pure and mixed stands.

4:2 Site description

Work was carried out at the Mabie 7 and Inchnacardoch 164 experiments, previously described in Section 3:2.

4:3 Methods

Methods were essentially identical for both experiments, all trees in the assessment plots being enumerated (assessment plots were 0.04 and 0.02 ha at Mabie and Inchnacardoch respectively).

It was decided to use regression equations developed by Mitchell et al. (1981) since these have been derived for young stands growing on sites with yield classes similar to those of the experiments. Unfortunately these regressions are based on trees with a breast height diameter of 5 cm, or greater, whereas many of those measured in this study were below this value. For small trees (less than 5cm breast height diameter) it is better to use root collar diameter (e.g. Rutter, 1955), since this is a readily defineable position. However, very little published material exists for young stands where this has been carried out and so this approach was rejected. The use of a regression for trees outwith the range for which it was constructed clearly will increase the uncertainty attached to the estimated dependent variable.

Diameter measurements were made at breast height using a pair of external diameter calipers. Two measurements were taken for each tree, one along a north to south axis and the other along an east to west axis. All calculations involving tree diameter are based on the mean value obtained from each pair of measurements.

Diameter values were used in conjunction with Mitchell et al's regressions (Table 4:1) to produce single tree estimates of foliage dry weight. Single tree values were summed to give a total for the assessment plot and extrapolated to a per hectare basis.

The weight of N contained in the foliage was derived by using estimated foliage dry weight and top whorl foliar N concentrations previously determined for Sitka spruce (Section 3:4) and hybrid larch (Section 5:1:4). Foliar N concentrations were not determined for the Japanese larch at Inchnacardoch, so calculations are based on an assumed value of 1.5%. This value is in the lower end of the range found by Leyton (1956) for Japanese larch growing at differing rates, and within the marginal growth range quoted by Everard (1973).

Applying top whorl foliar N concentrations to foliage for an entire tree will produce an overestimate of the amount of N contained in the crown, since concentrations normally decline down the crown (Maclean and Robertson, 1981). This overestimate may, or may not, be similar for larch and spruce depending on, 1) the sharpness of fall in concentration, and 2) the distribution of foliage in the crown.

Estimates of the N capital of the foliage are consequently based on a number of assumptions to which are attached certain errors. The results must therefore be regarded as highly approximate. It is hoped that the level of accuracey achieved is sufficient to identify differences between treatments.

TABLE 4:1

Coefficients of regression of foliage dry weight (kg) against tree basal area (m^2).

Species	a	b
Sitka spruce [1]	0.53	430.14
Hybrid larch [2]	1.07	241.79

1. GYC 14, age 22.
2. GYC 13, age 10.

4:4 Results

4:4:1 Experiment Mabie 7.

Basal area and mean tree basal area are both greatest in the OW treatment, although the difference between treatments is small (Table 4:2). Mean tree basal area for the spruce is 43% greater in the H treatment with derived values for foliage dry weight (Table 4:4) being, again, slightly higher in the OW treatment. Mean tree foliage weight in the mixture spruce exceeds that of the pure spruce as does the weight of N contained in the foliage (83% greater). Derived values for the weight of N contained in the foliage of the whole stand are also markedly greater (61%) in the H treatment (Table 4:4).

TABLE 4:2

Basal areas for the Mabie 7 experiment

	Treatment			
	OW	H		
		spruce	larch	total
Stems ha^{-1}	2372	739	1697	2436
Basal area (m^2ha^{-1})	9.4	4.2	4.5	8.7
Mean tree basal area (cm^2)	40	57	27	36

4:4:2 Experiment Inchnacardoch 164.

Basal area and the mean tree basal area are greatest in the JL/SS-N treatment, 100% and 153% greater, respectively (Table 4:3). Mean tree basal area for the spruce is 300% greater in the mixture treatment with derived values for stand foliage dry weight also being greater (Table 4:4). Mean tree foliage weight in the mixture spruce exceeds that of the pure spruce as does the weight of N contained in the foliage (400% greater). Derived values for the weight of N contained in the foliage of the whole stand are also substantially greater (167% greater) in the JL/SS-N treatment. The weight of spruce foliar N

in the mixtures exceeds that in the SS-N treatment despite the large disparity in tree numbers (Table 4:4).

TABLE 4:3

Basal areas for the Inchnacardoch 164 experiment.

	Treatment			
	SS-N	JL/SS-N		
		spruce	larch	total
Stems ha^{-1}	2175	615	1160	1775
Basal area (m^2ha^{-1})	3.8	4.2	3.4	7.6
Mean tree basal area (cm^2)	17	68	29	43

TABLE 4:4

Derived foliage weight and weight of foliar nitrogen for the Mabie 7 and Inchnacardoch 164 experiments ($kgha^{-1}$).

Treatment	Foliage dry weight	Foliar nitrogen
OW	5478 (2.3)	54(0.023)
H Spruce	2223 (3.0)	31(0.042)
Larch	3063	56
Total	5286	87
SS-N	3011 (1.4)	24(0.011)
JL/SS-N Spruce	2164 (3.5)	34(0.055)
Larch	2022	30
Total	4186	64

Bracketed values express data on a mean tree basis ($kg\ tree^{-1}$).

4:5 Discussion

Results from both experiments indicate a greater weight of foliar N in the mixture treatments, this being most marked at Inchnacardoch where it is accompanied by increased basal area and stand foliage weight. At Mabie the increase results solely from a higher foliar N concentration in the mixture treatment. While size and N content of individual spruce is greater in the mixtures at both experiments an overall increase in stand basal area (and foliage biomass) is seen only at Inchnacardoch.

An increase in the weight of foliar N contained in the mixtures is probably indicative of an overall increase in stand N capital. In young stands, in particular, a substantial portion of N in the stand may be contained in the foliage. For a young Pinus radiata. D. Don. stand (basal area $7.4m^2 ha^{-1}$, 2347 stems ha^{-1}) Madgwick et al. (1977) found that 85% of the N contained in the aerial biomass was present in the foliage.

In conclusion, mixture spruce are larger and contain more N than their equivalents in pure stands, while results suggest that the overall quantity of stand N is greater in the mixtures. A greater N capital in the mixture trees indicates a higher level of N uptake and availability. This suggests that larch can in some way exploit an N source which spruce cannot, with some of this N becoming available to the spruce. Any future study should attempt to verify these findings by actual biomass sampling.

Larch litter influences on N availability and cycling.

5:1 Nutrient withdrawal prior to abscission.

5:1:1 Introduction

Larch species are commonly reported as having foliar N concentrations which are higher than other conifers, approaching levels associated with deciduous hardwoods. Ovington (1956) found, on 3 sites, that larch (L. decidua. Mill., L. kaempferi) had the highest foliar N and P concentrations of a range of conifers, 1.24 to 2.32% and 0.18 to 0.22% respectively. Leyton (1956), examining the correlation of foliar nutrient levels with growth of L. kaempferi, found N concentrations of 1.13 to 2.28% and P concentrations from 0.15 to 0.47%, for a series of fertilizer inputs. Usova (1977) found larch (L. Siberica Ledeb.) needles to be higher in P than spruce or pine on the same site, as did Pogrebriak (1960).

Most deciduous species withdraw foliar nutrients before abscission; recent evidence suggests both a greater relative and absolute withdrawal at high foliar nutrient concentrations (Chapin and Kedrowski, 1983); therefore high foliar N levels may not be reflected by high N concentrations in litter. Tilton (1977) found that L. larcina (Du Roi) K. Koch had high N concentrations in its foliage (2.5%), but withdrew 64% during senescence; Chapin and Kedrowski (1983) demonstrated a 75% N withdrawal for this species. Schueller (1978) recorded a decline in N concentrations for L. decidua before needle fall.

The extent of withdrawal is important since it influences litter quality, particularly the C:N ratio, and consequently the pattern of decomposition and nutrient release.

In the present study hybrid larch foliar nutrient levels were assessed at the Mabie 7 experiment and the changes prior to abscission followed by sequential sampling. A year previously an identical sampling scheme was carried out at another site where small plot size severely limited the sampling

intensity, so the data is not presented here.

5:1:2 Site description

Sampling was conducted at the Mabie 7 experiment which is fully described in Section 3:2:1.

5:1:3 Methods

5:1:3a Field Sampling Procedure

Sampling was carried out from August through to November 1981 at 21 day intervals. 5 trees were randomly selected from each of the 3 H plots at each sampling data. For each tree a fully illuminated side shoot was removed from the top whorl. Shoots were stored in polythene bags for a maximum of 18 hours at 2-3°C prior to oven drying.

5:1:3b Chemical analysis

Shoots were oven dried to a constant weight at 85°C. For each sample the oven dry weight of 50 needles was determined, subsequent sample preparation and analysis for N, P and K was identical to that described in Section 3:3:2.

5:1:4 Results

Foliar concentrations of N, P and K were initially high, 1.82%, 0.48% and 1.50% respectively (Figure 5:1 and Appendix 2A). Subsequently, concentrations of N and K show a marked decline falling to 37.4% and 73% of their initial value. P concentrations remain constant during senescence, while needle weight declines to 72% of its initial value.

Expressing changes as a nutrient content per 100 needles (Figure 5:2, Appendix 2B) indicates a decline in all three elements prior to abscission; N, P and K falling to 26.6%, 73.6% and 53.8% respectively of their initial content.

FIGURE 5:1. CHANGE IN LARCH FOLIAR NUTRIENT CONCENTRATIONS AND NEEDLE WEIGHT AT MABIE 7 DURING ABSCISSION. MEANS OF 15 SAMPLES. ERROR BARS SHOW 95% CONFIDENCE LIMITS.

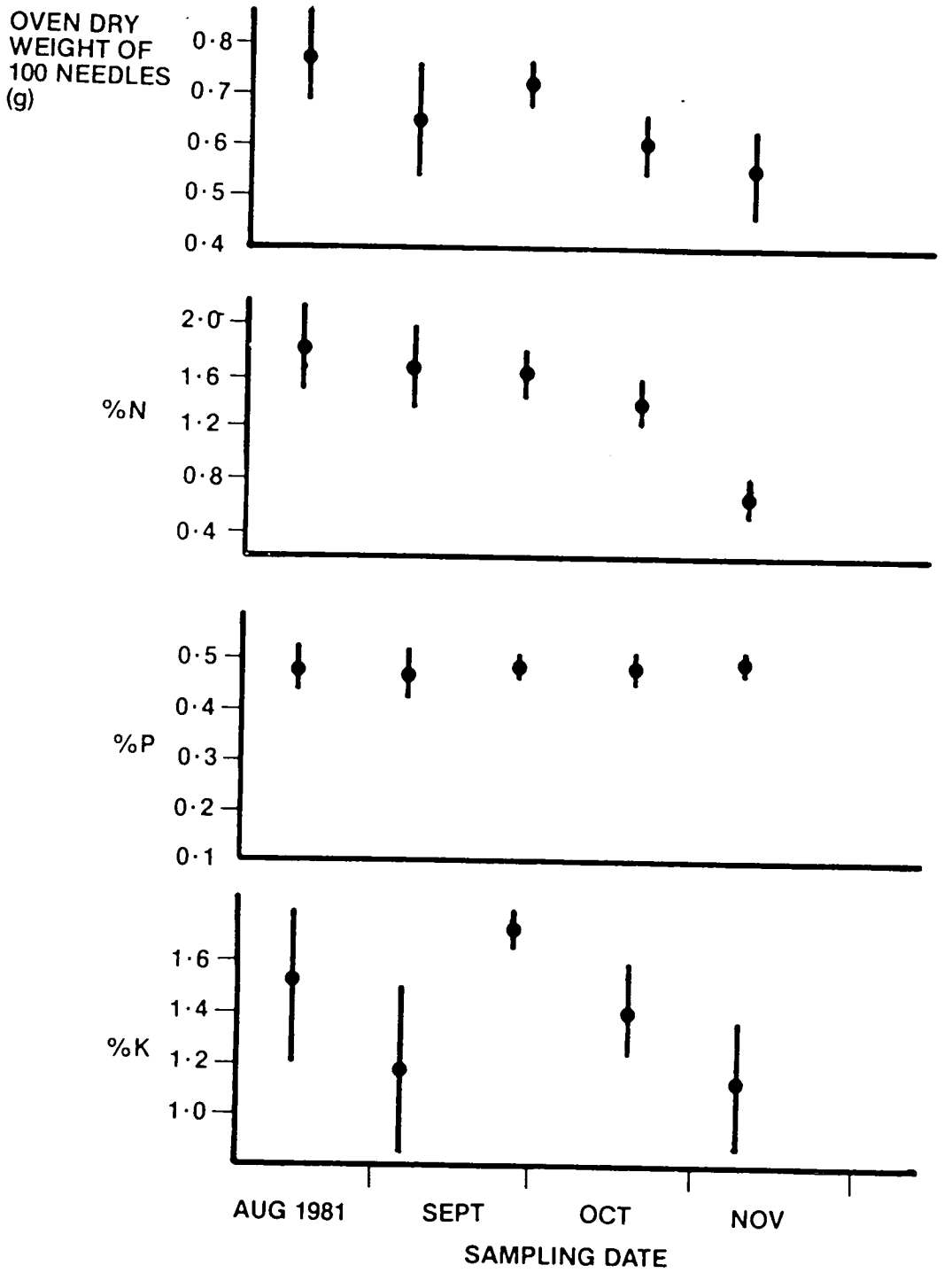
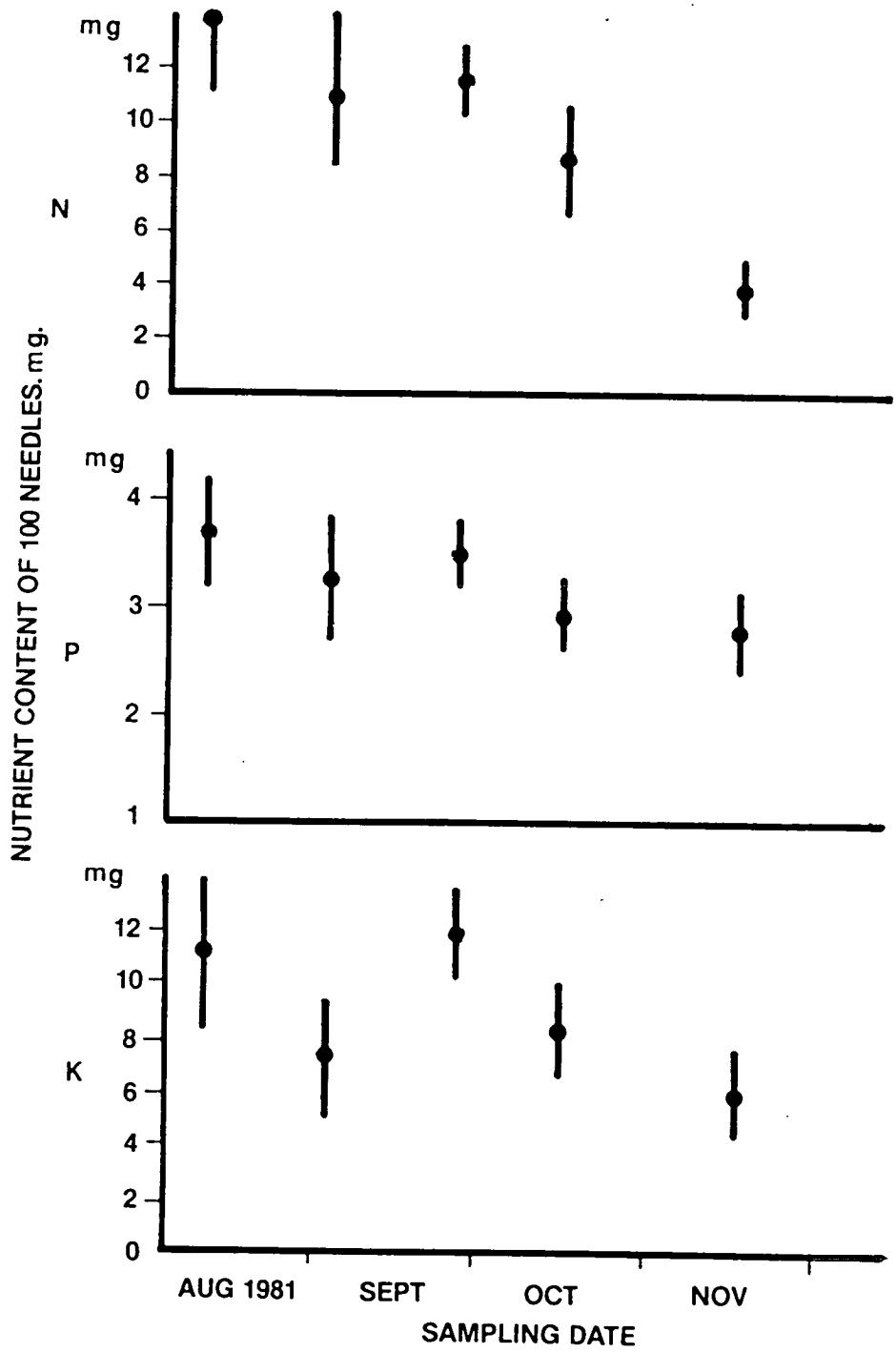


FIGURE 5:2. CHANGE IN LARCH FOLIAR NUTRIENT CONTENTS AT MABIE 7 DURING ABSCISSION. MEANS OF 15 SAMPLES. ERROR BARS SHOW 95% CONFIDENCE LIMITS.



5:1:5 Discussion

While foliar N concentrations were initially high, at a level associated with good growth for this species (Everard, 1973), marked reduction prior to abscission resulted in an absolute and relative impoverishment of the litter. A similar, but less dramatic, withdrawal and/or leaching loss is exhibited by P and K. The marked increase in K amount and concentration at the third sampling was surprising, K is highly mobile and usually continues to decline until abscission. This pattern was observed the previous year at a different site. The increase could be genuine due to contamination, perhaps from the sea which is very close to the site, or a result of sampling bias since needle weight also increased slightly at this time (larger needles are frequently associated with high foliar nutrient contents). However, the reduction in K content of 47% is similar to that reported for other deciduous species (Ryan and Bormann, 1982; Zimka and Stachurski, 1979).

These findings are in general agreement with those for other larch species (Chapin and Kedrowski, 1983; Schueller, 1978; Tilton, 1977). The process of N and P withdrawal has been studied in detail by Chapin and Kedrowski (1983); up to 92% of leaf N is present as proteins and nucleic acids, the levels of which decline in senescing leaves in association with increasing amino acid levels. At the same time protein and nucleic acid levels increase in stems, until spring when a decline is seen at the onset of growth. Davtyan and Kazaryan (1980) found that the content of weakly bound chlorophyll in L. kaempferi increased during the growth period, but fell rapidly in September, presumably as a result of hydrolysis and N withdrawal; chlorophyll has a high N content (Mengel and Kirkby, 1982). Most P is present in nucleic acids and lipids which decline in concentration during senescence, paralleled by an increase in the stem. Inorganic P in the foliage is initially low, but due to slow withdrawal its concentration increases to over 50% of total P at abscission.

Rate of withdrawal may increase during the period of abscission; Bares and Wali (1979) collected L. laricina litter sequentially and found a decline in N, P and K concentrations.

This may, of course, reflect differential abscission associated with foliage of different nutrient concentrations in the crown.

A decline in the concentration and amount of a nutrient during senescence can result from withdrawal and/or leaching loss. The extent of these processes and the sinks for withdrawn N were investigated in 2 further experiments.

5:2 Nutrient redistribution during abscission.

5:2:1 Introduction

Field sampling of larch foliage over the period of senescence has demonstrated a withdrawal (or loss) of N, P and K. The fate of these nutrients is clearly important to cycling within a larch, or larch/spruce, ecosystem.

Many workers have indicated storage of withdrawn nutrients in twigs, roots and foliage (for evergreen species), e.g. Chapin and Kedrowski (1983), Miller (1981). A change in the nutrient content of different tree components can be assessed by sequential biomass sampling, which may be tedious and time consuming for large trees. An alternative is to adopt a subsampling procedure (Comerford and Leaf, 1982a; 1982b), but this increases the variability attached to any estimate.

In the present study sequential harvesting of potted larch plants was chosen, on the assumption that the withdrawal and redistribution patterns in such plants would reflect those in older trees.

5:2:2 Experimental procedure

60 1+1 hybrid larch transplants were obtained from the Forestry Commission in March 1982, these were potted into 15cm diameter polythene pots using a 50:50 peat: sand compost, with a high nutrient reserve of added fertilizer. Plants were placed in an uncovered cold frame where they remained throughout the experiment.

Before the first sampling, plants were ranked according to height and the 10 largest and smallest plants rejected. 4 samplings were carried out at approximately 30 day intervals, commencing on 22.9.82 and continuing until complete litterfall had occurred (24.12.82). At each sampling 10 trees were randomly selected for destructive harvesting. Trees were split into 6 component parts: foliage, twigs (including the leading

shoot), bark (removed from the main stem), wood (from the main stem), woody root (woody material greater than 0.5cm in diameter) and non-woody root (material less than 0.5cm in diameter).

Components were dried to a constant weight at 85°C, cooled in a desicator and weighed. In addition, the oven dry weight of 100 needles was determined, in order to follow any change in needle weight. Subsequent preparation and chemical analysis was as described in Section 3:3:2.

5:2:3 Results

Litterfall commenced between harvest 2 and 3, and was complete by harvest 4. Total tree dry weight (Table 5:1) declined during the experiment due to needle loss, while the combined weight of perennial components remained more or less constant. Considerable variation is attached to weight estimates, particularly for certain components (Figure 5:4a, Appendix 3B). Consequently it is difficult to determine whether weight changes between harvests reflect genuine physiological change or result from variation in the sampled material. Needle weight declined by 29% between harvest 1 and 3 (Figure 5:4a, Table 5:2).

Foliar N concentrations declined during the experiment, paralleled by an increase in the N concentrations of all other components (Figure 5:3a, Appendix 3A). The quantity of foliar N also declined; due to withdrawal between harvest 1 and 2, and also leaf fall between harvests 2 and 3. This decline was associated with an increase in the N content of all other components (Figure 5:4b Appendix 3C), despite an overall dry weight decline in some cases. Expressed on the basis of needle nutrient content (Table 5:2), 82% of foliar N is removed, or lost, prior to abscission. Total tree N content was 58mg lower by the final harvest (Table 5:3).

Foliar P concentrations also exhibit a decline during the experiment, but to a lesser extent than N (Figure 5:3b, Appendix 3A). This fall being associated with a small increase in twig, bark, wood and woody root concentrations, while a decline occurred in the non-woody root. The quantity of foliar P also fell, initially through withdrawal alone. Needle P content (Table 5:2) fell by 54%. The relatively small change

in P concentrations plus variability in component weights makes changes in P content difficult to follow; P content of bark, wood and woody root shows an increase while that of the non-woody root falls, with twigs remaining constant (Figure 5:4c Appendix 3C). Total tree P content (Table 5:3) was 54mg lower at the final harvest.

Foliar K concentrations exhibit a very slight decrease, twig concentrations remained constant while bark and woody root concentrations increased, and those in the non-woody root decreased (Figure 5:3c, Appendix 3A). Needle K contents show a decline, but the response of other components is more variable. K content of the twigs fell, bark and wood contents increased, while the root system maintained a more or less constant K content (Figure 5:4d, Appendix 3C). Needle K content (Table 5:2) fell by 28%, total tree K content declined by 82mg (Table 5:3).

TABLE 5:1

Total tree dry weight (g) and weight of perennial components (total - needles). Mean values (n=10) and (95% confidence limits).

	Harvest 1	Harvest 2	Harvest 3	Harvest 4
Tree weight	38.31	35.58	30.67	26.22
	(4.916)	(4.079)	(5.935)	(2.204)
Total - Needles	27.35	27.45	27.77	-
	(3.219)	(3.554)	(5.438)	-

TABLE 5:2

Change in the weight (g) and nutrient content of 100 needles (mg). Mean values (n=10) and 95% confidence limits.

	Harvest 1	Harvest 2	Harvest 3
N mg	5.33	3.69	0.97
	(1.376)	(1.241)	(0.208)
P mg	1.14	0.86	0.52
	(0.313)	(0.313)	(0.205)
K mg	1.79	1.37	1.28
	(0.531)	(0.666)	(0.540)
Oven dry	0.256	0.202	0.182
Weight (g)	(0.065)	(0.051)	(0.033)

TABLE 5:3

Total tree nutrient content (mg) and nutrient loss between harvests 1 and 4. Mean values (n=10) and 95% confidence limits.

	N	P	K
Harvest 1	477.71	117.88	202.14
	(61.46)	(15.29)	(73.00)
Harvest 2	443.33	86.24	163.02
	(74.23)	(15.54)	(30.71)
Harvest 3	383.98	77.07	136.47
	(72.81)	(19.36)	(28.04)
Harvest 4	419.27	63.81	119.44
	(97.23)	(12.48)	(23.64)
Loss	58.44	54.07	82.70
	(104.33)	(17.90)	(45.46)

FIGURE 5:3 a CHANGE IN THE N CONCENTRATION IN DIFFERENT COMPONENTS OF 3 YEAR OLD LARCH PLANTS DURING NEEDLE FALL. ERROR BARS SHOW 95% CONFIDENCE LIMITS.

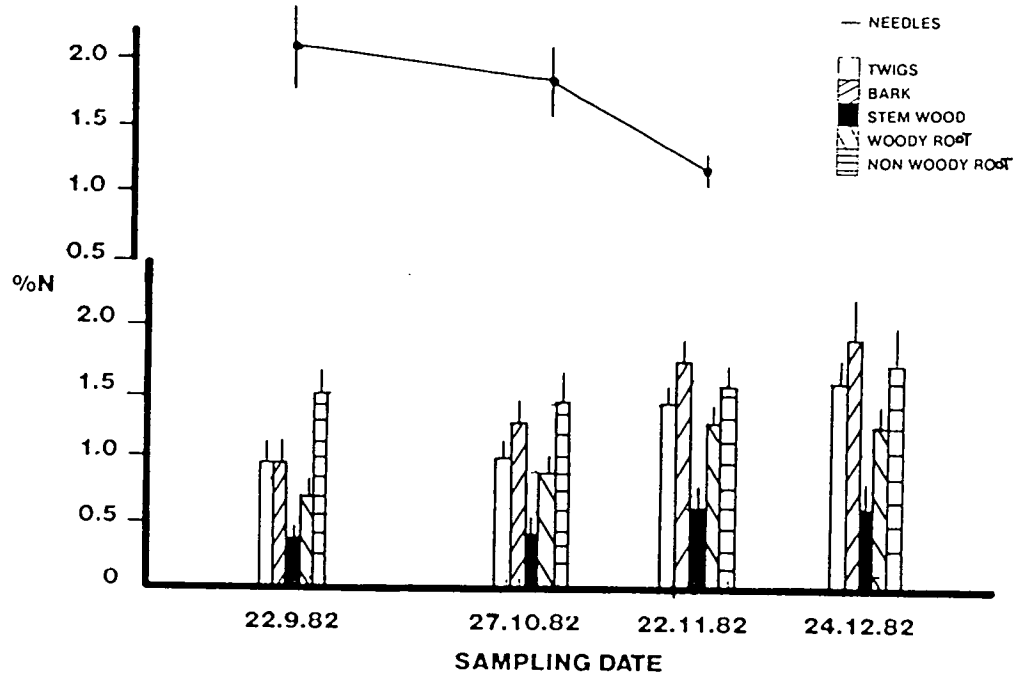


FIGURE 5:3b. CHANGE IN P CONCENTRATION OF DIFFERENT COMPONENTS OF 3 YEAR OLD LARCH PLANTS DURING NEEDLE FALL. ERROR BARS SHOW 95% CONFIDENCE LIMITS.

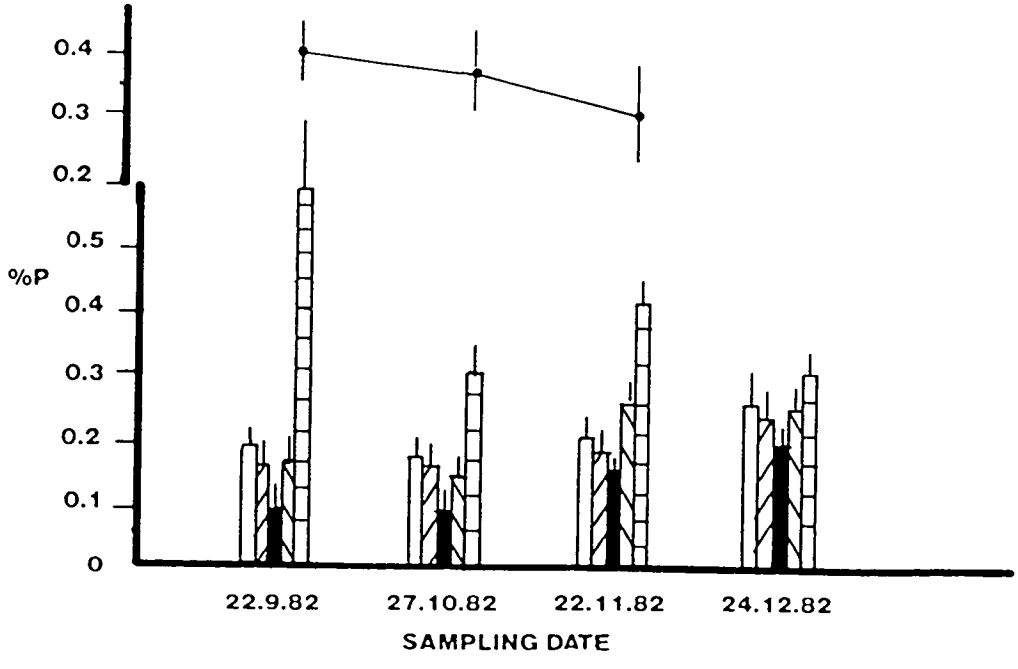


FIGURE 5:3c. CHANGE IN THE K CONCENTRATION IN DIFFERENT COMPONENTS OF 3 YEAR OLD LARCH PLANTS DURING NEEDLE FALL. ERROR BARS SHOW 95% CONFIDENCE LIMITS.

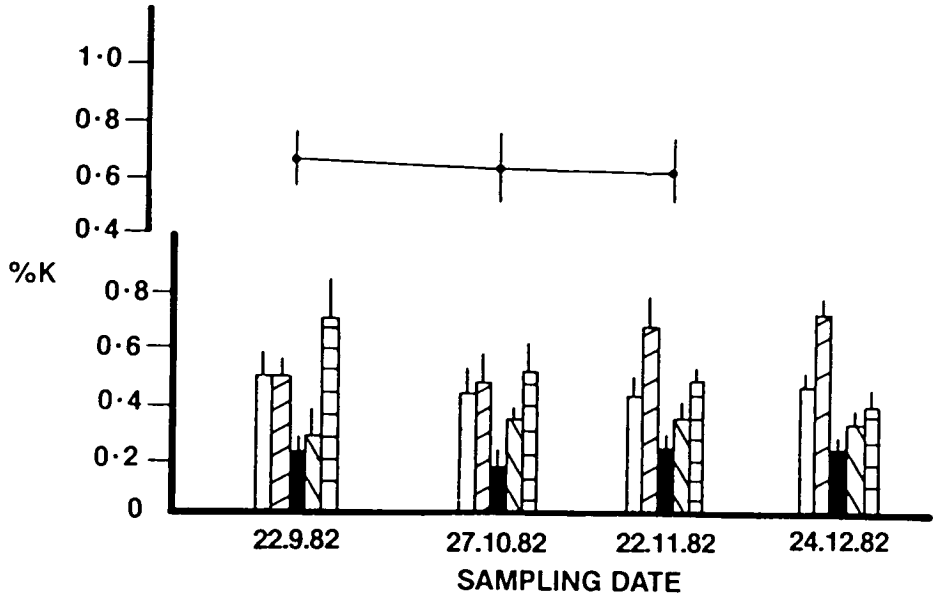


FIGURE 5:4a. CHANGE IN OVEN DRY WEIGHT (g) OF DIFFERENT COMPONENTS OF 3 YEAR OLD LARCH PLANTS DURING NEEDLE FALL. ERROR BARS SHOW 95% CONFIDENCE LIMITS.

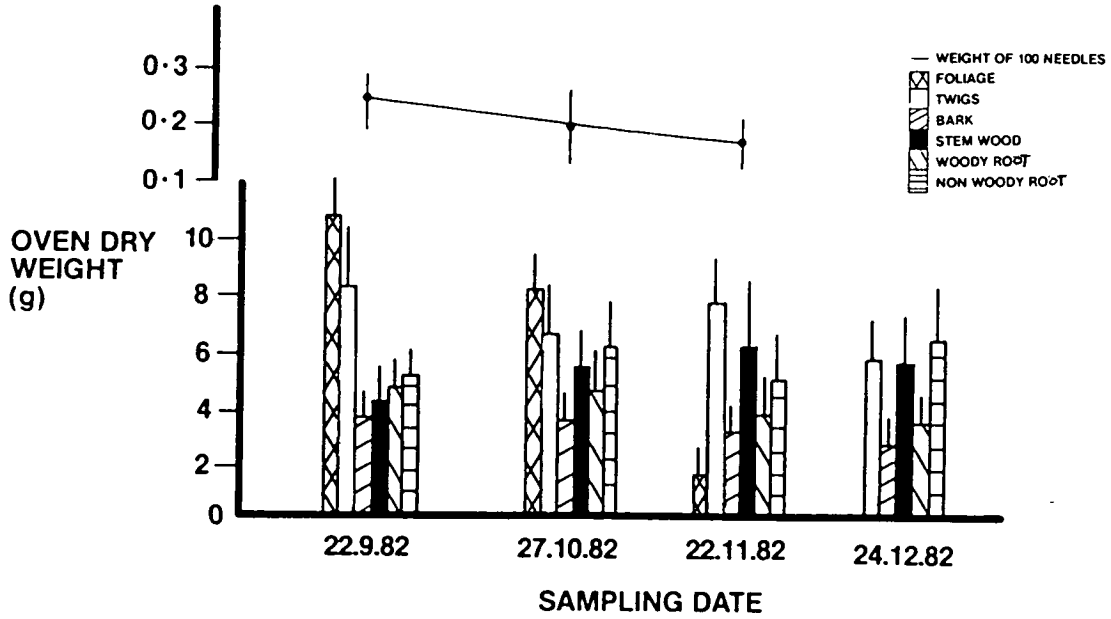


FIGURE 5:4b. CHANGE IN N CONTENT OF DIFFERENT COMPONENTS OF 3 YEAR OLD LARCH PLANTS DURING NEEDLE FALL. ERROR BARS SHOW 95% CONFIDENCE LIMITS.

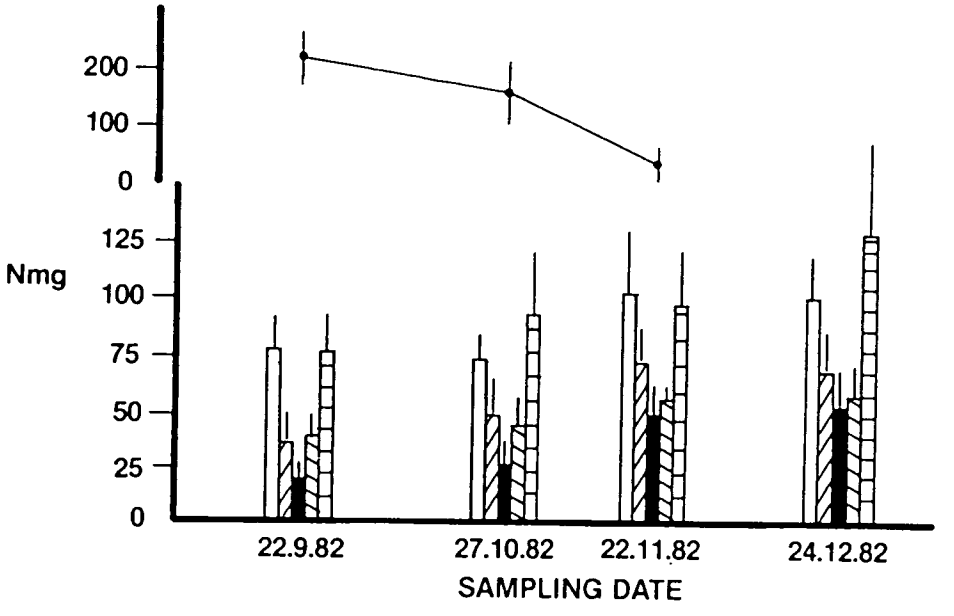


FIGURE 5:4c. CHANGE IN P CONTENT OF DIFFERENT COMPONENTS OF 3 YEAR OLD LARCH PLANTS DURING NEEDLE FALL. ERROR BARS SHOW 95% CONFIDENCE LIMITS.

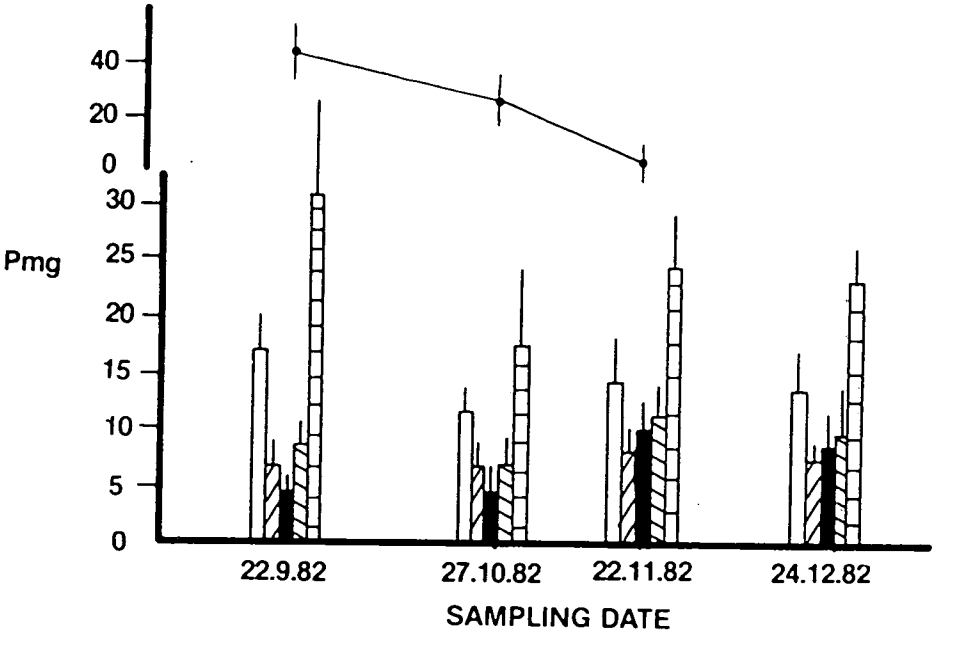
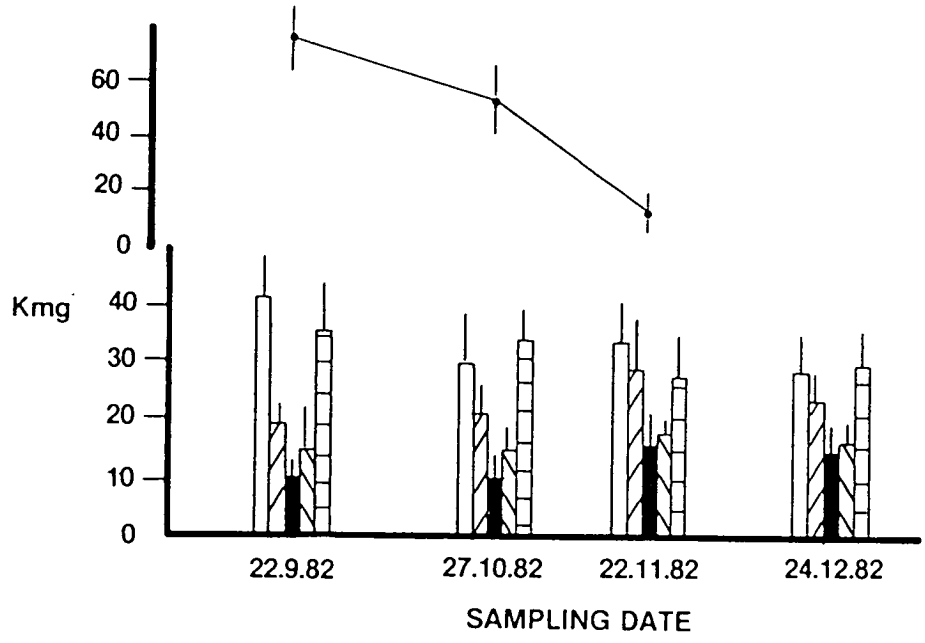


FIGURE 5:4d. CHANGE IN K CONTENT OF DIFFERENT COMPONENTS OF 3 YEAR OLD LARCH PLANTS DURING NEEDLE FALL. ERROR BARS SHOW 95% CONFIDENCE LIMITS.



5:2:4 Discussion

Needle and component concentration values suggest a withdrawal and redistribution of foliar N, P and K during senescence. Changes in tree nutrient content give conflicting results: indicating a withdrawal and redistribution of N but not P or K. However, loss values, calculated on the basis of tree nutrient content at the initial and final harvests, are associated with large error terms which may obscure withdrawal in the case of P and K.

If no withdrawal of N occurred a loss of 229mg (the initial quantity of foliar N) would be expected, however, the actual loss was only 58mg. This suggests an N withdrawal of 75% (171mg) which is close to the value predicted using needle data (82% or 188mg). This level of withdrawal agrees well with the 73% reduction found at Mabie 7. Unfortunately litter was not collected, which would have given a direct estimate of loss.

Predicting withdrawal, or loss, using needle data alone may be inaccurate since it is assumed that a) all needles abscise at the same N concentration, and b) that all needles abscise after the same relative weight loss. These assumptions may not be valid; Tilton (1977) found that L. laricina litter N concentrations declined over the period of needle fall, suggesting either a greater withdrawal towards the end of this period or that needles with a high N content abscise first.

While needle P content and tree concentration data suggest a withdrawal or loss of P, tree content declines by 54mg. This value is similar to the initial P content of 48mg found in the foliage, suggesting that no P is withdrawn. P concentrations changed to a lesser extent than those for N, this, plus variablitity in component weights may have obscured a geniune P withdrawal. The level of P withdrawal predicted from the foliage values, 54%, is considerably greater than the 26% found at Mabie 7. The withdrawal and redistribution of N is normally associated with a simultaneous withdrawal of P and K (e.g. Luxmoore et al., 1981; Zimka and Stachurski, 1979), although this is not always the case (Tilton, 1977).

The results for K follow a similar pattern, needle content and concentration data suggesting a withdrawal which is not reflected in tree K content, this declined by 86mg (similar to the initial foliar K content of 78mg). Again the small change in component concentrations and the associated variability in component weight may obscure a real withdrawal. The decline in needle content of 28% is below the value of 46% found at Mabie 7.

Despite considerable variability, results suggest a marked withdrawal and redistribution of foliar N and a probable smaller withdrawal of P and K, although it is possible that P and K are lost through leaching. Findings are in general agreement with results obtained at Mabie 7 and by other workers (e.g. Chapin and Kedrowski, 1983).

Budgets are based on the assumption that nutrient uptake and plant growth did not occur during the experiment, which will not have been the case. A related error was that of regarding the root system as a perennial component; while this is true for roots which have undergone secondary thickening fine root growth and death will have continued throughout the experiment, confounding attempts to follow changes in nutrient content. The usefulness of the approach adopted is limited since the changes which occur are small, relative to plant nutrient content, and obscured by high variability.

5:3 The leaching of soluble N, P and K from larch foliage and litter.

5:3:1 Introduction

Results presented in Sections 5:1 and 5:2 indicate a withdrawal or loss of nutrients from abscissing foliage, associated with the redistribution of a portion of these nutrients in the perennial organs of the tree. It is possible that a) leaching loss occurs from senescing foliage prior to abscission, and b) leaching loss may occur from litter immediately subsequent to litterfall.

It is generally accepted that leaves are most susceptible to leaching of N, P and other nutrients during autumn senescence (Tukey, 1970). Normally N and P are not readily leached from foliage (Morton, 1977), N losses only being large when high concentrations of nitrate are present (Tukey, 1970). However, on an annual basis leaching of foliage can account for 5-10% of annual N and P return to the forest floor (Cole and Rapp, 1980; Ryan and Bormann, 1982; Van Cleve and Alexander, 1981). Recently reported leaching losses from the senescing foliage of 3 tree species gave values of less than 0.6% for N and P; subsequent leachings gave little further loss (Chapin and Kedrowski, 1983).

Several workers have shown that litter may undergo an initial leaching phase which is not associated with microbial activity (Berg and Staaf, 1981; Nykvist, 1963). Leaching loss of N ranges from 25% to less than 1% (Berg and Staaf, 1981), being greater for deciduous than coniferous species. Leaf structure has an important influence on leaching loss which increases by a factor of 10 if litter is ground (Nykvist, 1963). Loss of N does not seem to be correlated with total N content (Berg and Staaf, 1981). The amount of rainfall during the period of senescence is probably important (Berg and Staaf,

1981; Chapin and Kedrowski, 1983), although Zimka and Stachurski (1979) found little effect of rainfall on the loss of N, P or K.

Leachable compounds present in the foliage and litter during litterfall tend to be of low molecular weight and highly mobile e.g.amino acids and inorganic P compounds (Chapin and Kedrowski, 1983). Such compounds are readily exploited by the microflora and have a short turnover time (Berg, 1978). Much of the N leached tends to be organic, amino acids and amino sugars, and can be readily used by fungi and probably mycorrhizas (Alexander, 1982; Heal et al., 1982). An input of readily metabolizable compounds during senescence may have a stimulating influence on the microflora.

5:3:2 Methods

5:3:2a Field sampling procedure

Foliage was collected from a hybrid larch stand in a Forestry Commission species/fertilizer experiment located on an upland raised bog at Leadburn, 18km south of Edinburgh. The stand has received standard inputs of P and K fertilizer but no N. A full site description is given in section 5:4:2.

At the time of collection, 24.10.80, litterfall had commenced. Needles were collected from the mid-crown position of four trees from which they were actively falling, and on which no green needles remained (i.e. all foliage was yellow and needles could be removed by gentle shaking of the parent branch). Needles were also taken from 4 trees which had just started to change colour, all foliage being predominantly green. Samples were stored in polythene bags at 3°C prior to analysis.

5:3:2b Chemical analysis

Samples were bulked into the 2 classes (green and yellow needles) and thoroughly mixed, 6 subsamples were oven dried and subjected to chemical analysis as described in section 3:3:2, to give initial N, P and K contents.

One g, oven dry weight equivalent, of fresh needle material was weighed into a 250ml plastic centrifuge bottle and 200ml of distilled H_2O added. 6 replicates were prepared for each colour class. Samples were gently shaken for 2 hours, left to soak for 20 hours then shaken for a further 2 hours. Needle

material was removed and the extract centrifuged at 2,500 r.p.m. for 20 minutes.

A subsample of the supernatant was analysed directly to estimate ammonium, nitrate, phosphate and inorganic K. Nitrate (nitrate and nitrite) was analysed by an automated colorimetric procedure (Henriksen and Selmer-Olsen, 1970), determination of other nutrients followed the procedure described in Section 3:3:2. A further subsample was digested before analysis to estimate total N, P and K, subtraction giving a value for the quantity of organically bound nutrient in the extract.

For the digestion procedure; 50ml of extract was transfered to a 100ml conical flask, to which was added 2ml of 36N H_2SO_4 and 1ml of 30% (100 volumes) H_2O_2. Flasks were heated on a hot plate until all the extract had evaporated and the H_2SO_4 started to fume, flasks were then covered with a watch glass and removed from the heat to cool. A further 1ml of H_2O_2 was added and the flasks reheated until fuming occurred when they were again covered and cooled. Digests were carefully washed into 50ml volumetric flasks and made up to volume using distilled H_2O. Samples were then analysed for N, P and K.

5:3:3 Results

Concentrations of N, P and K were higher in the green needles (Table 5:4). On leaching very little N was lost from the yellow needles, only 3.5% (Table 5:5). All this N was organic in nature. In contrast 47% and 71% of the P and K were leached (Table 5:5) both elements being present solely as the inorganic form (Table 5:6 and 5:7). Green needles leached greater relative and absolute quantities of nutrients. 16% of the N was leached (Table 5:5) of which approximately 50% was organic (Table 5:7) and 50% inorganic (Table 5:6). All inorganic N was present as ammonium. 47% and 91% of P and K were leached, again only the inorganic form was detected.

TABLE 5:4

Needle nutrient concentrations (mgg^{-1}). Mean values (n=6) and (95% confidence limits).

	N	P	K
Yellow needles	8.57	1.81	4.05
	(0.719)	(0.157)	(0.264)
Green needles	13.94	3.47	5.25
	(0.128)	(0.118)	(0.143)

TABLE 5:5

Quantity of inorganic and organic (Total) nutrient removed by water extraction, a) mg and b) as a percentage of initial content. Mean values (n=6) and (95% confidence limits).

		N	P	K
Yellow needles	a)	0.30	0.85	2.86
	b)	(0.000)	(0.070)	(0.080)
Green needles	a)	2.22	1.62	4.80
	b)	(0.321)	(0.159)	(0.381)
As a Percentage of initial content.				
Yellow needles	a)	3.50	46.96	70.62
	b)	(0.000)	(3.995)	(1.923)
Green needles	a)	15.93	46.69	91.43
	b)	(2.135)	(4.254)	(6.722)

TABLE 5:6

Quantity of inorganic nutrient removed by water extraction, a) mg and b) as a percentage of initial content. Mean values (n=6) and (95% confidence limits).

		Ammonium	Nitrate	P	K
Yellow needles	a)	0.00	0.00	0.85	2.86
	b)	(0.000)	(0.000)	(0.070)	(0.080)
Green needles	a)	1.18	0.00	1.62	4.80
	b)	(0.272)	(0.000)	(0.159)	(0.381)
As a Percentage of initial content.					
Yellow needles	a)	0.00	0.00	46.96	70.62
	b)	(0.000)	(0.000)	(3.995)	(1.923)
Green needles	a)	8.46	0.00	46.69	91.43
	b)	(1.805)	(0.000)	(4.254)	(6.722)

TABLE 5:7

Quantity of soluble organic nutrient removed by water extraction, mg and as a percentage of initial content. Mean values (n=6) and (95% confidence limits).

	N	P	K
Yellow needles	0.30	0.00	0.00
	(0.000)	(0.000)	(0.000)
Green needles	1.04	0.00	0.00
	(0.200)	(0.000)	(0.000)
As a Percentage of initial content			
Yellow needles	3.50	0.00	0.00
	(0.000)	(0.000)	(0.000)
Green needles	7.46	0.00	0.00
	(1.435)	(0.000)	(0.000)

5:3:4 Discussion

For both green and yellow needles very little N was leached in comparison with P and K. Greater relative and absolute amounts of all nutrients were leached from green needles indicating that withdrawal was not yet complete. The presence of inorganic N in leachate from green needles may reflect N hydrolysis prior to withdrawal. Lack of inorganic N in yellow needle leachate may indicate that this has been withdrawn, or perhaps lost by leaching in the field. The larger leaching losses for green needles indicates a potential leaching loss under field conditions. The presence of P in the inorganic form and N in the organic form agrees with the findings of Chapin and Kedrowski (1983).

The N loss of 3.5% from yellow needles is within the range of values most commonly reported (Berg and Staaf, 1981). Larch litter is not, therefore, a source of readily leachable N, although some loss may occur before litterfall. Leaching losses of P and K may be of greater significance.

5:4 Nutrient flux in throughfall beneath a larch and spruce canopy.

5:4:1 Introduction

Laboratory leaching of larch litter removed considerable amounts of P and K but very little N, although somewhat more organically bound N could be removed from larch foliage in a less advanced stage of senescence. Due to the artificial nature of the laboratory leaching and because this gave no measure of nutrient flux it was decided to collect throughfall during the period of larch senescence. It was thought that if larch throughfall were to return greater quantities of N to the forest floor than spruce it would be at this time. Deciduous canopies do become most leaky at senescence (Chapin and Kedrowski, 1983; Tukey, 1970).

Throughfall is not a simple measure of foliar leaching but reflects the interaction between the tree canopy and incoming precipitation. Once atmospheric inputs reach the canopy various structural characteristics will influence water storage and flow over canopy surfaces (Olson et al., 1981). Such characteristics will include stand density, canopy density and height (Lawson, 1967), stand age, species and foliage morphology (Henderson et al., 1977; Nihlgard, 1970), and seasonal loss of foliage (Madgwick and Ovington, 1959). Stage of growth of foliage is also important, i.e. young leaves or senescing foliage (Chapin and Kedrowski, 1983).

As water passes over a canopy its chemical nature will be altered by the processes of foliar leaching and absorption (Feller, 1977; Tukey, 1970), enrichment by impacted aerosols (Henderson et al., 1977; Likens et al., 1977) and fog or cloud droplets (Falconer, 1979), cation exchange (Eaton et al., 1973), and nutrient uptake or release by epiphytic microflora.

5:4:2 Site description

Sampling was conducted in hybrid larch and Sitka spruce plots (0.01 ha) which comprise part of a Forestry Commission species/fertilizer interaction experiment.

The experiment is located on an upland raised bog at Leadburn, 18km south of Edinburgh, at an elevation of 285m. Annual precipitation is about 1000mm with a potential water deficit of less than 25mmy^{-1} (Malcolm and Cuttle, 1983).

The bog falls into type 10B in the Forestry Commission classification (Pyatt et al., 1979), reaching a depth of 7m over boulder clay. Prior to afforestation the area supported extensive sheep grazing. The vegetation was dominated by C. vulgaris, E. vaginatum, and E. tetralix L., with an almost complete moss layer of mainly Sphagnum species. Other occasional species included T. caespitosum, E. angustifolium and Narthecium ossifragum Huds.

Cultivation, drainage, and planting were carried out in 1967, the area being established on single mould board ploughing at 1.8m spacing with 0.9m deep cross drains at 20m intervals. Plots received P at planting with subsequent inputs of P and K following normal Forestry Commission practice. There has been no input of N fertilizer.

5:4:3 Experimental methods

5:4:3aField sampling procedure

Sampling was conducted from 7.8.82 to 19.11.82 at approximately 14 day intervals. Both rain and throughfall were sampled using collectors consisting of 15cm internal diameter polyethylene funnels at 40cm above the forest floor. Samples were retained in 2 litre polyethylene bottles from which light was excluded by means of aluminium foil. Funnel placement was entirely random, with 10 funnels per plot. For rainfall, 4 funnels were placed in an adjacent clearing. A glass wool plug was placed in each funnel to collect particulate material (Feller, 1977), plugs were replaced at each collection.

On collection a sample volume was determined and a 200ml sub-sample retained for laboratory analysis. Samples were stored at 2-3°C for a maximum of 48 hours.

5:4:3b Chemical analysis

Sample pH was determined potentiometrically. A sub-sample was then analysed for ammonium, nitrate, phosphate, and potassium as described in Secion 5:3:2b. A second sub-sample was digested and analysed for total N, P and K according to Section 5:3:2b. Organic nutrient levels were determined by subtraction.

5:4:4 Results

Larch litterfall commenced between collections 4 and 5 and was complete by collection 7.

Ammonium levels in spruce throughfall generally exceeded those in rainfall and larch throughfall; quantities in larch throughfall were consistently less than in the incident precipitation (Table 5:8, Figure 5:5), and declined to zero over the last 3 collections (a decline also exhibited by rainfall but not spruce throughfall). Quantities of nitrate in throughfall were strongly correlated with the amounts in rain ($r=0.87$ for spruce, $r=0.94$ for larch), although the actual amounts are reduced by approximately 41% after passage through the canopies (Table 5:8. Figure 5:5). Larch throughfall contained more nitrate than that of spruce except for the last 2 collections when levels fell to zero; the quantities of nitrate returned in throughfall beneath the 2 canopies were identical (Table 5:8). Nitrate levels in larch throughfall fall to zero over the final 3 collections, coincident with a decline in spruce throughfall and rain.

Organic N levels were highly variable in both rain and throughfall (Figure 5:5), amounts in throughfall normally exceeding those in rain. Organic N returns beneath the 2 canopies were similar. Total N levels (organic and inorganic) in spruce throughfall usually exceeded those in rainfall and larch throughfall, amounts in larch throughfall were generally below those of the rain (Table 5:9. Figure 5:5). Total N in rain and larch throughfall decline over the last 3 collections, a pattern not exhibited by spruce throughfall.

Inorganic P (phosphate) was not detected in rain, or was present as trace amounts (Table 5:8, Figure 5:6). Quantities in spruce throughfall generally exceeded those beneath larch,

although the situation is reversed for the last 2 collections. Over the collection period more inorganic P was collected under larch (Table 5:8). Organic P showed considerable variability (Figure 5:6) and was detected in rain on only 2 occasions. Initially, levels were greater beneath larch but then the situation became more erratic. For the collection period similar amounts of organic P were collected beneath both canopies. Total P levels (organic and inorganic) in throughfall always exceeded those of rain, while larch throughfall generally contained more P than spruce (Table 5:9, Figure 5:6).

Only inorganic K (K^+) was detected and levels in throughfall always exceeded those of rain, with greatest amounts being collected under larch (Table 5:9, Figure 5:6).

A mean pH fall of 0.4 and 0.7 pH units was found for rain after passing through larch and spruce canopies respectively. Throughfall pH was always lower than that of rain except on one occasion (Figure 5:7), spruce throughfall always being slightly more acidic than larch.

TABLE 5:8

Inorganic N and P in rainfall and throughfall summed over the collection period (values in brackets show 95% confidence limits) $kgha^{-1}$

	Rain	Spruce throughfall	Larch throughfall
Ammonium	1.20	1.52	0.57
	(0.134)	(0.388)	(0.200)
Nitrate	0.78	0.46	0.46
	(0.129)	(0.082)	(0.082)
P	0.00	0.87	0.97
	(0.000)	(0.377)	(0.291)

TABLE 5:9

Total N, P and K in rainfall and throughfall summed over the collection period (values in brackets show 95% confidence limits) $kgha^{-1}$

	Rain	Spruce throughfall	Larch throughfall
N	2.30	2.60	1.64
	(0.250)	(0.582)	(0.459)
P	0.07	0.99	1.10
	(0.006)	(0.474)	(0.262)
K	1.10	4.41	6.39
	(0.083)	(1.465)	(1.112)

FIGURE 5:5. NITROGEN FLUXES IN RAIN AND THROUGHFALL.VERTICAL LINES SHOW 95% CONFIDENCE LIMITS.

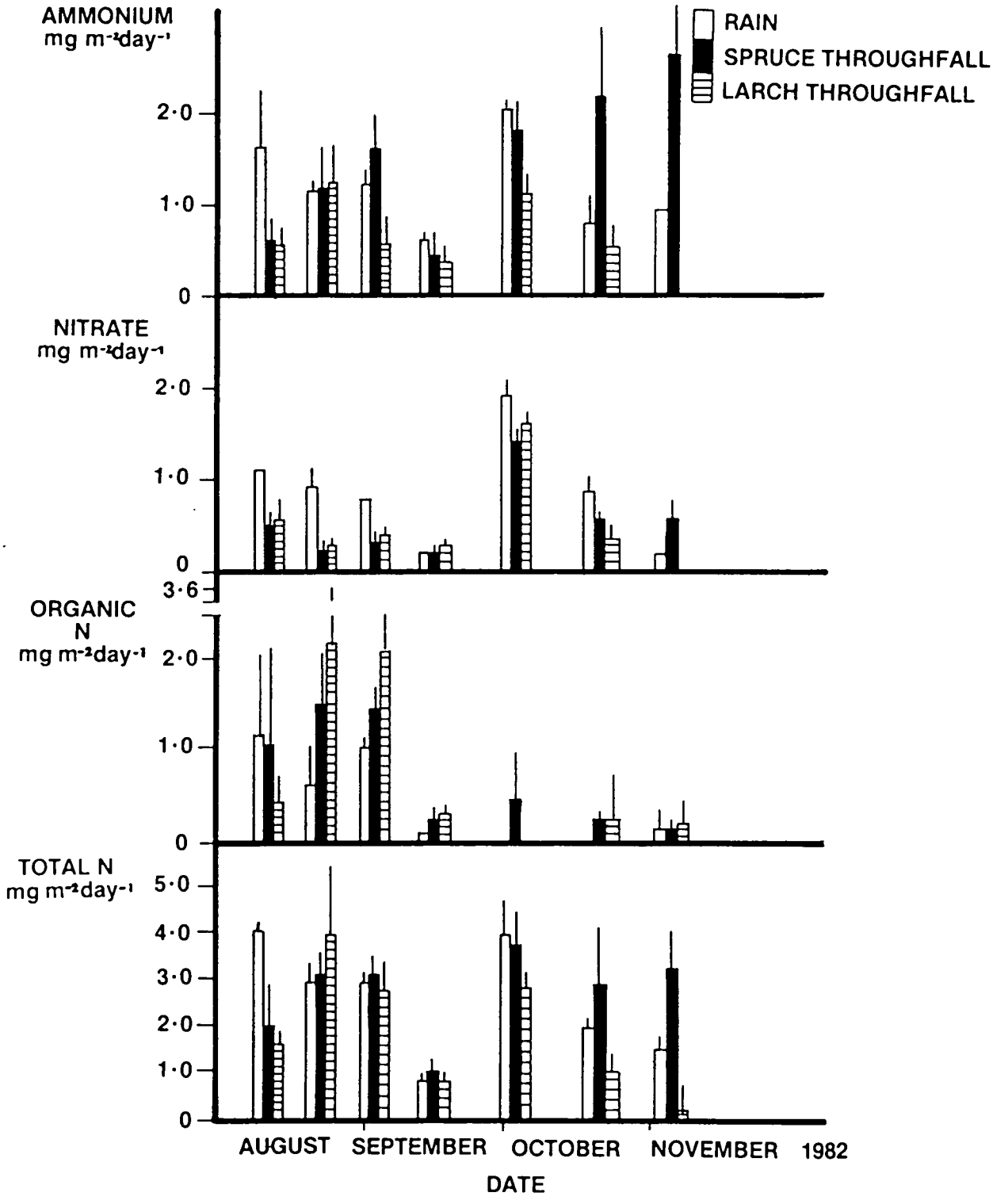


FIGURE 5:6. PHOSPHORUS AND POTASSIUM FLUXES IN RAIN AND THROUGHFALL. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS..

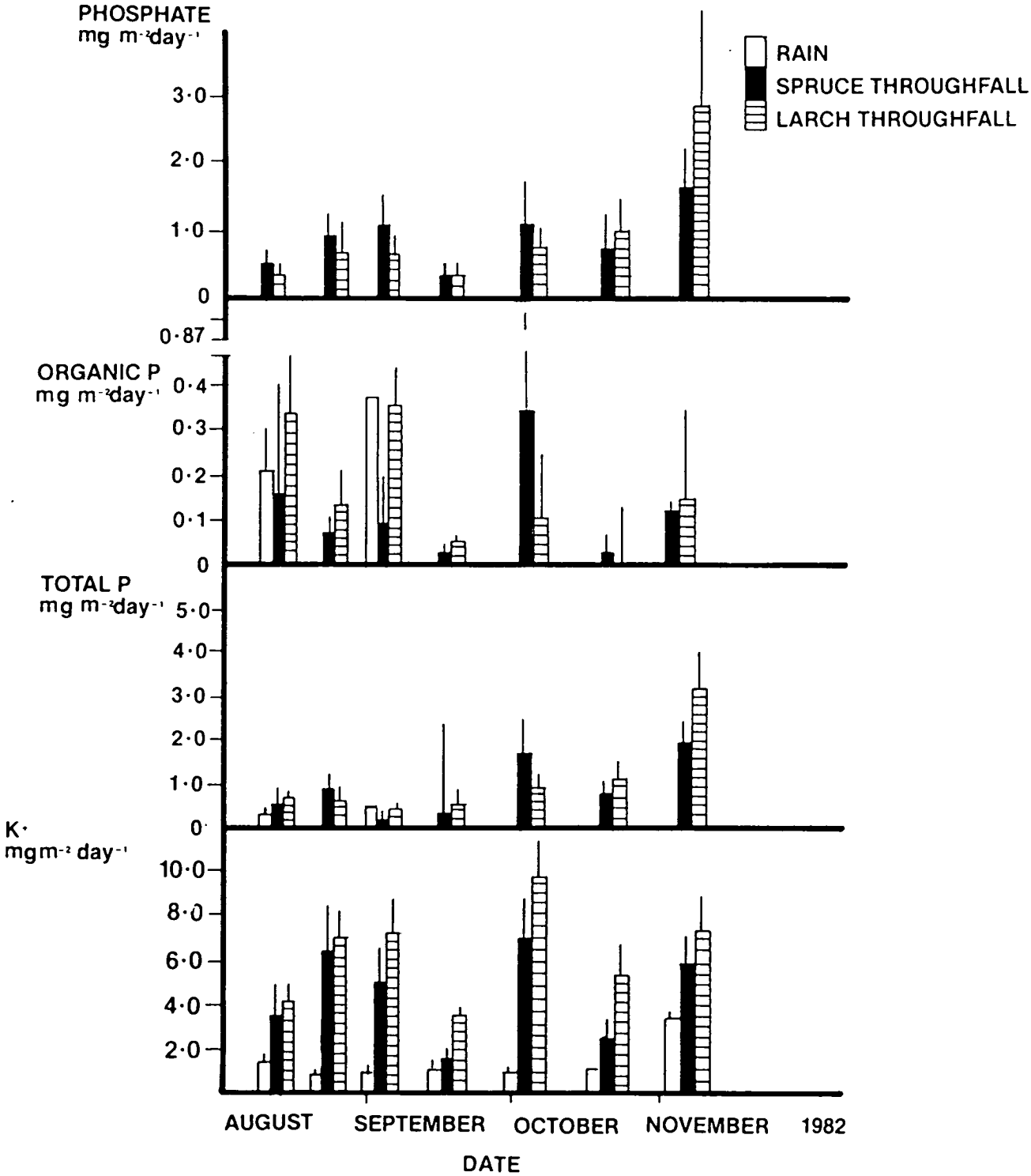
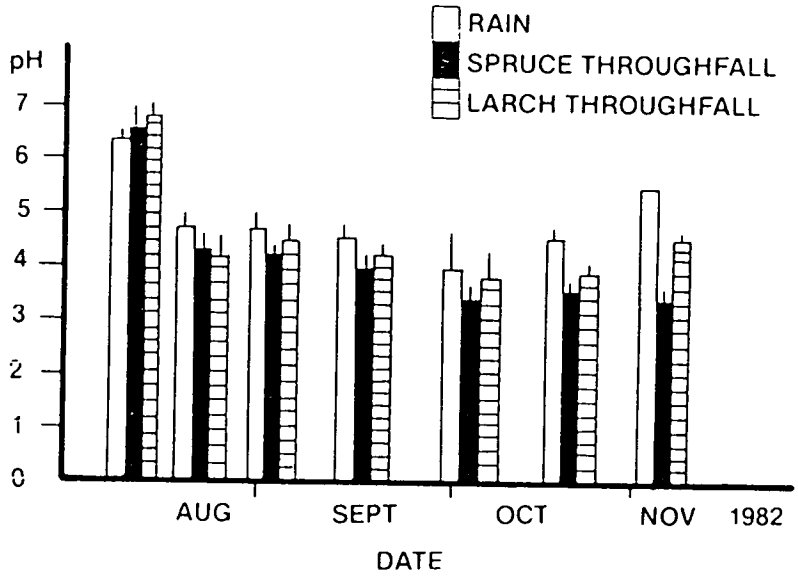


FIGURE 5:7.
pH OF RAIN AND THROUGHFALL. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS.



5:4:5 Discussion

The chemical constituents of throughfall are derived from several sources, these include bulk precipitation, impacted cloud or fog droplets, dry deposition, gaseous absorption by the canopy, and removal of chemicals from canopy tissues by leaching or ionic exchange (Olson et al., 1981).

Results follow the general trends found by other workers; a relative increase in organic N and P after rain has passed through the canopy (Verry and Timmons, 1977); high K levels in throughfall relative to rain (Feller, 1977); a general decline in throughfall pH relative to rain (Alcock and Morton, 1981); very low P levels in rainfall (Olson et al., 1981).

Larch throughfall transferred less N to the forest floor than spruce throughfall indicating that larch canopies do not become relatively more leaky for this element during senescence. On the contrary rainfall was actually depleted of N after passing through the larch canopy. The linear relation between nitrate levels in rain and throughfall suggests that this ion is not produced within the canopy, the reduction in throughfall nitrate levels relative to rainfall may result from conversion to other N forms or uptake and ion exchange mechanisms.

Larch foliage does appear to increase in leakiness for P, with levels in throughfall increasing over the last 3 collections, when values exceed those for spruce. Prior to this phase less P was present in larch throughfall, thus on an annual basis P input to the forest floor is probably lower under larch.

K was readily leached from both canopies, greater amounts always being found under larch, although there was no obvious increase in throughfall K content during senescence. It is likely that larch canopies return more K to the forest floor on an annual basis than spruce.

These findings are in accord with those of the leaching experiment which indicated that while P and K could be leached quite readily from larch litter and foliage only small amounts of N were lost. Throughfall was only collected for 3 months so it is possible that important relative differences occur outwith this period. However, leaching loss of elements from deciduous canopies is greatest during senescence (Chapin

and Kedrowski, 1983) so larch foliage is unlikely to contribute more N to throughfall at other times during the year.

Clarholm and Rosswall (1980) found that throughfall stimulated microbial activity, when moisture was non-limiting, due to the presence of soluble compounds. The greater input of K under larch, and the increased flux of P at the end of litterfall, may have a stimulating effect on microbial activity and decomposition. Additionally, soluble carbon levels may be important since the availability of carbon can limit microbial activity (Barber and Lynch, 1977). In quantitative terms, nutrient return in throughfall is not sufficient to account for increased N availablity in larch/spruce mixtures.

5:5 A comparison of Sitka spruce and hybrid larch litters as a source of N for Sitka spruce seedlings.

5:5:1 Introduction

Results presented in preceding sections indicate that larch withdraws N, P and K prior to leaf abscission; while P and K may be leached from senescing foliage the potential loss of N is low, these findings being substantiated by data for throughfall. Thus larch appears to be conservative in its use of N, nutrient withdrawal resulting in litter with a low N concentration. Chemical analyses alone do not indicate whether larch litter is a source of N potentially more available for Sitka spruce in mixture than is spruce litter. Since litter quality is dependent on many factors one might expect a difference in decomposition and N release between species growing on the same site.

It has been suggested that larch litter decomposes readily, giving rise to a better developed microflora than other conifers, resulting in rapid mineralization and nitrification (Lavrienko, 1965; Pogrebriak, 1960; Tikhonov, 1963). Ohta and Kumada (1978) indicate that mineralization rates of larch litter material were greater than other conifers and comparable to broadleaved species. However, Bornevie-Svendson and Gjems (1957) state that larch litter is slow to decompose, this was also found by Wittich (1936) who considered that claims for the rapid decomposition of larch litter were site specific and exaggerated, and by Mikola (1954).

Leyton and Weatherell (1959) found growth of Sitka spruce to be improved by litter amendments, height increment was positively correlated with the quantity of litter N added. They concluded that Japanese larch would be the best nurse species due to the high N concentration in its litter (1.7%) and a high annual litterfall. However, data presented in Section 5:1 indicates much lower N concentrations in larch litter, while

Bares and Wali (1979) and Tilton (1977) found litter N concentrations below 1% for L. laricina.

In the present study larch and spruce litters were assessed as an N source for Sitka spruce seedlings in a Pot experiment.

5:5:2 Methods

5:5:2a Litter collection

Hybrid larch and Sitka spruce litter were collected from a species/fertilizer interaction experiment, described in section 5:4:2. Both species had received identical fertilizer inputs (P and K at standard Forestry Commission rates, but no N).

Litter was collected in December 1980; for larch, freshly fallen material was readily identifiable by colour. For spruce, only surface material which was loose and not invaded by fungal hyphae was collected. Although Sitka spruce litterfall continues throughout the year it exhibits two seasonal peaks, in late autumn and early spring (Owen, 1954), therefore the bulk of material collected should have been freshly fallen. Since trees were only 13 years old litterfall was comprised almost entirely of needle litter.

Litter was air dried and stored at 3°C, sub-samples were oven dried and analysed to determine the concentrations of N, P and K. Sample preparation and subsequent chemical analysis was as described in section 3:3:2.

5:5:2b Experimental design

The experiment was conducted in an unheated greenhouse in 161cm^2 plastic pots. Two treatments were adopted for each litter type; 1) air dry litter was ground (0.5mm mesh) and mixed with washed coarse sand, approximately 1:27 by weight (0.1 N HCl extraction of washed sand removed only trace amounts of N, P and K, therefore the sand represented a zero nutrient input). Ground treatments were designated spruce/sand and larch/sand respectively. 2) unground air dry litter was placed directly in pots, with a 1cm deep mulch of quartz gravel. Unground treatments were designated spruce litter and larch litter respectively.

Litter was added to give a rate equivalent to 300 kgNha^{-1} in the case of ground litter, and 600 kg Nha^{-1} for unground litter (i.e. 0.48 and 0.96 g litter N per pot). Less litter was added

in the ground litter treatment as it was assumed that grinding would increase N availability.

A control treatment was included which consisted of washed sand with no N input, for comparison an inorganic N treatment (designated N. P. K.) which received ammonium nitrate equivalent to 150 $kgNha^{-1}$ (0.24g N per pot) was also included. All six treatments received P (as ground mineral phosphate) and K (as potassium chloride) at rates equivalent to 50 and 100 $kgha^{-1}$, being applied in quantities to copy Forestry Commission rates.

Pots were planted with single 1+0 Sitka spruce seedlings which had been graded to be 14-16cm in height. An initial sample of these seedlings (Table 5:10) indicated that variability in nutrient content was low.

Pots were placed on saucers to prevent loss of drainage water; however, drainage losses did occur from the unground litter treatment which required frequent soaking in warm weather. Additionally, algal growth was marked in many saucers.

30 replicates were prepared for each treatment and placed in a randomized block design. The experiment ran from 17.3.81 to 21.12.81.

5:5:2c Chemical analysis

At harvesting, trees (shoots and roots) were removed from pots, oven dried and weighed: this was also carried out for residual litter in the unground treatments. Both trees and litter were subjected to chemical analysis as described in section 3:3:2.

5:5:3 Results

All seedlings developed acute N deficiency symptoms (general soft chlorosis and a purple tinge to the foliage) within 4 weeks of planting, except for those in the N. P. K. treatment which maintained a normal healthy appearance. Control seedlings and those in spruce litter remained deficient throughout the experiment, however, those in unground larch litter reverted to a normal healthy colour some 20 weeks into the experiment, while there was a lessening of deficiency symptoms in the ground larch litter treatment at this time. Loss of deficiency symptoms in the unground larch litter was associated with the appearance of fungal fruiting bodies of Thelephora terrestris

Ehrene. ex. Fr. and Inocybe sp. in 50% of pots. Both these species are mycorrhizal (Last et al., 1983).

N, P and K contents of seedlings grown in the litter treatments (Table 5:10) are significantly greater than the control (Table 5:11). Seedling N and P contents in the unground litter treatments exceed the ground, with contents in the larch litter treatments (ground and unground) always exceeding those from spruce litter. The N contents of seedlings grown in larch litter are 110% (unground) and 22% (ground) greater than equivalent values for those grown in spruce litter.

Grinding appears to depress N release from larch litter more than it does from spruce litter. Highest N and K contents were found in the N. P. K. treatment, however, the P content was significantly lower than the litter treatments, but greater than the control. The control shows an increase in P and K content over that of the initial seedlings, but no increase in N.

Results for the change in unground litter N content (Table 5:12) indicate a decline in total N, but an increase in N concentration. A greater quantity of N is lost from larch litter than spruce, 9.5 and 4.9% of the total respectively. In both cases N loss from decomposing litter exceeds N recovered by the seedlings. Weight loss was greatest from larch litter, being 14.5% compared with 11.4% for spruce material. Losses of P and K greatly exceed amounts taken up by seedlings, being smallest for spruce litter.

TABLE 5:10

N, P and K content (mg) of Sitka spruce seedlings grown in hybrid larch or Sitka spruce litter. Mean values (n=30) and (95% confidence limits).

	N	P	K
Spruce litter	29.03 (3.268)	10.68 (1.026)	30.95 (3.483)
Larch litter	60.88 (5.275)	18.97 (1.374)	50.19 (4.727)
Spruce/sand	16.87 (1.349)	6.90 (0.578)	36.21 (3.052)
Larch/sand	20.54 (1.866)	11.31 (0.900)	36.75 (2.868)
N. P. K.	96.17 (8.077)	6.06 (0.529)	91.25 (9.626)
Control	12.81 (1.341)	2.35 (0.286)	26.71 (3.428)
Initial	11.65 (0.82)	1.94 (0.08)	8.33 (0.55)

TABLE 5:11

Significance of differences between treatment means in a T-test. * = significant at P = 0.05, ** = significant at P = 0.01, NS = not significant.

N mg	Spruce litter	Larch litter	Spruce sand	Larch sand	N.P.K.	Control
Spruce litter	–	**	**	**	**	**
Larch litter	–	–	**	**	**	**
Spruce/sand	–	–	–	**	**	**
Larch/sand	–	–	–	–	**	**
N.P.K.	–	–	–	–	–	**
Control	–	–	–	–	–	–
P mg						
Spruce litter	–	**	**	N.S.	**	**
Larch litter	–	–	**	**	**	**
Spruce/sand	–	–	–	**	*	**
Larch/sand	–	–	–	–	**	**
N.P.K.	–	–	–	–	–	**
Control	–	–	–	–	–	–
K mg						
Spruce litter	–	**	*	*	**	N.S.
Larch litter	–	–	**	**	**	**
Spruce/sand	–	–	–	N.S.	**	**
Larch/sand	–	–	–	–	**	**
N.P.K.	–	–	–	–	–	**
Control	–	–	–	–	–	–

TABLE 5:12

Litter weight, g pot^{-1}, nutrient content, mg pot^{-1}, and (nutrient concentration, %), for initial litter and after incubation with Sitka spruce seedlings. Mean values (n=30) ± 95% confidence limits.

Spruce	Weight	N	P	K
Initial	101.00	959.5 ± 73.73	70.7 ± 11.11	101.0 ± 4.04
		(0.95 ± 0.073)	(0.07 ± 0.011)	(0.10 ± 0.004)
After *	89.48	912.7 ± 52.10	89.5 ± 5.78	80.5 ± 6.72
	±4.333	(1.02 ± 0.028)	(0.10 ± 0.003)	(0.09 ± 0.004)
Larch				
Initial	93.20	960.0 ± 23.30	111.8 ± 5.59	111.8 ± 6.52
		(1.03 ± 0.025)	(0.12 ± 0.006)	(0.12 ± 0.007)
After *	79.67	868.4 ± 86.07	71.7 ± 6.61	47.8 ± 3.45
	±5.715	(1.09 ± 0.040)	(0.09 ± 0.005)	(0.06 ± 0.004)

* Includes residual fertilizer.

Table 5:13

Concentrations of N, P and K in spruce and larch litter prior to incubation with Sitka spruce seedlings. Mean values (n=5) and (95% confidence limits).

	%N	%P	%K
Spruce	0.95	0.07	0.10
	(0.073)	(0.007)	(0.004)
Larch	1.03	0.12	0.12
	(0.025)	(0.006)	(0.007)

5:5:4 Discussion

Larch litter appears to be a more readily available N source for spruce seedlings than Sitka spruce litter, for both ground and unground material. The greater release of N from larch litter does not appear to result from a high initial N concentration, since this is similar for both litter types (Table 5:13). Grinding and mixing of litter with sand reduced seedling N uptake. Part of this depression may be a consequence of the smaller quantity of N added in the ground treatment. Grinding normally stimulates N release due to a flush of mineralization from killed organisms and from enhanced decomposition of non-biomass sections of organic matter (Powlson, 1980). Why grinding depressed N release from larch litter more than from spruce (relative to the unground treatment) is uncertain. However, grinding will remove many of the physical constraints on decomposition which probably make spruce litter a more recalcitrant substrate than larch; resulting in a smaller difference in seedling N content between litter types in the ground treatments.

Mycorrhizal fruiting bodies were not apparent in the sand treatments; it is possible that greater N uptake from the unground larch litter was partly a result of more active mycorrhizal associations. Fruiting bodies were found only in the unground larch treatment and their appearance was coincident with the loss of N deficiency symptoms. However, fruiting body production may only indicate that conditions were more suitable for the reproductive stage of the fungus, rather than reflecting a greater overall activity. In addition, the sand used in the ground litter treatments may have been too fine to permit adequate aeration, resulting in adverse physical conditions for decomposer activity and mycorrhizal growth.

The apparent 20 week delay before N release occurred, when seedlings were N deficient, probably indicates an N accumulation phase prior to release. A period of both relative and absolute N accumulation is common in decomposing litter material (Berg and Staaf, 1981).

Seedlings grown in larch litter (ground and unground) have approximately twice the P content of those grown in spruce

litter. This reflects the greater P content of larch litter, while previous experiments have indicated that P can be readily leached from larch litter.

Nutrient amounts lost from the unground litters exceed uptake by the seedlings. This suggests that N, P and K were lost during the experiment; losses occurred due to overflow from saucers, algal growth in saucers, and fungal fruiting body production. These losses will have been minimal from the ground treatments which could be kept moist by the addition of water to the saucers, drainage losses were therefore zero. Nutrient loss values indicate substantially greater release of all 3 nutrients from larch litter, corroborating the results for seedling uptake.

5:6 N release from different combinations of hybrid larch and Sitka spruce litter during incubation with periodic leaching.

5:6:1 Introduction

Larch litter has been demonstrated to be a more readily available source of N for Sitka spruce seedlings than spruce litter. Release of N does not occur immediately but is delayed for some 5 months under greenhouse conditions (Section 5:5:3) suggesting an initial accumulation phase as the C:N ratio falls (Berg and Staaf, 1981). In order to follow this release larch litter was collected in summer some 8 months after litterfall, together with Sitka spruce litter from the same site. The two litters were incubated under laboratory conditions to compare rates of N release. Additionally, litters were mixed in several combinations to examine the possibility of positive interaction; the admixture of larch litter with other types has been suggested as being beneficial in terms of N release (Lavrienko, 1965).

5:6:2 Methods

5:6:2a Field collection of litter

Hybrid larch and Sitka spruce leaf litter were collected from the species/fertilizer interaction experiment described in Section 5:4:2.

Collection was carried out in July (1982), only surface material being taken. It is difficult to obtain comparable ages of larch and spruce litter without collecting material as it falls. Larch litter could be guaranteed as being approximately 8 months old; spruce litter may have been younger since some litterfall occurs in early spring (Owen, 1954). Despite such possible differences, litters can be said to reflect forest floor conditions at the time of sampling.

Litter was air dried and stored at 3°C prior to use.

5:6:2b Incubations

Litters were combined on an air dry weight basis to give 6 treatments, each with 4 replicates; L_0S_{10} (0.00g larch litter, 10.00g spruce litter), L_2S_8, L_4S_6, L_6S_4, L_8S_2 and $L_{10}S_0$. Litters differed slightly in moisture content so precise oven dry weight values are presented in Appendix 4A. Litters were placed in 250ml Buchner funnels using glass wool as a filter, funnels were covered with 25.4µm polyethylene film and incubated in the dark at 20°C. Initially funnels were flooded with distilled water and left for 24 hours to allow litter to hydrate, water was then removed under suction. Subsequently the incubations were leached with 200ml of distilled water poured over the litter surface at 30 day intervals. The experiment ran for 180 days.

Leachates were collected using suction and the volumes determined, a subsample was retained for chemical analysis.

5:6:2c Chemical analysis.

Litter samples were analysed for N, P and K before and after incubation; weight loss over the incubation was also assessed. Sample preparation and chemical analyses were as described in Section 3:3:2. Initial litter material was extracted with distilled water (2g air dry weight + 20ml water) for 5 hours and the extract pH determined potentiometrically.

Leachates were analysed for ammonium, nitrate and phosphate as described in Section 5:3:2b, pH was also determined.

5:6:3 Results

Initial N, P and K concentrations were greatest in larch litter (Table 5:14), the N concentration being more than twice that of the spruce material. The value is also greater than that recorded for freshly fallen larch litter (Table 5:13), although P and K concentrations are similar, pH of litter extracts was also higher for larch litter.

Treatment nutrient contents, showing the relative contributions of larch and spruce litter, are displayed in Appendix 4A. Due to the higher nutrient concentrations in larch litter, treatment nutrient contents increase with the proportion of larch material.

Total mineral N release (ammonium + nitrate) increased with the proportion of larch litter, being maximum for $L_{10}S_0$ and minimum for L_0S_{10} (Figure 5:8c, Appendix 4C). The larch litter content of treatments increases by equal increments from L_0S_{10} to $L_{10}S_0$. However, the increase in N release becomes greater as the proportion of larch material rises. This pattern is closely followed by ammonium (Fig 5:8a, Appendix 4C), although release increases more or less equally between the first 3 treatments, jumping dramatically in treatments L_6S_4 to $L_{10}S_0$. No nitrification occurred in the L_0S_{10} treatment, and was only detected in the presence of larch litter. Nitrification also increases with the proportion of larch material (Fig 5:8b, Appendix 4C), with treatments $L_{10}S_0$ and L_8S_2 being virtually identical. By the end of the incubation, nitrate is the dominant mineral N form in most treaments containing larch litter (Appendix 4C). Relative nitrification (nitrate:ammonium) increases with the quantity of larch litter from treatment L_0S_{10} to L_6S_4, then declines (Table 5:16). Inorganic P release follows a similar pattern to inorganic N release (Fig 5:8d, Appendix 4C).

Expressing inorganic nutrient release as a percentage of the initial nutrient content (Table 5:15) shows that relative N release also increases with the proportion of larch litter. The same result is seen for P, except that greater relative amounts are released.

Assuming no interaction between litters in the mixed treatments, one can use results from the single litter incubations to predict nutrient release values for the litter mixtures. For both N and P (Table 5:17), predicted values for treatments L_2S_8 to L_6S_4 exceed the measured values, while the prediction for L_8S_2 is less than the real result. Leachate pH declines during the incubation in all cases (Fig 5:9, Appendix 4C): initially pH was highest in the $L_{10}S_0$ treatment and lowest in the L_0S_{10}, however this situation is reversed by the end of the experiment. Analysis of residual litter after the incubation (Appendix 4B) shows that weight loss is negatively correlated with the proportion of larch litter. Total nutrient loss (initial content - final content) does not differ substantially between

treatments being approximately 53% for N and 67% for P. An attempt was made to separate residual material into larch and spruce components but this proved unsatisfactory due to a high proportion of amorphous material.

TABLE 5:14

Initial nutrient concentrations (%) and pH. Mean values (n=4) and (95% confidence limits).

	%N	%P	%K	pH
Sitka spruce	0.81	0.09	0.07	3.68
	(0.03)	(0.006)	(0.008)	(0.16)
Hybrid larch	1.72	0.13	0.10	3.90
	(0.10)	(0.005)	(0.005)	(0.36)

TABLE 5:15

Inorganic nutrient release (mg) in leachate over the incubation period, and as a % of the initial nutrient content. Mean values (n=4) and (95% confidence limits).

Treatment	Ammonium + Nitrate		P	
	mg	%	mg	%
L_0S_{10}	0.10	0.17	0.55	8.28
	(0.008)	(0.013)	(0.059)	(0.889)
L_2S_8	0.26	0.34	0.75	10.11
	(0.068)	(0.090)	(0.101)	(1.361)
L_4S_6	1.25	1.36	1.07	13.05
	(0.005)	(0.005)	(0.070)	(0.854)
L_6S_4	3.82	3.55	1.55	17.26
	(0.218)	(0.203)	(0.026)	(0.290)
L_8S_2	8.57	6.94	2.74	28.10
	(1.144)	(0.927)	(0.461)	(4.728)
$L_{10}S_0$	9.59	6.88	3.16	30.01
	(0.853)	(0.612)	(0.024)	(0.228)

TABLE 5:16

Relative nitrification
Mean values (n=4)

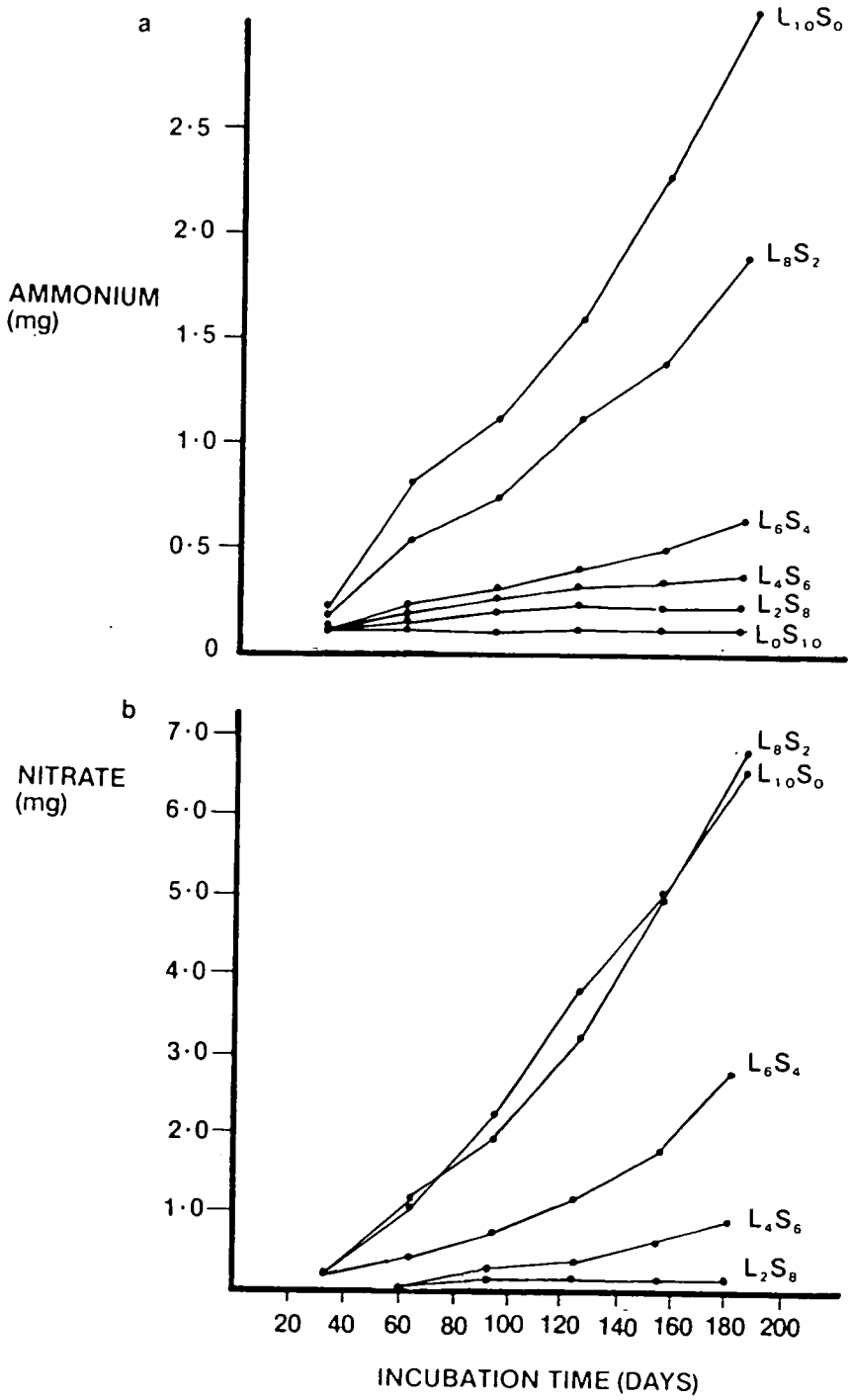
Treatment	Nitrate : Ammonium
L_0S_{10}	0.0
L_2S_8	0.2
L_4S_6	2.4
L_6S_4	5.1
L_8S_2	3.6
$L_{10}S_0$	2.2

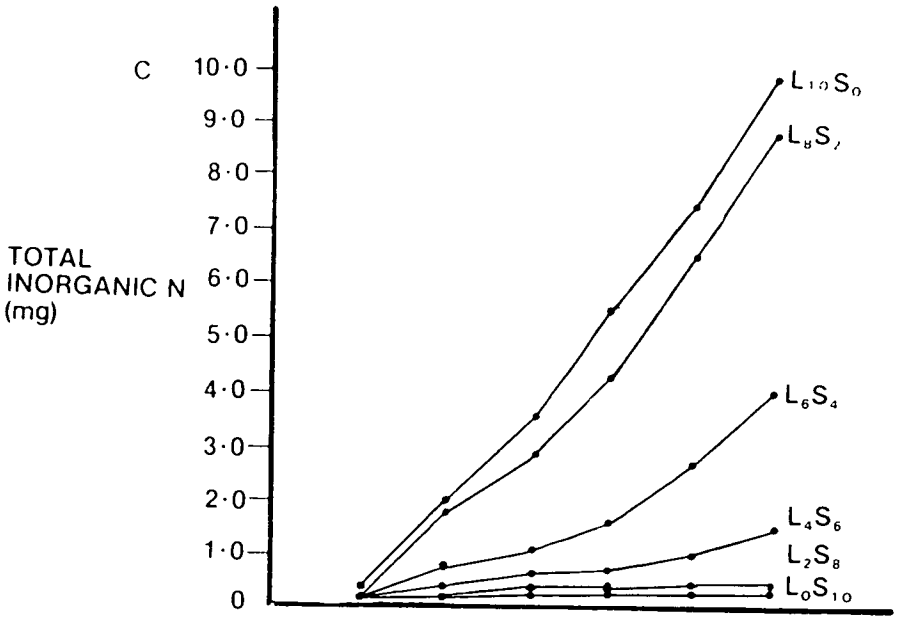
TABLE 5:17

Observed and (Predicted) mineralization values (mg) for N and P. Mean values (n=4).

Treatment	N	P
L_2S_8	0.26 (2.00)	0.75 (1.07)
L_4S_6	1.25 (3.90)	1.07 (1.59)
L_6S_4	3.82 (5.79)	1.55 (2.12)
L_8S_2	8.57 (7.69)	2.74 (2.64)

FIGURE 5:8. CUMULATIVE RELEASE (mg) OF INORGANIC NUTRIENTS FROM DIFFERENT COMBINATIONS OF LARCH AND SPRUCE LITTERS. MEAN VALUES (n = 4).




C
10·0
9·0
8·0
7·0
6·0
5·0
4·0
3·0
2·0
1·0
0
TOTAL
INORGANIC N
(mg)
L10S0
L8S2
L6S4
L4S6
L2S8
L0S10

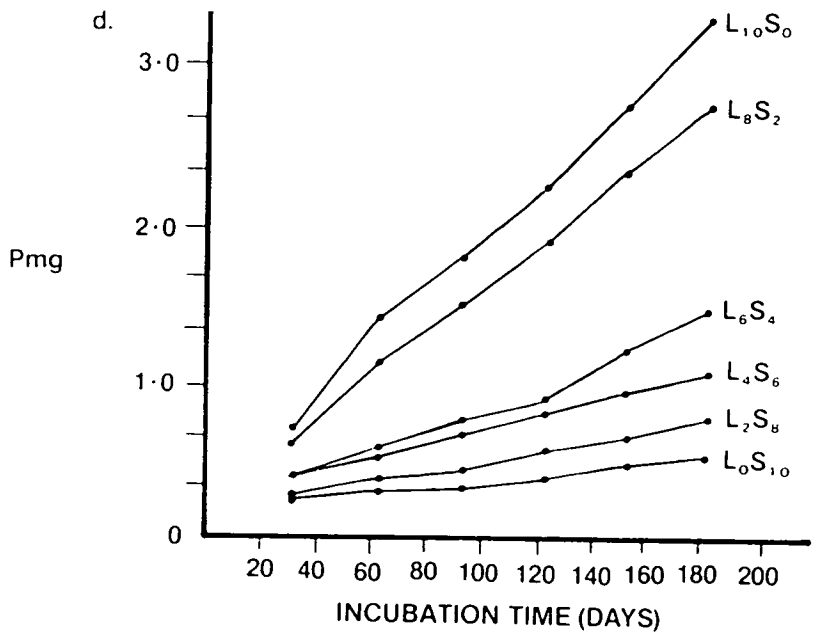
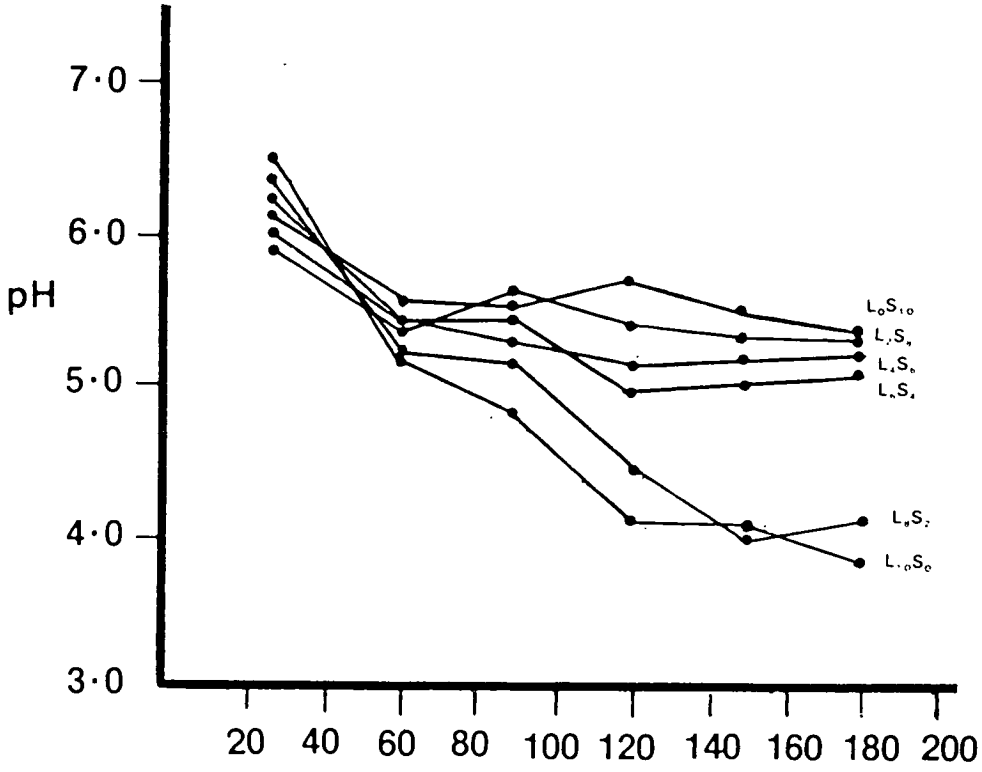

d.
3·0
2·0
1·0
0
Pmg
L10S0
L8S2
L6S4
L4S6
L2S8
L0S10
20 40 60 80 100 120 140 160 180 200
INCUBATION TIME (DAYS)

FIGURE 5:9.

LEACHATE pH FOR THE 6. TREATMENTS OVER THE INCUBATION PERIOD. MEANS VALUES (n = 4).



5:6:4 Discussion

8 month old larch litter had an N concentration 61% greater than fresh litter used in the pot experiment (although not from the same years litterfall) and released N readily when leached. Release (mineralization) is considerably greater (96 x) than the inorganic N released from Sitka spruce litter, which was collected at the same time. Differences must partially reflect the lower C:N ratio of larch litter (29:1 versus 61:1); indicating a shorter accumulation phase for larch litter since N concentrations of the fresh litters are similar. This assumes that litters are of comparable age. The smaller weight loss of larch material compared with spruce suggests that rapid early weight loss may have already occurred in the former, together with the associated accumulation of N.

Mineral N in leachates from spruce litter amounted to only 0.1% of the initial N content, despite a weight loss of 68%. Total N loss was much higher (52%) and comparable with larch litter. Clearly, the leaching/incubation system differs from the natural situation, where N is retained by the microflora, by allowing the removal of organic N (as microbes, soluble material and fine particulate matter) which is then no longer available for later mineralization. However the method should be suitable for comparative purposes and has been used to assess potentially mineralizable N, with considerable success, by other workers (e.g. Stanford and Smith, 1976).

Greater nitrification in the larch litter treatments probably reflects the higher level of mineralized NH_4^+, i.e. ammonium, competition for which is a major control on nitrifying populations. Relative nitrification increases with the proportion of larch litter up to L_6S_4, indicating that high ammonium levels alone do not explain the higher nitrifier activity in the presence of larch material. It is possible that the greater mineralization of P in the presence of larch litter stimulates nitrification (Verstrate, 1981). The decline in relative nitrification in treatment L_8S_2 and $L_{10}S_0$, despite high ammonium and P levels, may be due to the low pH values recorded for these treatments. It is interesting to note that nitrification occurred at pH 3.8 which conflicts with older, but not recent

views on the subject (Robertson, 1982).

Predicted values for the release of mineral N and P exceeded the actual results for treatments L_2S_8 to L_6S_4, suggesting a negative influence of spruce litter on N mineralization of larch material. However, for the L_8S_2 treatment the reverse is true indicating a positive interaction between the litters. Whether these findings reflect the field situation, where litter will tend to be deposited in discrete layers, is uncertain. The difference between actual and predicted values declines as the proportion of larch litter increases, as the negative influence of spruce litter is reduced.

These results agree well with those of the pot experiment (Section 5:5), indicating that larch litter is a more readily available source of mineral N than Sitka spruce litter under similar site conditions. The possible stimulatory effect on nitrification is of interest as other workers have noted this under field conditions (e.g. Lavrienko, 1965).

The use of distilled water to leach funnels will not have removed all exchangeable ammonium, although most nitrate will have been removed. Leaching should have been carried out using potassium chloride to ensure complete removal of exchangeable ions. Mineral N recovery does not therefore equate with mineralization which will have been underestimated. Accumulation of ammonium during the course of the incubation probably accounts for the high levels of nitrification detected in some treatments.

The high litter weight loss recorded over the experiment, plus the associated loss of total N, suggests that considerable quantities of particulate material were removed in leachate. Loss of such potentially mineralizable material will have influenced subsequent mineralization.

5:7 Larch litterfall in a mixed larch : spruce stand.

5:7:1 Introduction

Results presented in preceding sections indicate that larch withdraws N, P and K prior to leaf abscission; while P and K may be leached at this time the potential loss of N is low, these findings are substantiated by data for throughfall. Thus larch appears to be conservative in its use of N; however larch litter is a more readily available N source for seedlings than Sitka spruce litter, despite comparable N concentrations in the fresh material. It is necessary to quantify the larch litter input in mixed stands to assess its importance in N cycling, and as a potential source of N for Sitka spruce.

5:7:2 Site description

Larch litterfall was collected in the Mabie 7 experiment, described in Section 3:2:1.

5:7:3 Methods

5:7:3a Field sampling procedure

Larch litterfall was collected over the period of abscission (August - November 1981) in each of the three H treatments. 10 plastic buckets (24cm internal diameter) were randomly placed on the flat plough position (undisturbed ground surface) in each stand. Buckets had drainage holes to prevent the accumulation of rain water. Collections were initially conducted at 30 day intervals, being reduced to 15 days over the period of peak litterfall. For each bucket, samples were oven dried and bulked over the collection period.

5:7:3b Chemical analysis

Bulked oven dry samples were weighed to give the total weight of litterfall. Subsequent sample preparation and chemical analysis for N, P and K were identical to that described in Section 3:3:2.

5:7:4 Results

Litterfall amount and nutrient content did not differ significantly between the treatment plots, results were therefore combined to give a single set of values (Table 5:18).

TABLE 5:18

Weight ($kgha^{-1}$), nutrient concentration (%), and nutrient content ($kgha^{-1}$) of larch litterfall in the Mabie 7 experiment. Mean values (n=30) and (95% confidence limits).

Weight	%N	%P	%K	N	P	K
986.5	0.68	0.11	0.13	6.75	1.03	1.33
(85.11)	(0.036)	(0.005)	(0.005)	(0.659)	(0.097)	(0.114)

5:7:5 Discussion

The quantity of larch litterfall and amounts of N, P and K returned to the forest floor are extremely low in comparison with data for other temperate forests (Bray & Gorham, 1964; Rodin & Bazilevich, 1967). However canopy structure is still very open and full leaf area has yet to be attained. Additionally larch occupies only 75% of the stand.

Values are also low in comparison with the predicted foliar weight of 3063 $kgha^{-1}$ in Section 4. Assuming a weight loss of 28% prior to abscission (Section 5:1), predicts a litterfall of 2205 $kgha^{-1}$, considerably in excess of the measured value of 986.5 $kgha^{-1}$. The discrepancy may be due in part to restricting collectors to the flat plough position only, which may inadequately reflect litterfall in the stands as a whole.

The discrepancy does not influence the main result which is that larch litter contributes only small quantities of N, P and K to the forest floor. Of this total N only a small fraction will become available in the first year; applying the mineralization value of 6.88% obtained in Section 5:6 would give an N release of approximately 0.93 $kgha^{-1}$ in the year following litterfall. It seems unlikely that the quantitative influence of larch litter, in terms of N release, can be an important factor for the N nutrition of Sitka spruce in mixed stands.

Net N mineralization in pure spruce stands and larch/spruce mixtures as measured by field and laboratory incubations.

6:1 Introduction

Annual net N mineralization is an important factor limiting production in non-fertilized forest ecosystems (Miller, 1981; Nadelhoffer et al., 1983; Williams, 1983). Factors influencing mineralization have been previously discussed; mixed and pure stands may differ in terms of substrate quality, decomposer organisms, and microenvironment. Consequently it seems reasonable to suppose that differences may exist in the quantities of N made available annually by mineralization.

Net N mineralization can be estimated by calculating the mean change over time in mineral N concentration (mgg^{-1}) of replicate soil samples incubated in situ or laboratory conditions. Since root uptake and leaching losses are prevented, the change in mineral N concentration gives an estimate of mineralization.

Traditionally, estimates of potentially mineralizable N have been based on aerobic laboratory incubations, conducted in closed systems under constant moisture and temperature conditions (Keeney, 1980). For agricultural soils, such methods have, in general, given results highly correlated with N uptake by plants grown in potted soils under greenhouse conditions. The highly refined incubation technique of Stanford et al. (1974) has shown extremely good correlation with crop growth. Cumulative N mineralization is proportional to the square root of incubation time (Stanford and Smith, 1972), consequently potentially mineralizable N can be estimated from incubation studies lasting only 3 to 4 weeks. Aerobic incubation results from forest soils have been shown to correlate

with tree growth (Tamm and Petersen, 1969; Van den Driessche and Webber, 1977 : Van Praag and Weissen, 1973).

An alternative technique where samples are incubated under warm anaerobic conditions was derived by Waring and Bremner (1964). Results from such incubations have been correlated with tree growth in some cases (Shumway, 1978), although the suitability of the technique seems to vary with different habitat types (McNabb et al., 1978).

Since N mineralization is strongly influenced by moisture and temperature (Popović, 1980) more reliable estimates of field mineralization may be obtained from samples incubated under field conditions. Such studies normally involve composite, homogenised samples placed in containers which permit gas exchange but prevent loss of mineral N through leaching and plant uptake. The vast majority of these studies have used polyethylene bags, although Rapp et al. (1979) used perforated metal cans while Williams (1983) used plastic pots. In situ incubations have gained some popularity as a means of estimating rates of N mineralization and have been adopted by a number of workers; e.g. Ellenburg (1977); Glavac and Koenies (1978); Melillo (1981), Nadelhoffer et al. (1983); Pastor et al. (1984); Popović (1980); Powers et al.,(1978): Runge (1974); Van Pragg and Weissen (1973); Westerman and Crothers (1981); Williams (1983).

Two approaches may be adopted in the use of field incubations; 1) long term incubation of material from one collection date (Williams, 1983) with or without periodic subsampling to follow the pattern of mineralization; 2) sequential collection and incubation of material over a much shorter time interval (Popović, 1980). The first approach has the advantage that the extended incubation period should yield results which are not influenced by the initial manipulation of the material; Popović(1980) indicates that for soils low in N, or where fine root concentrations are high, a short incubation period (less than 6 weeks) may not be sufficient to reduce the impact of initial immobilization on the final result. However, the first approach does not permit the integration of changes in soil moisture (unless incubations are not fully enclosed) or sub-

strate quality and quantity (e.g. fine root turnover), a problem partially resolved by the sequential sampling approach.

The exclusion of rainfall and throughfall from incubations may be an important artefact, even with the sequential approach which permits broad changes in soil moisture levels to be followed. The microbial biomass, especially bacteria, are stimulated by rainfall even when moisture is non-limiting, due to mineral elements present in the rain (Clarholm and Rosswall, 1980). Williams (1983) detected significant, but variable, differences in N mineralization between field incubations left open to the rain and ones which were not. Additionally, short term wetting and drying cycles which stimulate mineralization (Heal, 1979) are excluded from many incubation studies.

Whether fine roots killed during sample collection should be removed or included in the incubation is uncertain. Fine root turnover can be large (Fogel, 1983) with rates of decomposition being extremely rapid (Ford and Deans, 1977) or similar to above ground fine litter components (Berg et al., 1982c). It is arguable that roots killed during sample preparation may be insignificant in terms of annual turnover; however artificially caused root death will not coincide with normal phenology and may provide a substrate dissimilar to roots which may have undergone natural mortality, perhaps with senescence. An additional artefact of both field and laboratory incubations is the absence of living roots and mycorrhizas. Gadgil and Gadgil (1975) have demonstrated antagonism between mycorrhizal symbionts and decomposer organisms, while a positive influence of the rhizosphere on decomposition and mineralization has been postulated for some time (Stone and Fisher, 1969).

Normally mineral N concentrations in the soil are low (Cole, 1981), in long term incubations concentrations rise to artificially high levels in the absence of plant uptake and leaching loss. Such high concentrations may have qualitative and quantitative effects on the microflora, influencing nitrification and subsequent mineralization. This problem should be avoided by sequential incubations.

Incubation studies may be criticised for their severe

manipulation of the sample material (Van Praag and Weissen 1973). Additionally, the need to prevent loss of mineralized N necessitates some degree of sample isolation from the ambient soil environment. Consequently, conditions in incubations are not comparable with those in undisturbed soil layers (Williams, 1983); although in situ studies go some way to reconcile these problems. Sample manipulation can be reduced by the use of undisturbed samples (e.g. Rapp et al., 1979); since this precludes mixing of material to produce a uniform substrate variation may become a problem. Natural variation in soil N and mineralization can be considerable (see Keeney, 1980). Carey et al. (1981) rejected the use of undisturbed individual samples because of high variation encountered during a pilot study. Since the act of sample collection, root severance, and isolation introduces many artefacts into the incubation system it may be arguable whether intact samples mimic the real system to a greater degree than those which have been homogenised.

The present study makes use of both field and laboratory incubation techniques to examine potential differences in N mineralization in pure spruce and larch/spruce mixtures. All incubations used homogenised composite material, but towards the end of the experiment some undisturbed samples were incubated for comparative purposes.

6:2 Methods

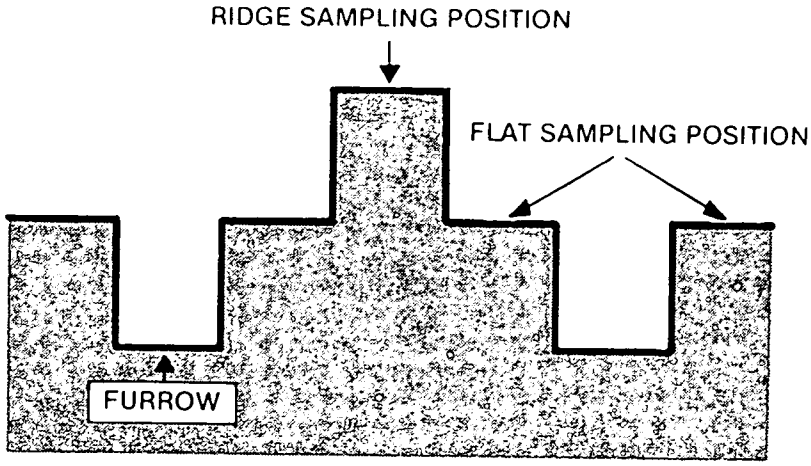
6:2:1 Field sampling procedure

Sampling was conducted in the Mabie 7 and Inchnacardoch 164 experiments described in Section 3:2.

Mabie 7: for each of the 3 OW and H treatment plots, samples were taken from 10 randomly selected points on the ridge and flat plough positions respectively (Figure 6:1). Samples were collected to a depth of 9cm using a 6.6cm internal diameter corer; aluminium rings within the corer permitted the sample to be divided into 3 depth sections, 0-3, 3-6 and 6-9cm. The surface sample included L.F.H. material while deeper samples were entirely of peat. For each treatment plot, samples from a given position (ridge or flat) and depth were bulked then homogenised. Any living plant material was removed

FIGURE 6:1.

DIAGRAMATIC SECTION ACROSS PLOUGHING TO INDICATE SAMPLING POSITIONS FOR MATERIAL USED IN FIELD AND LABORATORY INCUBATIONS.



(Mosses etc.) along with larger roots, while an attempt was made to reduce the quantity of fine root material. On the last 4 sampling occasions an extra 4 cores were taken from each treatment plot to allow the incubation of undisturbed material. At the start of the experiment an additional 30 cores were taken from the ridge and flat positions of both treatments for bulk density determinations.

Inchnacardoch 164: Material from this experiment was used in a single laboratory incubation. For each of the 5 SS-N and JL/SS-N treatment plots 5 cores were taken from both the ridge and flat positions as described above. Collection was carried out in December 1982.

6:2:2 Incubation

For incubation under field conditions, bulked homogenised material from a given treatment, plough position, and depth, was repacked into an aluminium corer ring ($103cm^3$) to its original bulk density. Initially this was achieved by weighing core sections using a spring balance, until sufficient accuracy ($< \pm$ 15%) could be obtained by eye. Material was carefully removed from the ring and wrapped in 25.4μm thick polyethylene film (this may have been too thick to permit free movement of oxygen and carbon dioxide, Bremner and Douglas ,1971). The incubation package was replaced within the treatment of origin at the correct position and depth. Each incubation had 6 replicates.

To examine the possible influence of microclimatic differences between plots on net mineralization (independent of substrate quality) material was exchanged between treatments. Thus OW samples were incubated in the H treatment and vice versa. Incubations were for 30 days, except for a 60 day incubation in winter (December - February 1983). On collection the sampling/incubation procedure was repeated.

For the last 4 incubations the 0 - 3cm sections of the additional cores were incubated intact, without root removal or homogenisation.

Subsamples of fresh material were retained for laboratory determinations of initial mineral N, moisture content, and pH.

Incubations under laboratory conditions were run using material from both experiments. With Mabie material incubations were run concurrently with those in the field on 4 occasions. For each of the OW and H treatments material from the treatment plots was bulked to give 1 composite sample for each plough position and depth. 20g portions of each sample were weighed into 250ml conical flasks and incubated under moist aerobic conditions in the dark at 20°C. Flasks were stoppered with cotton wool and the moisture content maintained by the addition of water every 5 days. Samples were replicated 4 times and the incubations run for 30 days. Procedure was identical for material from Inchnacardoch except that 40g samples were used and mineralization assessed after 30 and 60 days. Subsamples of fresh material were retained for laboratory analysis.

6:2:3 Chemical analysis

Mineral N (ammonium, nitrate and nitrite) was extracted by shaking samples (10g fresh weight) for 1hr with 200ml 1N KCl, extracts were stored at 3°C prior to analysis. Core samples were stored at this temperature for a maximum of 72hrs before extraction. Concentrations of ammonium and (nitrate + nitrite)-N in extracts from fresh and incubated samples were determined by colorimetric methods adapted to a continuous flow system (Crooke and Simpson, 1971; Henriksen and Selmer-Olsen, 1970).

Moisture contents of fresh and incubated samples were determined on subsamples dried to a constant weight at 85°C, while pH was recorded potentiometrically, in distilled water at a solid : liquid ratio of 1 : 25, on bulked material.

Soil bulk densities were used to convert mineral N concentrations in soil to real content values expressed on an area basis (Appendix 5A).

6:3 Results

No nitrate was detected in either the soil exchangeable pool or incubated material throughout the course of the experiment: consequently references to mineralization or mineral N indicate ammonification or ammonium.

Moisture contents of material placed in incubation packages showed little or no change compared with those measured for

fresh material at the start of the incubation.

F-tests indicated that variances differed between means, therefore a variation of the normal T-test approximating the method of the Fisher-Behrens test was adopted (Snedecor and Cochran, 1967) in the analysis of results.

6:3:1 Field incubation

a) Comparison of net N mineralization in the OW and H treatments.

Treatments and plough positions exhibited similar seasonal patterns of net mineralization, although quantities differed (Figures 6:2 and 6:3, Appendix 5B). Mineralization increases from low levels (or immobilization) from January to April, peaking during May and June. Levels fall between June and July, increasing to a second, larger, peak during August and September. Levels then fall to their low winter values in November. This apparent seasonal pattern is only inferred since results were obtained over 3 years, data being incomplete for any given year.

A common seasonal pattern is also exhibited by treatments and plough positions for changes in the soil ammonium pool (Figures 6:2 and 6:3, Appendix 5C), with maximum values occurring in March 1982. Soil ammonium levels do not exhibit consistent treatment differences, although OW values tend to be higher when levels peak. There is little correlation between changes in the soil ammonium pool and net mineralization, except for the period February to July 1982, when changes in soil ammonium between sampling dates broadly follow the pattern of mineralization.

Marked treatment differences are apparent for both plough positions; ridge mineralization values in the H treatment exceed those in the OW on 10 of 13 occasions (9 of these significantly, Appendix 5B), and 11 of 13 occasions for the flat (9 significantly, Appendix 5B). Summing monthly mineralization values to produce an annual estimate (Appendix 5A) produces a total of 28 (29) $kgNha^{-1}yr^{-1}$ for the OW treatment and 60 (65) $kgNha^{-1}yr^{-1}$ for the H treatment; depending whether the 1982 or (1983) February to April values are chosen.

Soil moisture content also varies seasonally (Figure 6:4),

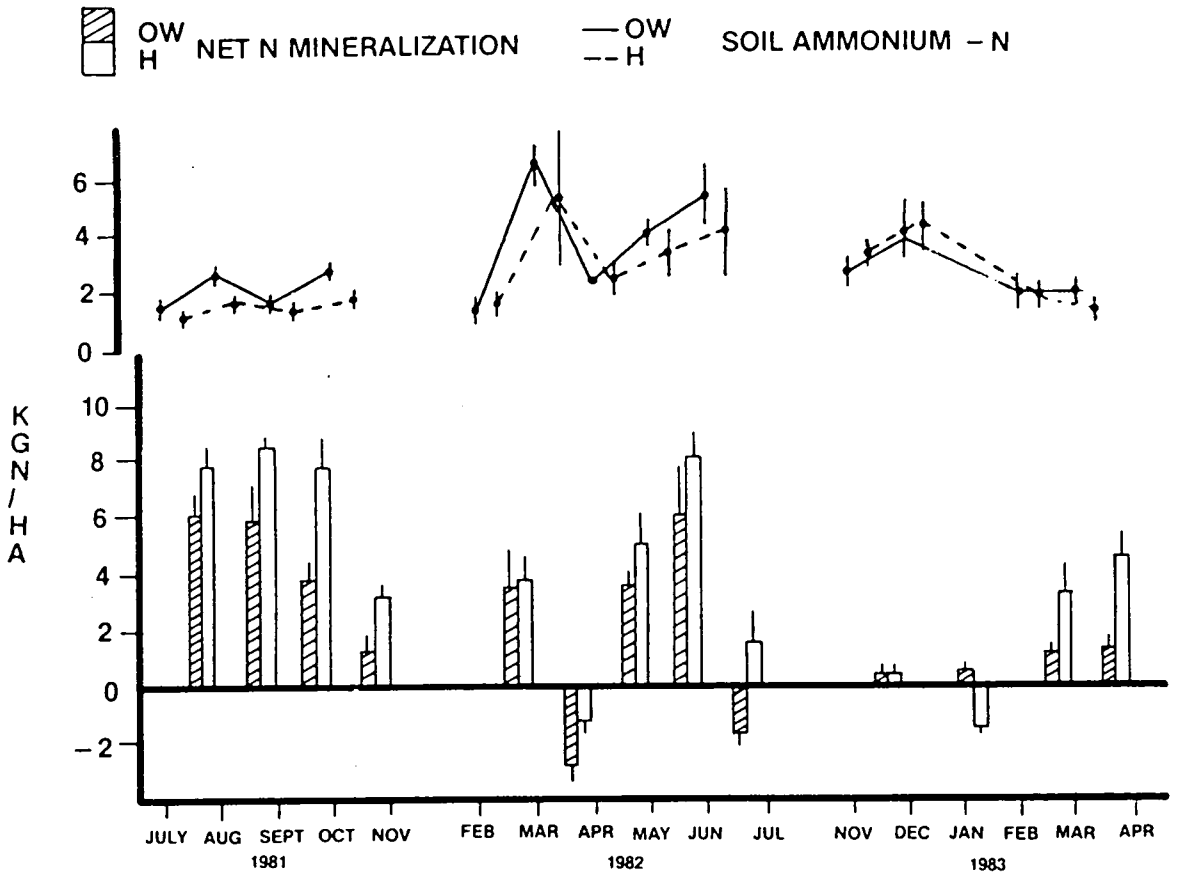


FIGURE 6:2. SEASONAL PATTERNS OF NET N MINERALIZATION IN THE RIDGE POSITION OF THE OW AND H TREATMENTS IN 0-9 cm SOIL. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS. SOIL POOLS OF AMMONIUM – N ARE SHOWN AT THE START OF EACH INCUBATION PERIOD.

VALUES OF SOIL AMMONIUM - N FOR THE TWO TREATMENTS ARE OFFSET TO PERMIT INCLUSION OF CONFIDENCE LIMITS.

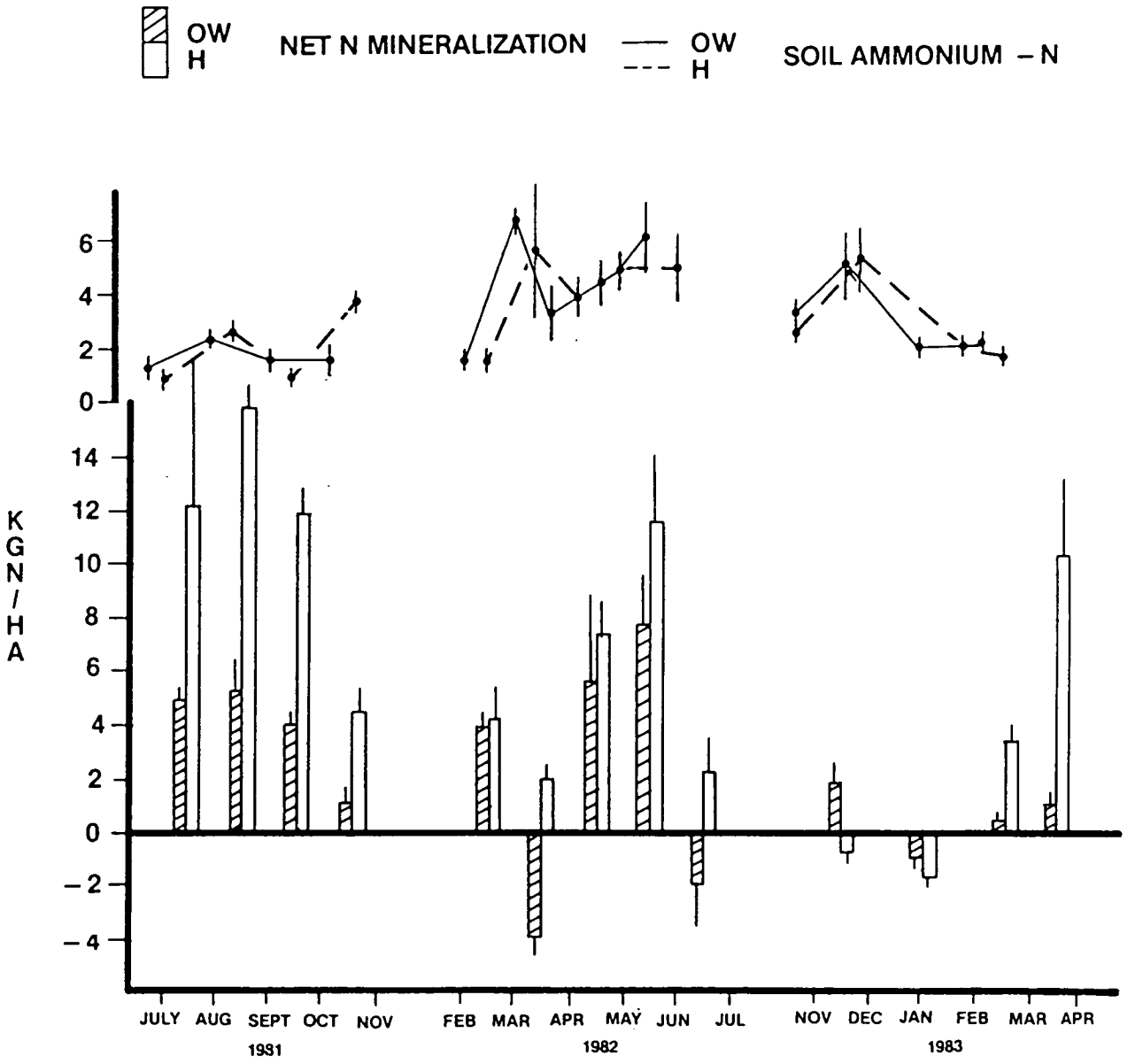


FIGURE 6:3. SEASONAL PATTERNS OF NET N MINERALIZATION IN THE FLAT POSITION OF THE OW AND H TREATMENTS IN 0-9 cm SOIL. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS. SOIL POOLS OF AMMONIUM – N ARE SHOWN AT THE START OF EACH INCUBATION PERIOD.

VALUES OF SOIL AMMONIUM - N FOR THE TWO TREATMENTS ARE OFFSET TO PERMIT INCLUSION OF CONFIDENCE LIMITS.

driest values being recorded in summer and early autumn. Treatment differences are only significant for the ridge position (Table 6:1), with the H treatment being consistently drier. Moisture values for the flat position are very similar, differences being non-significant, although H values tend to be lower. Greatest between treatment differences occur during the dry period July to October 1981. Moisture contents show no correlation with net mineralization or soil ammonium.

Soil pH does not differ significantly between treatments (Table 6:2), however H treatment values are consistently higher by approximately 0.05 units.

TABLE 6:1

Soil moisture content (% fresh weight). Mean values (n=78) for the incubation period and (95% confidence limits).

	Ridge			Flat		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
OW	69.5	78.0	79.6	78.0	82.1	83.0
	(1.9)	(1.4)	(1.1)	(1.7)	(1.0)	(1.0)
H	65.3	72.4	75.3	75.2	81.0	82.4
	(3.6)	(3.0)	(2.3)	(3.4)	(1.5)	(1.3)
	*	*	*	NS	NS	NS

Differences between treatment means are significant at P=0.05 (*) or are not significant (NS) in a T-test.

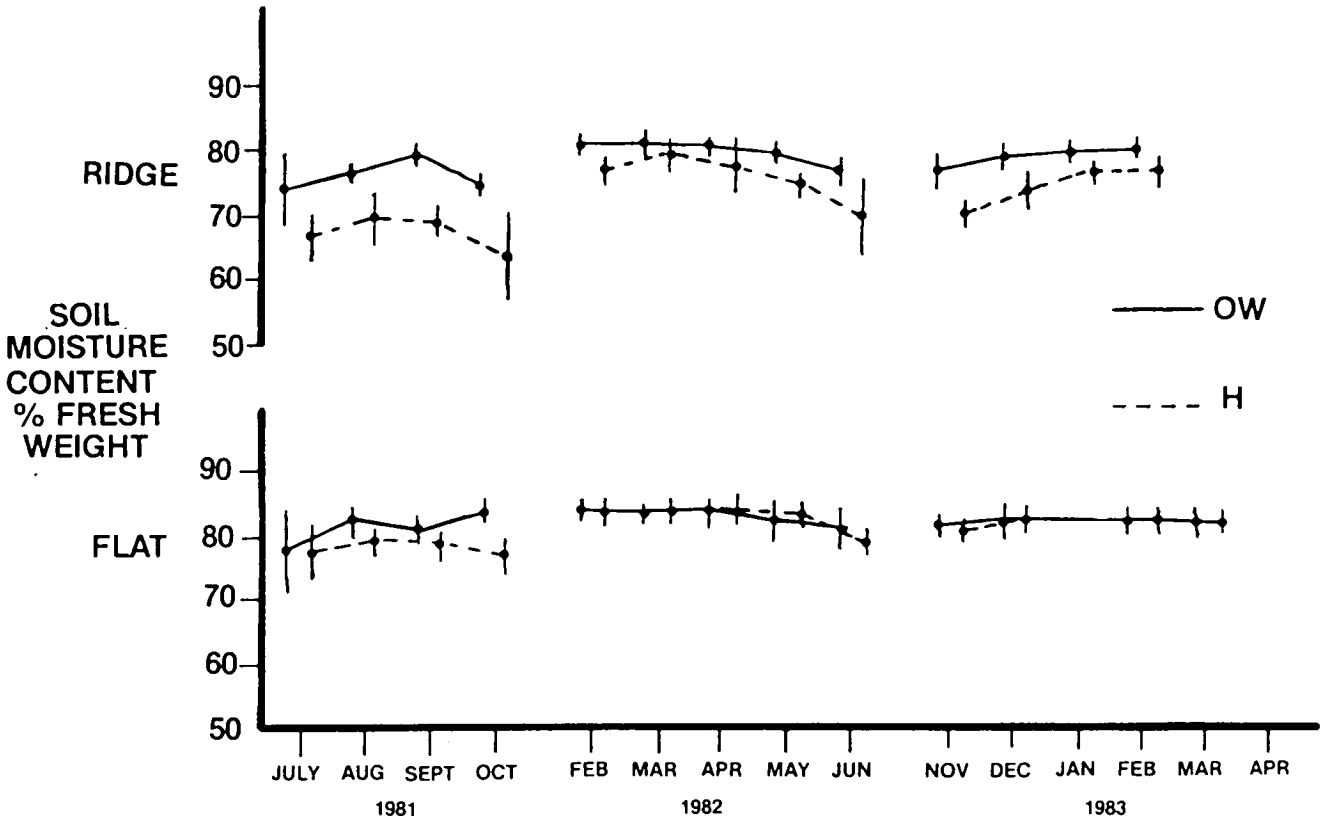


FIGURE 6:4. SOIL MOISTURE CONTENT IN THE OW AND H TREATMENTS FOR THE RIDGE AND FLAT POSITIONS (3-6 cm depth). VERTICAL LINES SHOW 95% CONFIDENCE LIMITS.

VALUES FOR THE TWO TREATMENTS ARE OFFSET TO PERMIT INCLUSION OF CONFIDENCE LIMITS.

TABLE 6:2

Soil pH. Mean values (n=13) for the incubation period and (95% confidence limits).

	Ridge			Flat		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
OW	3.43 (0.13)	3.35 (0.14)	3.27 (0.15)	3.38 (0.16)	3.32 (0.15)	3.30 (0.14)
H	3.48 (0.15)	3.40 (0.14)	3.34 (0.14)	3.54 (0.17)	3.36 (0.13)	3.33 (0.14)
	NS	NS	NS	NS	NS	NS

Differences between treatment means are not significant at P=0.05 (NS) in a T-test.

b) Reciprocal incubation of H and OW material under both H and OW conditions.

For sample material from either treatment, and both plough positions, the incubation site (i.e. an OW or H plot) has virtually no influence on net mineralization (Figures 6:5 and 6:6, Appendix 5B). Taking OW ridge material, mineralization values for incubation under the two conditions differ significantly on only 4 of the 13 occasions. For OW flat material significant differences occur on only 5 occasions. A similar result is seen for H material, with significant differences occurring on only 3 occasions for the ridge and only 1 occasion for the flat (Appendix 5B). For differences which do occur, the influence of site is not consistent.

Summing monthly mineralization values (Appendix 5A) for an annual estimate gives 28 (29) $kgNha^{-1}yr^{-1}$ for OW material incubated under OW conditions compared with 27 (28) $kgNha^{-1}yr^{-1}$ for the same material incubated under H conditions. The pattern is repeated for H material with 60 (65) $kgNha^{-1}yr^{-1}$ under

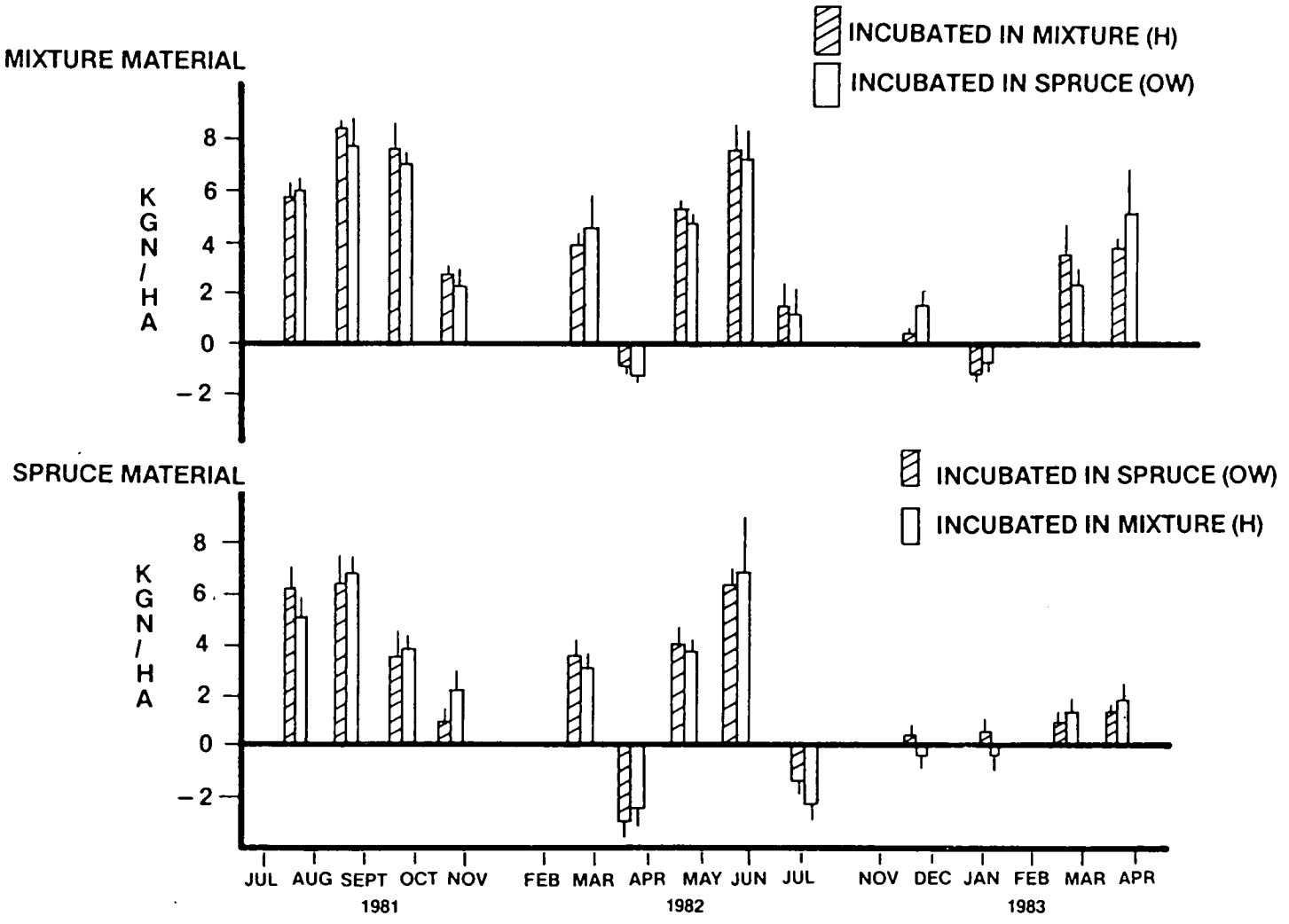


FIGURE 6:5. COMPARISON OF NET N MINERALIZATION IN THE RIDGE (0-9 cm) FOR SPRUCE AND MIXTURE MATERIAL INCUBATED IN BOTH SPRUCE AND MIXTURE STANDS. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS.

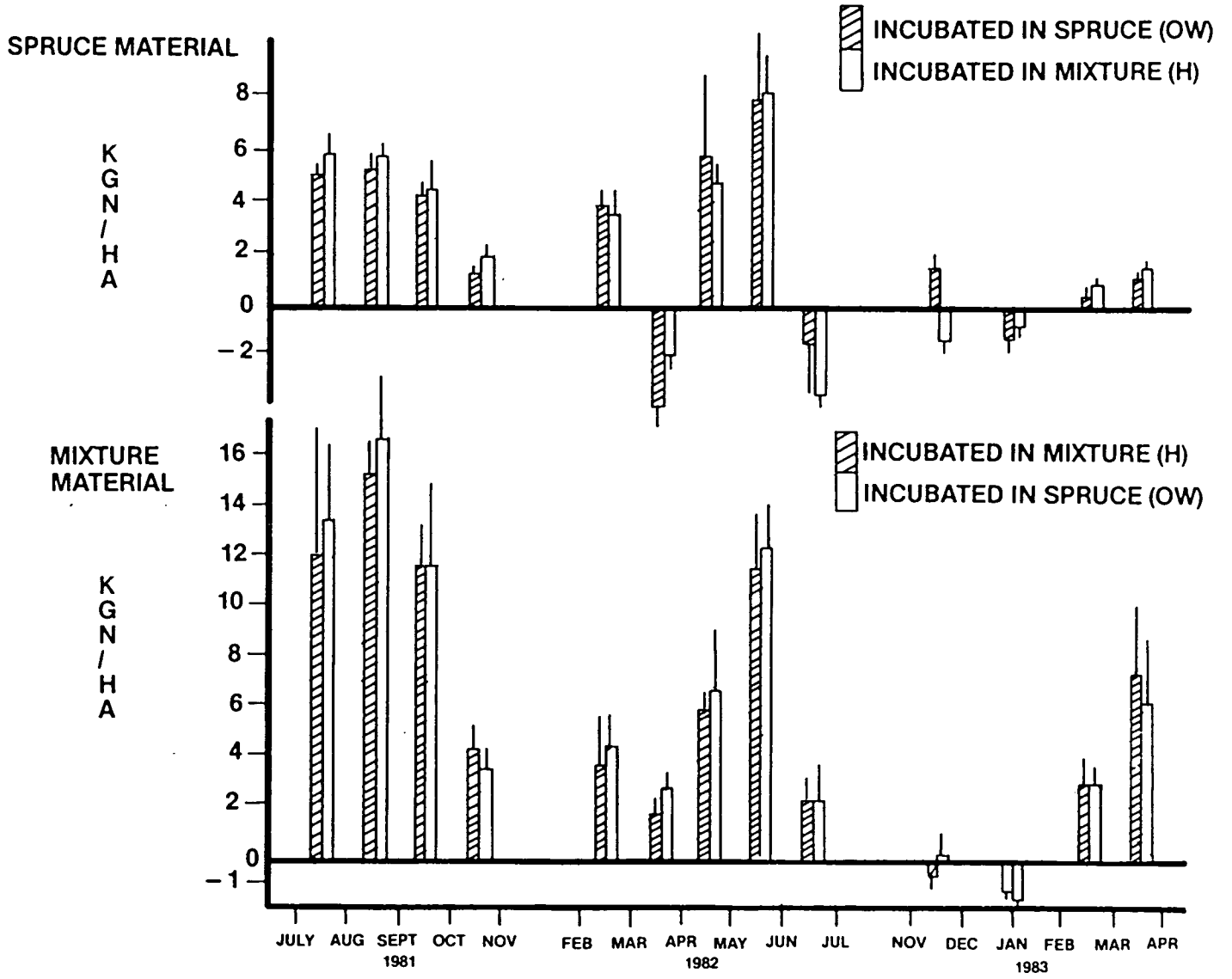


FIGURE 6:6. COMPARISON OF NET N MINERALIZATION IN THE FLAT (0-9cm) FOR SPRUCE AND MIXTURE MATERIAL INCUBATED IN BOTH SPRUCE AND MIXTURE STANDS. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS.

H conditions and 63 (67) $kgNha^{-1}yr^{-1}$ under OW conditions, using February to April 1982 or (1983) values respectively.

c) Comparison of ridge and flat plough positions

Comparison of net N mineralization values for OW and H material (Figures 6:2 and 6:3 , Appendix 5B) indicates relatively little difference between the ridge and flat positions for the OW treatment, however, a considerable difference is apparent for the H treatment. Mineralization differs significantly between ridge and flat on only 4 occasions for OW material but on 9 occasions for H treatment (Appendix 5B).

Summing values to give an annual estimate gives 27 (28) $kgNha^{-1}yr^{-1}$ for the ridge compared with 29 (29) $kgNha^{-1}yr^{-1}$ for the flat in the OW treatment. In the H treatment these values are 44 (49) and 68 (74) $kgNha^{-1}yr^{-1}$ respectively.

Soil moisture levels are considerably greater in the flat position of both treatments (at all depths), this difference being more marked in the H treatment (Table 6:1). Soil pH values do not differ between the two positions (Table 6:2).

d) Variations with depth

There is a tendency for most mineralization to occur in the 0-3 cm layer of the H treatment, for both plough positions (Figure 6:7, Appendix 5D). This is most marked for the period July to November 1981, when a similar trend is observed in the OW treatment (Figure 6:8, Appendix 5D). Outwith this period mineralization at other depths assumes a greater importance. Increased mineralization in the 0-3 cm layer occurs on fewer occasions in the OW treatment. Summing respective depth values (Table 6:3) indicates that 48-34% of OW mineralization and 58-54% of H mineralization takes place in the upper layer.

Moisture content increases with depth in all cases, while differences in moisture contents between treatments and plough positions are reduced (Table 6:1), pH declines with depth in all cases.

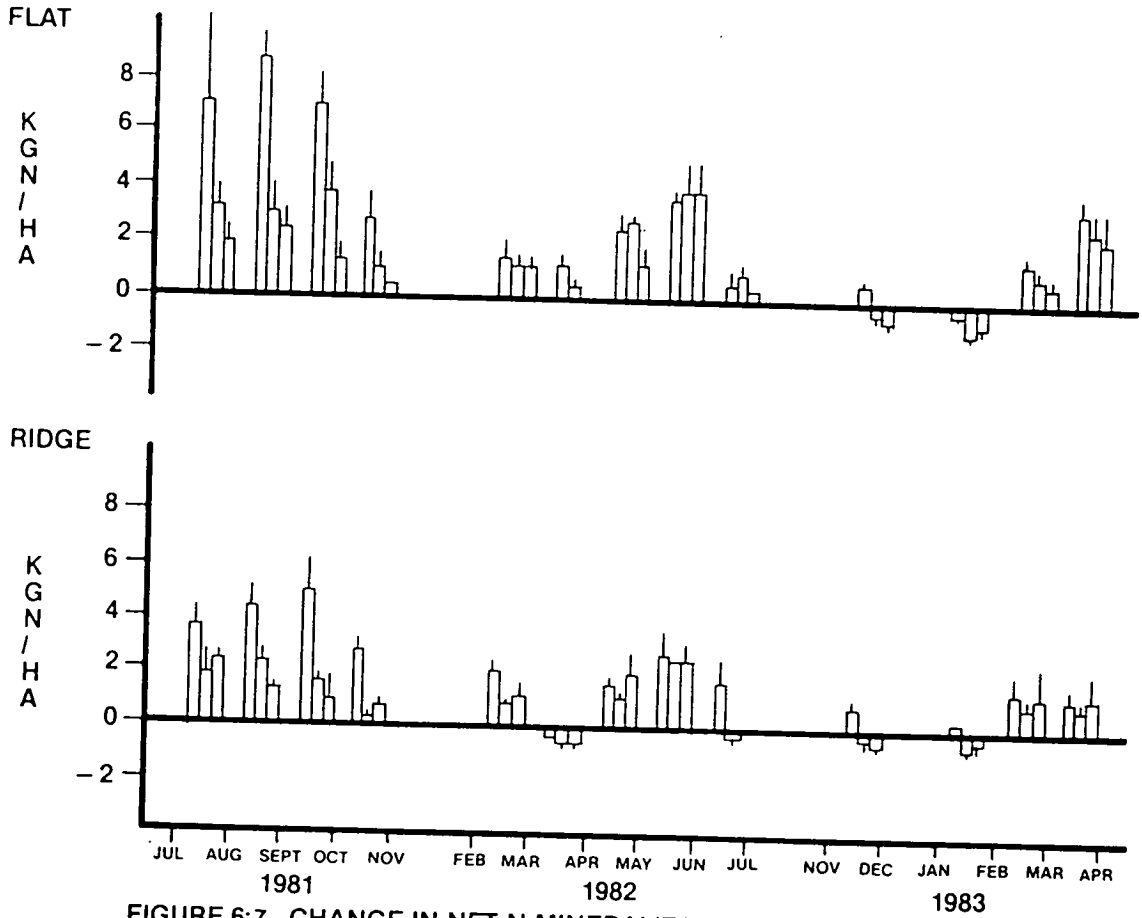


FIGURE 6:7. CHANGE IN NET N MINERALIZATION WITH DEPTH, 0-3, 3-6, 6-9 cm, FOR THE H TREATMENT IN BOTH RIDGE AND FLAT PLOUGH POSITIONS. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS.

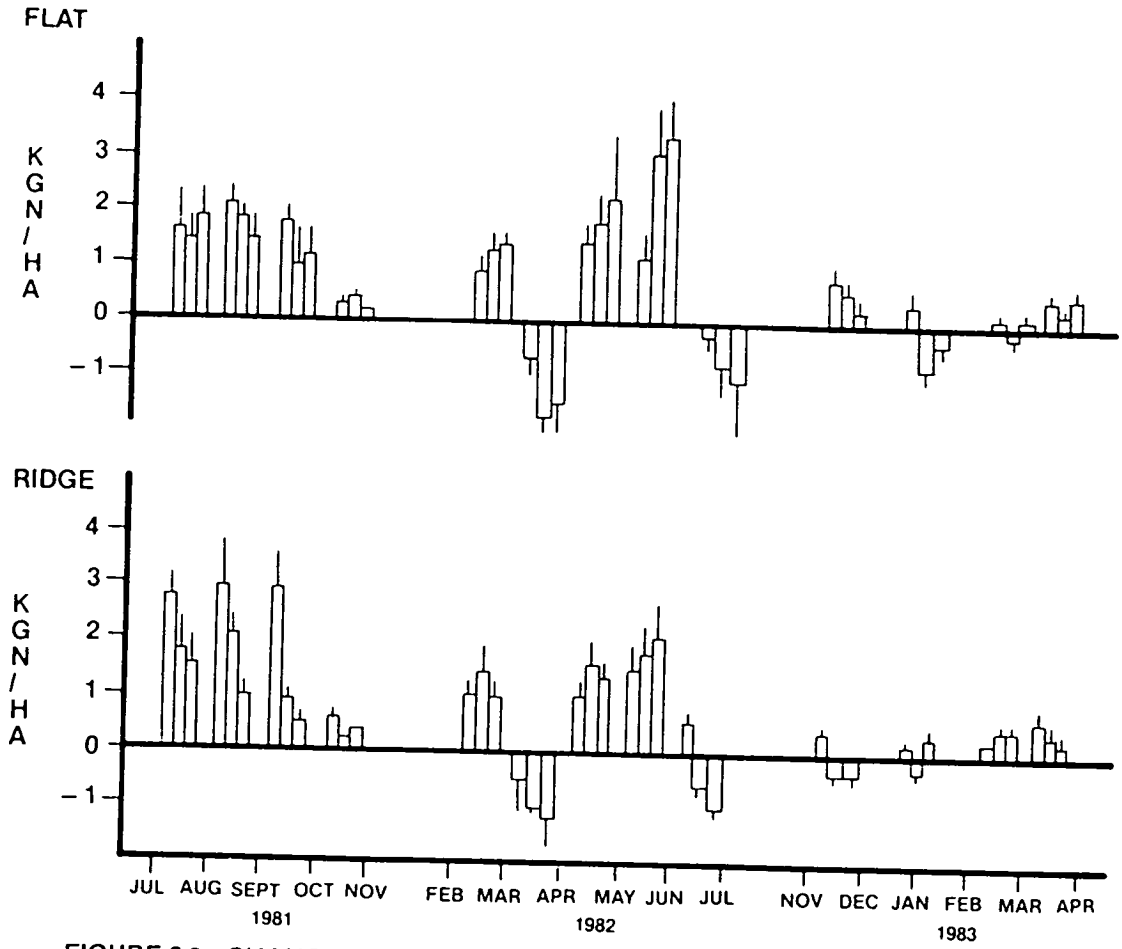


FIGURE 6:8. CHANGE IN NET N MINERALIZATION WITH DEPTH, 0-3, 3-6, 6-9 cm, FOR THE OW TREATMENT IN BOTH RIDGE AND FLAT PLOUGH POSITIONS. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS.

TABLE 6:3

Net N mineralization at different depths*, $kgha^{-1}$.

	Ridge			Flat		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
OW	13	8	6	10	9	10
H	25	9	9	36	18	13

* using February - April 1982 values.

e) Intact Cores

Results for the incubation of intact cores (0-3 cm) were extremely variable (Appendix 5E) making interpretation and comparison with the main experiment difficult. Considering only results with 95% confidence limits less than the mean value shows no clear effect of sample mixing on mineralization. For both OW and H material 50% of intact cores gave mineralization values greater than equivalent mixed material and 50% mineralized less.

Mineralization values of intact H cores exceed OW cores in virtually all cases. For the final incubation only, intact cores gave mineralization results which were very similar to those for mixed material (cf. Appendix 5E with Appendix 5D).

6:3:2 Laboratory incubations

a) Comparison of N mineralization in pure spruce (OW, SS-N) and mixture (H, JL/SS-N) material.

Marked treatment differences are apparent for both experimental sites. For Mabie 7, mineralization of H material significantly exceeds that of OW material for all 4 incubations, and both plough positions (Figure 6:9, Appendix 5F). Treatment differences are greatest for the flat plough position. Summing the 4 incubations and extrapolating to an annual value gives 110 $kgNha^{-1}yr^{-1}$ for the OW treatment and 179 $kgNha^{-1}yr^{-1}$ for the H.

For Inchnacardoch 164; mineralization of JL/SS-N material significantly exceeds that of SS-N material for both plough

FIGURE 6:9. NET N MINERALIZATION FOR LABORATORY INCUBATIONS OF MABIE 7 MATERIAL. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS. 0-9 cm DEPTH.

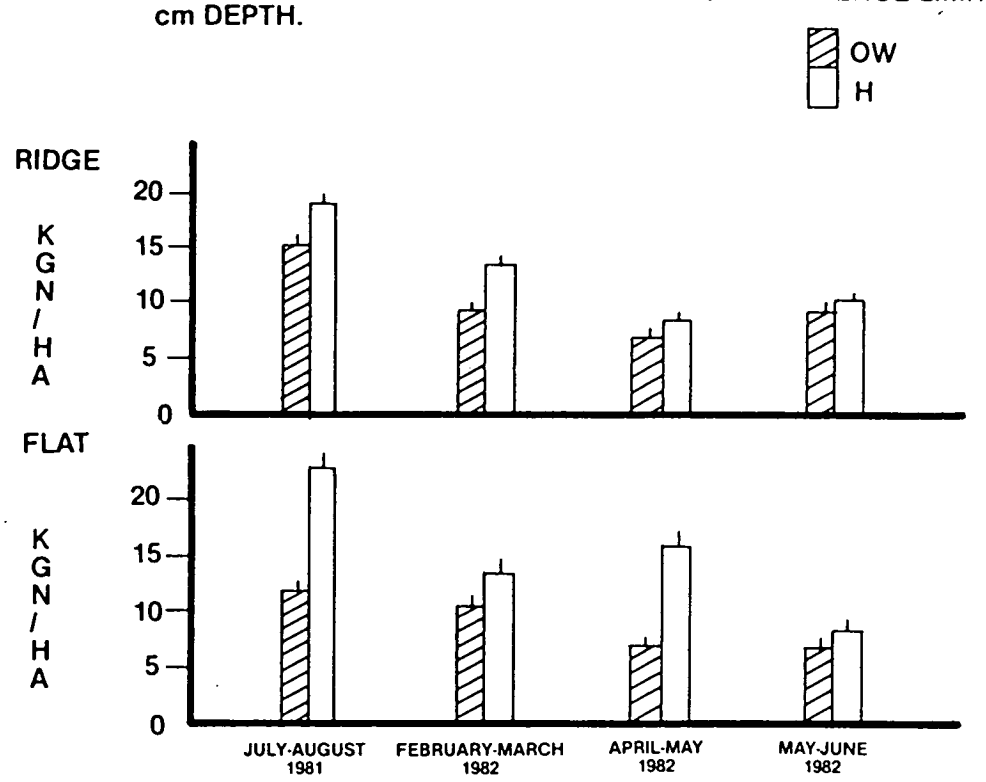
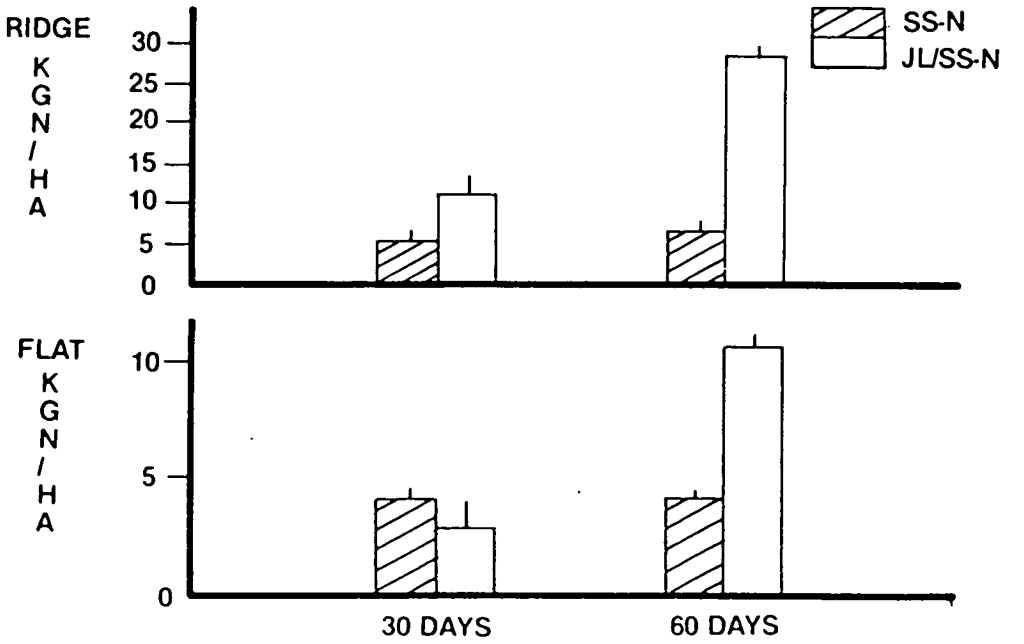


FIGURE 6:10. NET N MINERALIZATION AFTER 30 AND 60 DAYS FOR LABORATORY INCUBATIONS OF INCHNACARDOCH 164 MATERIAL. VERTICAL LINES SHOW 95% CONFIDENCE LIMITS. 0-9 cm DEPTH.



positions, after 60 days (Figure 6:10, Appendix 5G). After only 30 days the pattern is the same except for JL/SS-N ridge material which mineralized less than the SS-N. Summing values and extrapolating to 1 year gives 32 $kgNha^{-1}yr^{-1}$ for the SS-N and 109 $kgNha^{-1}yr^{-1}$ for the JL/SS-N treatment.

b) Comparison of ridge and flat plough positions.

For Mabie; OW material shows little difference in mineralization between plough position (Figure 6:9; Appendix 5F). Summing values for the 4 incubations gives 39 $kgNha^{-1}$ for the ridge and 36 $kgNha^{-1}$ for the flat. Mineralization of H material shows a greater positional difference, summing values gives 49 $kgNha^{-1}$ for the ridge and 65 $kgNha^{-1}$ for the flat.

With material from Inchnacardoch the pattern is different, for both SS-N and JL/SS-N incubations, mineralization of ridge material exceeds flat. Differences do not relate to pH or soil moisture (Appendix 5H).

c) Changes with depth.

For Mabie; OW and H material from both plough positions shows greatest mineralization in the 0-3 cm layer. The difference in surface mineralization accounts for 80% of the treatment difference for ridge material and 93% for flat material (Table 6:4). Mineralization for the 3-6 and 6-9 cm deep layers is very similar for the 2 treatments, for both plough positions (Table 6:4, Appendix 5I).

Inchnacardoch flat material shows greatest mineralization in the surface layer for both treatments; for the ridge, however, mineralization at the other depths is more important (Table 6:4, Appendix 5G).

d) Comparison of the field and laboratory incubations.

Summing field and laboratory incubation results for equivalent periods gives a field value of 22 $kgNha^{-1}$ and a laboratory value of 37 $kgNha^{-1}$ for OW material. For the H treatment these values are 32 and 60 $kgNha^{-1}$ respectively. Assuming a Q_{10} of 2 (Alexander, 1977) and a mean field temperature of 10°C (Williams, 1983) laboratory values can be reduced by a half. Thus for OW material the value becomes 18.5 $kgNha^{-1}$, while that for H material becomes 30 $kgNha^{-1}$ These values are 84% and 94% of the equivalent field results.

TABLE 6:4

Net N mineralization at different depths for laboratory incubated material ($kgha^{-1}$). Mabie values are the sum of 4 incubations, Inchnacardoch values after 60 days.

	Ridge			Flat		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
Mabie						
OW	22	8	9	14	10	12
H	30	9	10	41	12	12
Inchnacardoch						
SS-N	2	2	3	2	1	1
JL/SS-N	5	15	11	7	1	4

6:4 Discussion

Annual net mineralization in the field amounted to 28 $kgNha^{-1}yr^{-1}$ under pure spruce stands and 60 $kgNha^{-1}yr^{-1}$ under mixture stands; values which are comparable with those quoted for natural coniferous forest, 30-50 $kgNha^{-1}yr^{-1}$ (Gosz, 1981). The values are low in comparison with those measured in temperate deciduous forest, which averages 110 $kgNha^{-1}yr^{-1}$ (Melillo, 1981). Mineralization of 72 $kgNha^{-1}yr^{-1}$ was found by Glavac and Koenies (1978) from a spruce stand in Germany, while Williams (1983) obtained a field estimate of 67 $kgNha^{-1}yr^{-1}$ under fast growing ($23m^3ha^{-1}yr^{-1}$) Sitka spruce on a brown forest soil (inherently more fertile than the deep peat sites in this study).

The annual N requirement of natural temperate coniferous forest averages 46 $kgha^{-1}$ (Cole and Rapp, 1981); managed stands generally require more N to sustain higher rates of growth (Cole, 1981, Keeney, 1980). Miller et al. (1979) found that an annual N uptake of 69 $kgha^{-1}$ was required to maintain maximum growth rate of Corsican pine ($19.7m^3ha^{-1}yr^{-1}$) on N deficient sand. This level of N supply and growth rate are very similar to the mineralization value and associated growth rate found by Williams (1983) for Sitka spruce.

A mineralization rate of 28 $kgNha^{-1}yr^{-1}$ would seem insufficient to support a high rate of growth, while 60 $kgNha^{-1}yr^{-1}$ should be capable of sustaining a much increased growth rate. This is in agreement with findings for height growth, N status, and foliar N capital described in sections 3 and 4. It is noteworthy that the relative difference in N mineralization between treatments (2:1) and the difference in foliar N capitals (1.6:1) are very similar, while absolute levels of mineralization are more than adequate to account for the observed foliar N capitals.

Clearly, conditions within the incubation packages will not truly reflect those in the adjacent soil and therefore it is uncertain the extent to which measured net N mineralization approaches the real value. However, laboratory incubation results mirror the treatment differences found in the field; while the adjusted laboratory totals (Q_{10}) are virtually identical to those in the field, for the equivalent period. Manipulation of material prior to incubation does not appear to

have an overriding effect upon the results; incubation of intact cores does not alter the observed treatment differences, and for one set of incubations results from mixed and intact material were very similar. Agreement between the different methods suggests that the field incubation technique adopted in this study genuinely reflects treatment differences.

Mineralization exhibits a similar seasonal pattern under spruce and mixture stands suggesting a common causative factor. Moisture and temperature are normally considered as having a major interactive effect on mineralization (Popović, 1980), although the former did not obviously influence the pattern of mineralization in this study. The only indication of a moisture related effect comes from mixture ridge material at Mabie, this mineralizes at a rate below that of the flat position, where moisture levels are higher. Such a difference is not apparent for pure spruce material, where ridge moisture levels exceed those in the mixture.

Changes in the exchangeable ammonium pool follow virtually identical patterns in both treatments, which show no correlation with soil moisture and little correlation with net N mineralization. It might be expected that changes in the soil ammonium pool would follow the pattern of mineralization, high exchangeable levels being recorded after periods of active mineralization and vice versa. This pattern does exist for the period February to July 1982 but is not apparent at other dates. Such a pattern would not be expected in the presence of effective root (mycorrhizal) uptake of mineralized N which would damp fluctuations in the exchangeable pool. It is probable that mycorrhizas can respond extremely rapidly to periods of high N availability (Ingestad, personal communication), preventing marked changes in the exchangeable pool except when mycorrhizal activity is low. The similarity of soil ammonium levels between treatments merely reflects the ability of the mixture trees to effectively exploit the higher rate of mineral N production.

Increased mineralization in the mixtures is not a result of moisture conditions, while the similarity of mineralization rates between reciprocal incubations suggests that temperature differences, if they occur, are not important. This indicates,

circumstantially, that differences are due to factors such as; substrate quality; decomposer community; N-fixation; or mycorrhizosphere influences on the decomposition of organic matter. Mineralization levels and differences between treatments, are greatest in the surface layer. This could indicate an influence of larch litter which appears to release N more readily than spruce litter (Section 5:5), although total amounts are small.

No nitrate or nitrification were detected during the course of this study. This is not immediately surprising since low pH, low ammonium levels, and anaerobic conditions tend to suppress nitrification (Alexander, 1977). Nitrate levels in coniferous systems tend to be an order of magnitude below those of ammonium (Cole, 1981), which tends to dominate in these ecosystems (Borman and Likens, 1979; Reiners, 1981). Ellenberg (1971) cites several studies in temperate forests which showed no nitrification, while Melillo (1977) and Pastor et al. (1984) have identified forest sites where mineralization may be high but no nitrification occurs. Recently nitrification has been shown to occur under what were previously considered adverse conditions (Robertson, 1982) and forest tree species have been shown to be able to exploit nitrate in some cases (Adams and Attiwill, 1982). Williams (1983) detected nitrification under Sitka spruce but on a more fertile site, additionally his incubation technique permitted the accumulation of artificially high ammonium levels which would have removed the competitive control on nitrifying organisms. Failure to detect nitrate in the soil solution was more surprising but nothing above 0.001 mgl^{-1} (the detection limit) was found.

N mineralization of forest floor and peat material from pure and mixed stands as estimated by plant uptake and long term laboratory incubation.

7:1 Introduction

Laboratory and field incubation studies indicate that litter and peat from mixture stands supports greater mineralization than equivalent material taken from beneath pure spruce. Such studies estimate net mineralization and do not consider the ability of plants to compete for N as it is turned over within the microbial pool (Heal et al., 1982) or to exploit soluble organic N sources (Van Cleve and White, 1980).

To assess whether plants would be able to obtain more N from incubating samples than indicated by net mineralization studies, pure spruce and mixture material were incubated in the presence of birch (Betula pendula Roth.) seedlings. The same material was incubated concurrently in the absence of plants to compare the N mineralization estimates obtained by the two methods.

7:2 Methods

7:2:1 Field sampling

Litter and peat were collected in September 1981 from the Mabie 7 experiment described in Section 3:2:1. Samples were collected from the ridge and flat plough positions of the OW and H treatments with the sectional corer used in the field incubation study. For both treatments, 30 samples were taken from each plough position and depth (0-3, 3-6 and 6-9 cm) the material was bulked, homogenised and roots removed. Samples were stored at 3°C before use, subsamples were retained for determination of moisture content, pH and initial mineral N status.

7:2:2 Incubation

For each sample, 50g fresh weight was weighed into a 7cm square plastic pot; pots were placed on saucers to prevent loss of drainage water. 10 replicates were prepared for each treatment. Pots were arranged in a randomized block design in a heated greenhouse (mean temperature 20-30°C) with 16 hours artificial daylength. After 2 days, to permit settling of the peat material, each pot was planted with 1 newly germinated birch seedling. The experiment was run for 120 days after which plants (shoots + roots) were harvested; plant oven dry weight (85°C) and nutrient content were determined.

In addition, 30g fresh weight of each sample was weighed into a 250ml conical flask; flasks were plugged with cotton wool and incubated in the dark at 20°C. Field moisture levels (60-82% fresh weight) were maintained by addition of water every 5 days. At 30 day intervals 5g of material was removed from each flask and analysed for mineral N. 4 replicates were prepared for each sample and the incubation run for a total of 120 days.

7:2:3 Chemical analysis

Mineral N was extracted by shaking 5g (fresh weight) of sample with 100ml 1N KCl for 1 hour, extracts were filtered and analysed colorimetrically for ammonium and (nitrate + nitrite) - N (Section 5:3:2). Plant material was analysed for N, P and K as described in Section 3:3:2. Sample pH was determined potentiometrically in a water : sample suspension (2.5:1).

7:3 Results

N mineralization was calculated from plant uptake (Table 7:1, Appendix 6A, Appendix 6B). Mineralization values were not derived for P and K since both treatments had received identical inputs of PK fertilizer at standard Forestry Commission rates (Section 3:2:1).

N mineralization was greatest in H material (Figure 7:1, Table 7:1). Differences between treatments were most marked for 0-3 cm material, from both ridge and flat positions, although a considerable treatment difference also exists for 3-6 cm flat material. Absolute values and treatment differences decline with depth; greater mineralization occurs in flat

material, at all depths, for both treatments (this is most marked for H material). N mineralization in H samples exceeded the OW by a factor of 1.5 (Table 7:1).

The patterns of P and K uptake (Figure 7:1, Appendix 6A) are essentially identical to those described for N mineralization, both being greatest in the H treatment. Nutrient uptake ratios (Table 7:2) are very similar for the two treatments.

Laboratory incubation results (Figure 7:1, Table 7:1, Appendix 6C) are very similar to the mineralization values based on plant uptake. Greatest mineralization occurred in H material, while amounts and treatment differences decline with depth for both plough positions. Ridge and flat mineralization values are very similar for OW material, while for H material mineralization is greatest for the flat.

Nitrification was only apparent after 90 days (Appendix 6C); nitrate levels were consistently higher in the H material, although absolute amounts were small.

A reasonable relationship exists between mineralization estimates derived by the two methods ($r=0.80$), greatest differences occurred for flat material while ridge values were very similar (Table 7:1). Mineralization values based on plant uptake are generally higher than those from the laboratory incubation.

TABLE 7:1

N mineralization ($kgha^{-1}$) assessed by plant uptake and laboratory incubation.

	Plant uptake	Laboratory incubation
Ridge		
OW	44.7	44.6
H	59.1	49.9
Flat		
OW	67.4	33.6
H	106.5	73.7
Total		
OW	59.8	37.3
H	90.7	65.7

FIGURE 7:1. N MINERALIZATION ESTIMATED FROM PLANT UPTAKE AND LABORATORY INCUBATION (mgg^{-1}), AND PLANT UPTAKE OF P AND K (mg). VERTICAL LINES SHOW 95% CONFIDENCE LIMITS.

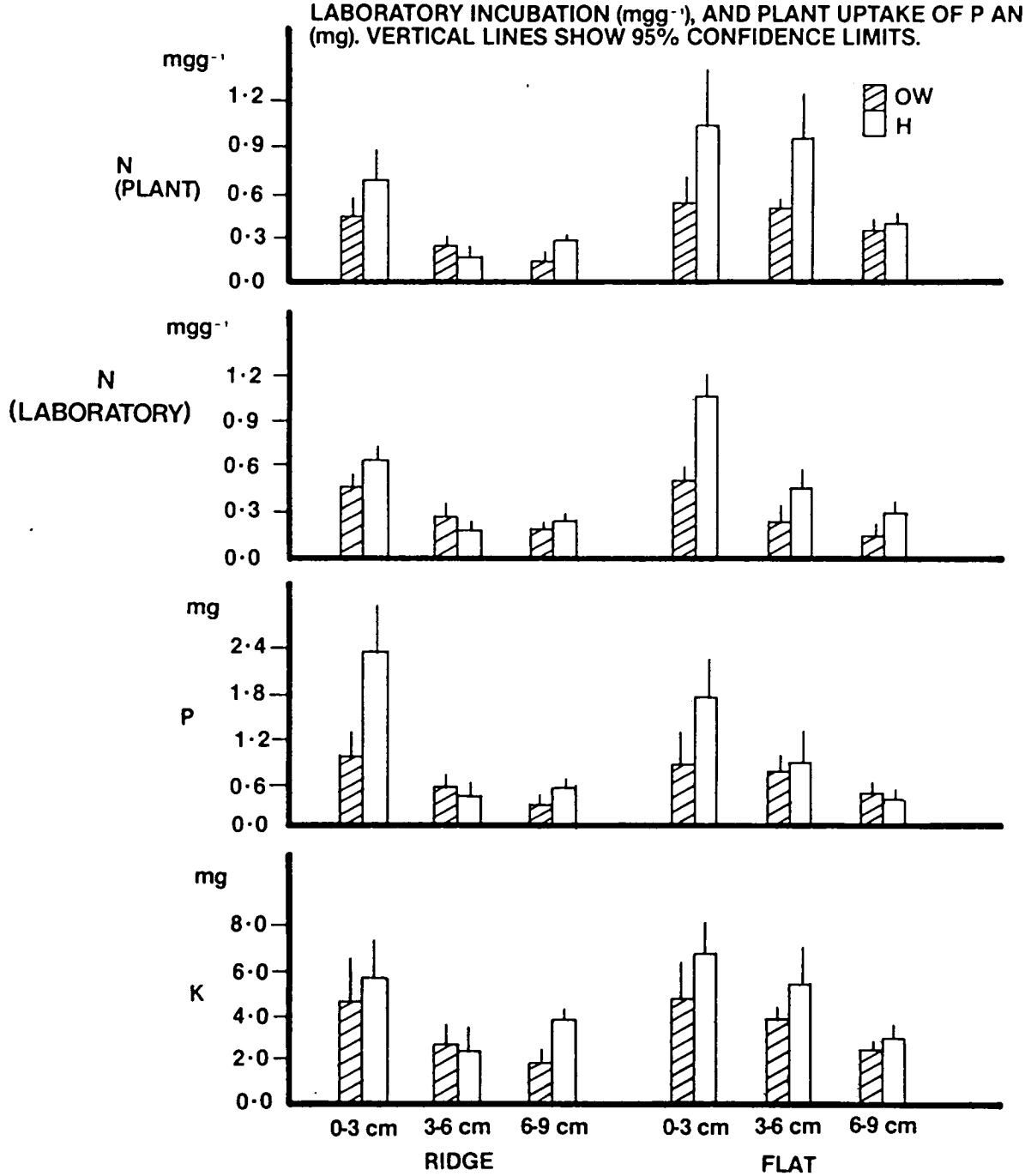


TABLE 7:2

Nutrient uptake ratios.

	N:P	N:K
Ridge		
OW	6.4	1.1
H	4.5	1.2
Flat		
OW	5.9	1.2
H	6.6	1.4

7:4 Discussion

The results agree well with previous field and laboratory incubation studies (Section 6); indicating greater N mineralization in H material, with values being greatest in the 0-3cm layers and flat position. Since, for the plant uptake experiment, other factors were equal, these differences must reflect differences in substrate quality. In contrast with previous incubations nitrification was detected, but only after 90 days. This was almost certainly due to the artificially high accumulation of ammonium towards the end of the incubation.

N mineralization values based on plant uptake exceeded those from the normal incubation; this may reflect plant uptake of soluble organic N and possible competition for N being turned over in the microbial biomass; additionally, the presence of plant roots and a rhizosphere, with their combined exudates may have stimulated N mineralization (Rambelli, 1973). However, temperature levels will have been greater for this incubation and fluctuations will have occurred, both of which are likely to have increased mineralization. Therefore it is possible that estimates of net annual mineralization in Section 6 may be rather lower than the amount of N which is actually exploitable by the trees. The ability of plants to use soluble organic N and to compete for gross mineralization products has been indicated by several workers (Heal, et al., 1982; Van Cleve and White, 1980; Williams, 1983).

Greater uptake of P and K from H material probably does not reflect greater availability since both treatments have received identical regular inputs of these elements as fertilizer. Rather greater N availability in the H material has resulted in greater relative growth rates, with balanced nutrient uptake resulting in increased uptake of P and K. This is supported by the nutrient uptake ratios.

Estimating differences in mineral N availability in pure spruce and mixture stands using ion exchange resin bags.

8:1 Introduction

Laboratory incubations to assess potentially mineralizable N can provide useful indices of substrate quality but do not integrate short and long term environmental changes. Also, single incubations do not reflect sesonal differences in substrate quality and quantity. Field incubations go some way to overcoming these limitations but, in common with laboratory methods, involve considerable sample manipulation. Lysimetry is an alternative, however, results are not analagous to an incubation but reflect net mineralization and system retentivity against mass flow. Lysimeters may therefore identify relative differences in nutrient availability but do not accurately measure mineralization. Lysimetry also involves sample manipulation and isolation; material within lysimeters may experience different temperature and moisture regimes compared with the surrounding soil mass. Additionally, considerable volumes of leachate require to be stored and analysed.

Ion exchange resin bags can remove nutrients from mass flow and receive ions by diffusion. Their potential use in field and laboratory situations has been demonstrated (Binkley, 1982; Smith, 1979). Obvious advantages are that bags can be placed with minimal soil disturbance, no leachate need be collected and long time intervals can be allowed between collections. In addition, resins should be reuseable. Results obtained from resin bags are likely to equate with those from lysimetry, perhaps being slightly higher due to the possibility of diffusion from the surrounding soil. The method will not therefore give a quantitative estimate of mineralization. Possible problems involve the best form of container, continuity of contact with

the soil to allow mass flow and diffusion, microbial growth, and resin durability. Since resins are only selective in terms of the normal exchange series sufficient resin must be allowed so that the system does not become saturated with ions which are not of interest to the experimenter.

Where resin bags are placed within or below living root systems results may only reflect changes in the soil solution integrated over the collection interval.

Ion exchange resin bags were placed in the Mabie 7 experiment, as an alternative to incubation techniques, to assess N availability.

8:2 Methods

8:2:1 Resin bags

20g (moist weight) of cation exchange resin, (Amberlite 1R-120) with hydrogen as the exchangeable ion, and 28g of anion exchange resin (Amberlite 1RA-401) with hydroxyl ions as the exchangeable ion, were placed in nylon mesh bags prepared from stockings. The resin mixture gave approximately 50 milli equivalents (meq.) of cation exchange and 53 meq of anion exchange. 5% of the exchange capacity was saturated with mercuric chloride to prevent microbial growth.

Bags were placed immediately beneath the litter layers in the OW and H treatments of the Mabie 7 experiment (Section 3:2:1), at both ridge and flat plough positions. For the H treatment bags were further split between pure larch rows and the spruce triplets. Each position was replicated 18 times. Bags were also buried within polythene bags to check possible leakage of ions from the nylon. Bags were placed in February 1983 with an initial collection of 6 bags per position in June (120 days) and a final collection in August (200 days).

8:2:2 Chemical analysis

Resin was removed from the bags, mixed, weighed, and half the resin extracted with 200 ml 1N KCl in a shaker for 1 hour. Initial laboratory based tests indicated complete removal of ammonium, nitrate and phosphate by this method. Extracts were filtered and stored at 3°C prior to analysis.

Samples were analysed for ammonium, nitrate and phosphate using automated colorimetric procedures previously described

(Section 5:3:2). The procedure failed to work for phosphate due to some form of interference. Results were calculated as mg bag^{-1} which is equivalent to $kgha^{-1}$ since bag surface area was approximately 100 cm^2.

8:3 Results

Ammonium and nitrate levels tend to decline between the first and second collections (Table 8:1). Ammonium levels were highest in the H treatment for both the larch and spruce triplet positions, with no consistent differences between plough positions in either treatment. Nitrate values are greater in the H treatment for the flat position, however differences for the ridge are more variable. Total mineral N amounts are always greater in the H treatment, although all values are very low.

TABLE 8:1

N flux (mg bag^{-1})* from resin bags.
Initial collection (120 days). Mean values (n=6) and (95% confidence limits).

Position	Ammonium	Nitrate	Ammonium + Nitrate
Ridge			
H Larch	0.26(0.11)	0.033(0.007)	0.29 (0.12)
H Spruce	0.16(0.02)	0.035(0.005)	0.20 (0.02)
OW	0.14(0.01)	0.040(0.017)	0.18 (0.01)
Flat			
H Larch	0.35(0.20)	0.060(0.047)	0.41 (0.25)
H Spruce	0.22(0.05)	0.036(0.005)	0.26 (0.05)
OW	0.16(0.02)	0.023(0.009)	0.18 (0.03)

* Bag area $\simeq$ 100 cm^2. Therefore values may also be read as $kgha^{-1}$.

Table 8:1 cont:-

Final collection (200 days). Mean values (n=12) and (95% confidence limits).

Position	Ammonium	Nitrate	Ammonium + Nitrate
Ridge			
H Larch	0.18(0.05)	0.033(0.010)	0.21 (0.06)
H Spruce	0.18(0.08)	0.057(0.014)	0.24 (0.09)
OW	0.11(0.04)	0.035(0.015)	0.15 (0.05)
Flat			
H Larch	0.14(0.06)	0.039(0.011)	0.18 (0.07)
H Spruce	0.16(0.04)	0.056(0.013)	0.22 (0.05)
OW	0.12(0.04)	0.031(0.011)	0.15 (0.05)

8:4 Discussion

The decline in mineral N uptake between sampling dates could reflect sample variation; alternatively the decline could be real and result from the period of extremely dry weather between collection dates. Mass flow requires the movement of a wetting front while diffusion requires a short, continuous water phase between soil and resin; both are unlikely under dry conditions. Additionally resins do not function if allowed to dry out completely and will crack when re-wetted with a reduction in efficiency. All resin bags had become completely dry by the final collection.

The quantities of mineral N collected were extremely low, this must result partially from the dry conditions. Since bags were placed beneath the litter layers where fine root concentrations were high it is probable that mineral N, made available by mineralization, was removed from solution before reaching the bags. If this is the case, bags would reflect the normal solution concentration of mineral N which is known to be very low for the site (Section 6:3).

Bags did detect the presence of low levels of nitrate, approximately an order of magnitude below ammonium, a normal situation for coniferous forest (Cole, 1981). This contrasts with incubation results and routine analysis of mineral N levels by KCl extraction, when no nitrate was detected. The nitrate was probably atmospheric in origin and did not result from nitrification. The results agree with previous findings by indicating greater N availability in the mixture treatment.

The usefulness of resin bags for assessing nutrient availability in the field is uncertain, their use may by limited to situations where moisture levels remain sufficiently high to prevent drying out of the resin.

Assessing the presence or absence of N fixation in larch, spruce and mixture stands.

9:1 Introduction

A possible explanation for improved spruce N status in mixed stands could be N fixation, although this is not normally an important component of the N cycle in temperate coniferous forest. Forest floor material from larch, spruce and mixture stands was assessed for N fixation using the acetylene reduction assay (Hardy et al., 1973).

9:2 Methods

9:2:1 Field sampling

Samples were taken from the flat plough position of the forest floor with the soil corer used for the field incubation (Section 6:2:1), only the 0-3 cm section being retained for analysis. Sampling was restricted to this position since it was there that greatest N mineralization had been monitored. Samples were taken from the Leadburn experiment (Section 5:4:2) and the Mabie 7 experiment (Section 3:2:1) in May 1983. For the former, 10 cores were taken from the Sitka spruce and hybrid larch stands respectively; for the latter, 20 cores were taken from the OW and H treatments respectively. Cores were stored in polyethylene bags at 3°C prior to analysis.

9:2:2 Laboratory analysis

Cores were left at 20°C overnight then placed in polyethylene bags with a 'suba seal' attachment. Bags were previously turned inside out and left for 12 hours, then reinverted to ensure no build up of ethylene. Half the cores of each treatment were amended with 5 ml of 5% glucose solution to stimulate microbial activity. Acetylene, with ethylene as an internal standard, was added to each bag and a 0.5 ml sample taken after a few minutes. Cores were then incubated at 20°C for

5 hours and a second 0.5 ml sample taken. Gas samples were analysed using a Pye Unicam series 104 gas-liquid chromatograph. Comparison of results for the initial and final gas samples permitted acetylene reduction, and therefore N fixation, to be determined.

9:3 Results

No N fixation was detected in any of the sample material; under the conditions of measurement rates were therefore below 1 $kgha^{-1}yr^{-1}$.

9:4 Discussion

Failure to detect N fixation was not surprising since most published findings for temperate forest indicate low levels or no fixation (e.g. Sucoff, 1979). It is possible that fixation occurs on a strictly seasonal basis and was missed by the single sampling date, ideally a series of samples should be taken throughout the year. However, failure to obtain fixation even with a preincubation at 20°C and a glucose amendment suggests that N-fixing organisms are not present.

Rhizosphere fixation was not assessed directly, however root material was present in the cores and should have remained viable since the assay was conducted within 24 hours of sampling.

The amount and distribution of mineral elements in forest floor and peat material beneath pure spruce and larch/spruce stands.

10:1 Introduction

Analysis of litter and peat material was carried out to characterise possible site differences brought about by the different treatments and to provide background site information. Additionally, sampling in the mixture stands was conducted so that within stand differences could be identified.

10:2 Methods

10:2:1 Field sampling

Sampling was conducted in October 1982 at the Mabie 7 experiment (Section 3:2:1). Samples were taken using the sectional corer already described; 30 cores were taken from the OW treatment for the ridge and flat respectively, cores were subdivided into 0-3, 3-6 and 6-9 cm sections. The 0-3 cm section was further divided into litter and peat material. An identical sampling scheme was used in the H treatment, however pure larch rows and spruce triplets were sampled separately.

10:2:2 Laboratory analysis.

Living vegetation (mosses etc.) and root material were removed from the samples which were then oven dried at 85°C before being weighed.

Subsequent analysis for N, P and K was as described in Section 3:3:2. In addition, samples were analysed for calcium (Ca) by atomic absorption spectroscopy.

10:3 Results.

The amounts of N and P in the 0-9 cm layer are essentially identical for the different sampling sites (Table 10:1). K however is greater in the OW treatment, particularly for the ridge position; the reverse is seen for Ca which shows greater accumulation in the flat position of the H treatment.

N concentrations tend to be higher in larch and spruce litter from the H treatment; P concentrations are also highest in this treatment, but for larch material only (Table 10:2). K concentrations are highest in OW material while Ca concentrations are greatest in spruce and larch litter from the H treatment.

TABLE 10:1

Quantities and distribution of mineral elements in litter and peat material from pure spruce (OW) and mixture (H) treatments. Mean values (n=30) and (95% confidence limits).

R = Ridge, F = Flat.
1, 2 and 3 = 0-3, 3-6 and 6-9 cm depth sections.
L and P = litter and peat for the 0-3 cm section.

Section	OW	H (Larch)	H (Spruce)
N gm^{-2}			
R_1 L	14.17 (2.18)	13.21 (2.06)	11.82 (1.42)
R_1 P	37.47 (5.70)	38.71 (5.78)	40.63 (5.12)
R_2	58.89 (6.13)	58.65 (7.01)	58.56 (5.78)
R_3	60.53 (5.20)	62.76 (5.05)	61.87 (5.03)
F_1 L	11.15 (2.26)	13.01 (1.57)	14.74 (1.81)
F_1 P	39.88 (5.37)	40.66 (4.38)	38.16 (4.80)
F_2	59.58 (7.08)	47.28 (5.72)	54.30 (5.43)
F_3	54.26 (6.12)	58.98 (6.77)	64.04 (5.67)

Table 10:1 cont:-

P gm^{-2}			
R_1 L	1.86 (0.60)	1.94 (0.78)	1.60 (0.77)
R_1 P	1.68 (0.29)	2.05 (0.52)	2.02 (0.77)
R_2	1.61 (0.38)	1.30 (0.25)	1.25 (0.18)
R_3	1.66 (0.46)	1.07 (0.16)	1.14 (0.20)
F_1 L	1.19 (0.40)	1.62 (0.48)	1.41 (0.50)
F_1 P	2.03 (0.20)	2.42 (0.41)	1.93 (0.24)
F_2	2.73 (0.40)	1.75 (0.25)	2.30 (0.28)
F_3	1.92 (0.26)	2.11 (0.29)	2.28 (0.22)
K gm^{-2}			
R_1 L	2.50 (0.89)	0.82 (0.19)	0.77 (0.08)
R_1 P	3.11 (0.89)	2.24 (0.50)	2.36 (0.35)
R_2	4.01 (1.10)	2.12 (0.39)	2.39 (0.42)
R_3	3.38 (0.98)	1.91 (0.36)	1.92 (0.35)
F_1 L	1.85 (0.82)	1.18 (0.16)	1.18 (0.19)
F_1 P	3.27 (0.93)	2.27 (0.25)	2.27 (0.23)
F_2	3.09 (0.39)	2.58 (0.33)	2.86 (0.24)
F_3	2.32 (0.34)	2.70 (0.37)	2.88 (0.31)
Ca gm^{-2}			
R_1 L	5.98 (1.56)	6.92 (1.94)	6.04 (2.22)
R_1 P	12.00 (2.51)	15.95 (3.68)	15.25 (3.42)
R_2	12.53 (2.65)	12.13 (2.01)	13.01 (2.12)
R_3	7.68 (1.69)	7.23 (1.16)	8.49 (1.33)
F_1 L	2.34 (0.96)	6.07 (1.39)	4.20 (1.28)
F_1 P	5.56 (1.41)	14.32 (2.85)	8.75 (2.19)
F_2	7.55 (1.74)	12.89 (2.85)	8.02 (1.63)
F_3	5.27 (1.09)	6.17 (1.08)	5.35 (0.96)

TABLE 10:2

Nutrient concentrations in litter material from pure spruce (OW) and mixture (H) treatments. Mean values (n=30) and (95% confidence limits).

	%N	%P	%K	%Ca
OW				
Ridge	1.28	0.18	0.21	0.56
	(0.04)	(0.06)	(0.06)	(0.13)
Flat	1.32	0.14	0.21	0.31
	(0.08)	(0.03)	(0.05)	(0.08)
H (Larch)				
Ridge	1.46	0.21	0.09	0.75
	(0.07)	(0.08)	(0.01)	(0.17)
Flat	1.37	0.18	0.13	0.65
	(0.08)	(0.05)	(0.02)	(0.14)
H (Spruce)				
Ridge	1.39	0.19	0.09	0.68
	(0.06)	(0.07)	(0.01)	(0.22)
Flat	1.44	0.14	0.12	0.44
	(0.08)	(0.05)	(0.02)	(0.03)

10:4 Discussion

Total quantities of N and P are essentially identical for H and OW treatments, while larch and spruce positions within the H treatment are also very similar. A greater N concentration in H litter material is consistent with the greater N mineralization found in this treatment; however, most mineralization occurred in the flat where OW and H (larch) litter N concentrations are least different. Greater amounts and concentrations of Ca in H litter may also have influenced N mineralization due to locally enhanced pH conditions. A difference in Ca, and K, levels may have resulted from, a) differences in uptake, b) differences in leaching loss to lower horizons, or c) transport from deeper in the profile by roots and subsequent deposition in litterfall. This latter explanation seems unlikely since rooting is probably restricted by a high water table outwith the summer period.

Chemical estimates of N availability and organic N fractions under spruce and larch/spruce mixtures.

11:1 Introduction

A developing stand of trees does not possess a closed N cycle until after canopy closure; initially, nutrient demands for growth must be met by the soil and atmospheric inputs. The capture and retention of atmospheric nutrients is inefficient before canopy closure due to incomplete site occupancy, consequently virtually all demand must be supplied from the soil. Rates of N mineralization and the tree's ability to exploit soil N sources will determine the rate of growth at this stage; the latter is influenced by the morphology and intensity of rooting and properties of the mycorrhizosphere.

Certain coniferous species appear to possess a rhizosphere which can mineralize or otherwise render available a fraction of soil N (largely organic) resistant to microbial degradation under previous vegetation. Fisher and Eastburn (1974), Fisher and Stone (1969) and Stone and Fisher (1969) demonstrated greater availability of N and P in the root zone of larch, which extended beyond the canopy. There was little effect on total N or P. The effect was transient, lasting approximately 30 years, this being consistent with the mineralization of a finite N pool. They observed a similar effect with pines but little or no effect with spruce. O'Carroll (1978) postulated that enhanced growth of Sitka spruce in mixture with Japanese larch was due to greater N mineralization. Growth of pine seedlings in soil which previously supported a pine crop was poorer than for soil from pasture or eucalypt forest (Skinner and Attiwill, 1981) which might suggest loss of a labile N source. Hewett (1966) found that Auracaria cunninghamii Ait. showed improved growth and N status when underplanted beneath

southern pines, suggesting this was a result of increased N availability or accretion. Bevege and Richards (1970) used a chemical fractionation method to demonstrate that more labile forms of organic N were reduced beneath pines, with slow replenishment from refractory sources, due to mineralization of the labile pool associated with greater N availability. This was associated with a decline in native organic matter but not total N, and improved growth of A. cunninghamii. Jones and Richards (1977) have demonstrated the same phenomena for pines but not eucalypts and attributed it to properties of the pine rhizosphere.

Thus pioneer species such as larches and pines seem able to exploit organic N sources unavailable to previous vegetation (Gosz, 1981). a characteristic poorly developed in late successional species like spruces (Stone and Fisher, 1969). The effect is most likely to be due to rhizosphere organisms, rather than mycorrhizas which cannot readily utilise humus bound N (Lundberg, 1970).

No difference was found in total soil N levels between pure spruce and mixture stands (Section 10), however differences do exist in rates of mineralization and these may be expressed in the size of different N fractions. Extraction/fractionation techniques based on chemical methods are crude and cannot readily be related to organic N pools of biological significance (Paul and Juma, 1981). Most approaches give an estimate of the active organic phase and a more recalcitrant phase; recent work indicates that this is a gross simplification and that many different fractions are involved (Jansson, 1981). In addition chemical estimates of labile organic N often fail to correlate with estimates based on biological methods (Paul and Juma, 1981). However, Stone and Fisher (1969) and Jones and Richards (1977) obtained apparently useful information using chemical methods for comparative purposes.

In this study 2 methods were adopted; 1) extraction using boiling water (Brönner and Bachler, 1980) which gives an index of readily hydrolysable N, probably of biomass origin and low molecular weight organic compounds; 2) 6 N HCl extraction (the method used by Jones and Richards, 1977), again

gives an estimate of hydrolysable N which probably includes more resistant material than the boiling water method.

11:2 Methods

Both extractions used material collected for the field incubation study which was in excess of actual requirement.

11:2:1 Boiling water extraction

2g of air dry, ground (0.5mm mesh), material was weighed into a 250ml conical flask and 100ml of distilled water added. The solution was boiled under reflux for 1 hour cooled, and the residue filtered. 50ml of filtrate was digested using 2ml 36N H_2SO_4 and 2ml 100 volumes H_2O_2, samples were made up to 50ml with distilled water and analysed for ammonium using the automated colorimetric method previously described (Section 3:3:2).

11:2:2 6N HCl extraction

The method is essentially that of Bremner (1965); 1g of air dry, ground (0.5mm mesh), sample was weighed into a 250ml conical flask and 20ml 6N HCl added. The solution was boiled under reflux for 12 hours, cooled and filtered. The filtrate was made up to 100ml with distilled water and a 10ml subsample digested and analysed as described above. Total sample N content was determined by the usual acid digest procedure (Section 3:3:2).

11:3 Results

Less N was extracted by the boiling water method compared with 6N HCl (Table 11:1 and 11:2). Greater quantities of N were extracted with boiling water from H material, except for the 3-6 and 6-9 cm depths on the ridge (Table 11:1).

Results for the HCl fractionation are inconsistent, with no clear treatment differences; extractable levels were highest for flat material and tended to decline with depth, being highly correlated with the total N level ($r=0.90$).

TABLE 11:1

Boiling water extractable N (mgg^{-1}). Mean values (n=6) and (95% confidence limits).

Ridge (cm)	H Material	OW Material	F^1
0 - 3	5.00 (0.70)	4.95 (0.46)	0.07 N.S.
3 - 6	3.40 (0.56)	4.13 (0.79)	6.16 *
6 - 9	3.77 (0.81)	4.41 (0.68)	2.21 N.S.
Flat (cm)			
0 - 3	6.99 (0.53)	6.31 (0.65)	6.49 *
3 - 6	6.09 (0.25)	5.98 (0.39)	0.23 N.S.
6 - 9	6.49 (0.35)	5.49 (0.14)	87.77 *

F^1 Value :- * = significant difference between treatment means, N.S. = non-significant difference between treatment means at P = 0.05 for a 2-way anovar.

TABLE 11:2

Total, hydrolysable and non-hydrolysable N (mgg^{-1}) following extraction with 6N HCl. Mean values (n=6) and (95% confidence limits).

H Material

Ridge (cm)	Total N	Hydrolysable N	Non-hydrolysable N	Hydrolysable: Non-hydrolysable N
0 - 3	13.30 (0.04)	8.51 (0.64)	4.79 (0.64)	1.78
3 - 6	11.00 (0.02)	7.10 (0.59)	3.90 (0.57)	1.82
6 - 9	10.90 (0.07)	7.43 (0.55)	3.47 (0.52)	2.14
Flat (cm)				
0 - 3	14.50 (0.08)	9.82 (1.04)	4.68 (1.04)	2.10
3 - 6	12.30 (0.07)	9.12 (0.29)	3.18 (0.29)	2.87
6 - 9	13.00 (0.07)	8.21 (1.18)	4.79 (1.18)	1.71

OW Material

Ridge (cm)				
0 - 3	12.50 (0.07)	8.71 (0.49)	3.79 (0.49)	2.30
3 - 6	11.70 (0.07)	7.41 (0.14)	4.29 (0.14)	1.73
6 - 9	11.80 (0.08)	7.57 (0.58)	4.23 (0.59)	1.79
Flat (cm)				
0 - 3	14.30 (0.09)	9.71 (0.22)	4.59 (0.22)	2.12
3 - 6	13.00 (0.08)	9.01 (1.03)	3.99 (1.03)	2.26
6 - 9	14.00 (0.08)	10.14 (0.38)	3.85 (0.38)	2.63

11:4 Discussion

Boiling water extraction results suggest a greater availability of readily hydrolysable N in H material, however, the results correlate poorly (r=0.45) with mineralization results in the field for the same material (July - August 1981). This suggests that the method is not suitable for organic soils.

The HCl fractionation gave no clear result; if it is assumed that larch can mineralize a mobile N pool unavailable to spruce one might expect, a) a decline in total native N, b) a decline in the hydrolysable fraction, c) a slower decline in the non-hydrolysable fraction to replenish the hydrolysable pool, d) a decrease in the ratio of hydrolysable:non-hydrolysable N. Beveage and Richards (1970) demonstrated (d) in the absence of (a), (b) or (c), while Jones and Richards (1977) demonstrated all the possibilities; in both cases for pines. Failure of the method to identify treatment differences in this case suggests either no differential rhizosphere effect, or unsuitability of the extraction method to an organic soil. Both the cited studies dealt with mineral soils with low N contents, it is likely that peat contains too much N for a useful comparison to be made using chemical methods.

General discussion and conclusions.

12:1 General discussion

Foliar analysis has demonstrated a definite improvement in Sitka spruce foliar N status in the presence of larch, for stands growing on N deficient deep peats in the absence of N fertilizer. This improvement is reflected in increased height and diameter growth, while estimates of stand foliar N capital suggest a greater quantity of N in the mixture tree biomass. At both experimental sites where work was conducted, improvement in the growth and N status of mixture spruce does not become manifest until some 7-10 years from planting.

During early growth pure spruce exhibits similar or rather better height increment and N status than mixture spruce. At Mabie 7, better growth of the pure spruce in the years immediately subsequent to planting is the result of a 2,4-D weed control which was applied to this, but not the mixture, treatment. At Inchnacardoch 164, the early difference results from an input of N fertilizer in 1967 which was limited to the pure spruce treatment. While growth and N status of mixture spruce continued to improve, both declined in the pure stands 7-10 years from planting. Such a decline is commonly observed for Sitka spruce on deep unflushed peats where acute N deficiency may develop some 8 years from planting (McIntosh, 1983). It is possible that where silvicultural inputs are the same a mixture effect may be noticeable even earlier in the life of a stand.

A mixture effect would not be expected in the first few years of stand development, since initially trees grow as individuals with no interaction between stand members. If greater N availability in mixtures was root related an effect would only be expected once trees had reached a size sufficient for contact to occur. Similarly, if litter played a part in the

mechanism time would be required for material to accumulate and N release to occur. There is no evidence from the data collected that indicates a sudden improvement in the growth and N status of mixture spruce, rather growth of the pure spruce suddenly declines while that of the mixture spruce continues to improve. The relative difference in spruce growth therefore results from a limitation being imposed on the pure stands which does not appear to be imposed on the mixtures. This limitation appears to be a reduction in the availability of N which is maintained, and even increased, in the presence of larch.

Thus initial N supply seems sufficient to meet early growth demands in both pure and mixed stands. In part this will be due to the low initial N requirement of the trees which can probably be met by temporarily improved rates of mineralization following cultivation (Powlson, 1980). In addition, the application of ground mineral phosphate at planting can cause increased mineralization of native organic N (Carey et al., 1981). However, early tree growth is exponential and is associated with an exponentially increasing demand for N (Ingestad, 1982). The sudden fall in spruce growth and N status 7-10 years from planting is almost certainly the result of N supply becoming inadequate, perhaps with the exhaustion of a labile N pool released as a result of cultivation and fertilization. Since both pure spruce treatments examined in this study had received a fertilizer input or weed control, not given to the mixtures, it is probable that if these inputs had not been given N supply would have become inadequate at an earlier date. The increase and maintenance of N status and growth in the mixture spruce indicates that N supplies have continued to remain at a satisfactory level.

If stand N capital did not differ between pure and mixed stands the maintenance of N status and improved growth of the mixture spruce could be explained in terms of competitive ability; assuming spruce to be a better competitor for available N than larch would mean that a greater portion of stand N might be exploited by the spruce, delaying or preventing the onset of deficiency. However, this explanation is not consistent

with the greater estimated foliar N capital of the mixture stands.

A greater estimated N capital in mixture tree biomass indicates greater N uptake which must be associated with greater N supply or availability. Thus larch makes N available to spruce, which is not available under pure spruce conditions; this indicates an ability of larch to mobilize or otherwise obtain N which spruce cannot, with some portion of this N becoming available to the spruce. Relatively poor performance of the larch at both experimental sites suggests that spruce may obtain N to the detriment of the larch. Unfortunately pure larch stands did not exist on these sites to allow a direct comparison.

Enhanced N availability in the presence of larch must reflect an improvement in soil N availability since atmospheric inputs do not appear to differ significantly between pure and mixed stands, while biological N fixation was not detected. Increased availability could result from roots exploiting a greater soil volume in the mixtures, this seems unlikely since soil moisture values gave no indication of drier conditions at depth in the mixture stands. Assuming that the volumes of soil exploited by roots are similar for pure and mixed stands then larch must be able to mobilize N which cannot be mobilized by spruce. Some workers have suggested that pioneer species such as larch and pine can mineralize a fraction of soil organic N which was unavailable to previous vegetation, an ability not possessed by late successional forms like spruce (Bevege and Richards, 1970; Jones and Richards, 1977; Skinner and Attiwill, 1981), due to special attributes of their rhizosphere microflora (Stone and Fisher, 1969). Chemical analysis of the peat and fractionation of the organic N did not identify any differences in total N, or the size of hydrolysable and non-hydrolysable pools, between mixed and pure stands. Some workers have noted a reduction in total native N and hydrolysable N under pioneer species due to greater mineralization associated with the rhizosphere (Jones and Richards, 1977, 1978).

Rates of N mineralization, assessed by field and laboratory incubations, were significantly higher in mixed stands with most mineralization occurring in the upper 3 cm, although differences also occurred at depth. There appears to be no significant influence of microclimate on mineralization rates between pure spruce and mixed stands. Differences must therefore relate to substrate quality. Higher mineralization in the surface layer will in part result from various physical cycles exhibiting greatest amplitude at the soil surface. However, it also infers an influence of surface, and probably below ground, litter. Larch litter is a secondary N source, consequently N released from litter alone could not lead to a greater mixture N capital, although it might be a supplier of N to the mixture spruce. Larch litter does appear to release N more rapidly than Sitka spruce litter, despite a marked withdrawal of nutrients during senescence and low levels of leachable N.

N release from decomposing larch litter is preceded by a delay of some 5 months associated with a fall in the C:N ratio. It is probable that in the field larch litter does not release N until the year following litterfall. N release from larch litter will therefore be a function of cumulative litterfall over the life of the stand. The input of N measured in larch leaf litterfall was 6.8 $kgNha^{-1}$, representing the maximum input from litter up to the date of collection, with previous inputs being considerably lower. Thus the cumulative input of litter over the stands life will represent a small quantity of N, certainly insufficient to support a mineralization value of 60 $kgNha^{-1}yr^{-1}$ as suggested by the field incubation. Root litter inputs were not assessed but most recent work (Fogel, 1983) suggests that below ground inputs are considerably greater than above ground. However, it is unlikely that even the cumulative combined litter input could supply sufficient N to explain the measured mineralization rate.

A component of this mineralized N must therefore come from the mineralization of native organic N present in the peat, which appears enhanced in the presence of larch. Litter inputs under pure spruce were not measured but it is unlikely that

they represent a major cumulative input of N; trees in these plots exhibit needle retention of up to 7 years. However the measured mineralization rate of 28 $kgNha^{-1}yr^{-1}$ probably requires less mineralization of native organic matter to support it. Greater mineralization of native N was not indicated by the chemical fractionation technique or by differences in total N levels. Since peat has a high N concentration relatively small changes in total N may not be detected, even though they may represent quite substantial amounts of N on an area basis. The presence of larch may stimulate N mineralization through below and/or above ground influences. The former might include effects due to the rhizosphere, mycorrhizas, and perhaps rooting intensity. The latter would have to involve a stimulatory influence on decomposition at the litter/peat interface, perhaps as a result of the microflora and fauna supported by larch litter.

Attempts to assess the relative importance of root effects were largely inconclusive or unsuccessful. As previously described, attempts to identify a positive rhizosphere effect by chemical methods were inconclusive. Root exudates may be an important source of available carbon in forest ecosystem, additionally N may be exuded as amino acids and other highly available forms (Smith, 1976). An attempt was made to collect larch root exudates in plastic tubes filled with fine sand, but this proved unsuccessful. A further approach to isolate root related mechanisms involved an experiment where 1+1 transplants of larch and spruce were planted pure and in mixture in horticultural peat. The peat was inoculated with a water/soil suspension using material from pure or mixed stands. Litter was removed so that significant interactions would only occur between root systems. Unfortunately the experiment had to be abandoned due to almost complete destruction of the root systems by weevil larvae (Otiorrhynchus species).

Current mineralization values in the mixture stands, 60 $kgNha^{-1}yr^{-1}$, should be sufficient to support good spruce growth. Williams (1983) estimated net N mineralization to be 67 $kgNha^{-1}yr^{-1}$ under a fast growing ($23m^3ha^{-1}yr^{-1}$) Sitka spruce stand, while Miller et al. (1979) found that an annual N uptake of 69 $kgha^{-1}yr^{-1}$

was required to maintain maximum growth rate of Corsican pine (19.7 $m^3 ha^{-1}yr^{-1}$). Cole (1981) grew Douglas fir under conditions of theoretically unlimited N supply and obtained an uptake of 78 $kgha^{-1}yr^{-1}$, if groundflora were included total uptake was 215 $kgha^{-1}yr^{-1}$. These values for tree uptake at high rates of growth are very similar, Cole's data indicate that N supply may have to be considerably in excess of tree requirement in the presence of a ground flora; trees cannot necessarily exploit 100% of estimated mineralization. Rates of mineralization associated with the pure spruce are clearly inadequate to support high rates of growth, consistent with results for foliar analysis, height increment, and stand appearance.

Current differences in mineralization rates are more than adequate to account for differences in estimated foliar N capitals, even if these values are doubled to approximate total N capitals. However present rates of mineralization may not necessarily reflect previous rates, although relative differences may be similar. Major differences will not have existed before years 7-10 from planting, when a mixture effect first becomes apparent. Since trees respond to N supply by changing their relative growth rate (Ingestad, 1982) the progressive rise in mixture spruce height increment may well reflect a gradual increase in N mineralization. Consequently cumulative mineralization over the life of the mixtures may be much lower than suggested by the present rate, and more in line with quantity of N estimated in the foliar biomass.

Criticism of techniques adopted in this study have been largely dealt with in the relevant sections. Considering the overall approach, certain data could have been more useful and complementary if collected from the same site, e.g. throughfall could have been collected at Mabie 7. Spruce litter inputs in pure and mixed stands were largely ignored, such information would have been useful for comparative purposes. Experiments to assess rates of N release from litters should have been run in conjunction with field studies which followed the process of weight loss and nutrient release under field conditions, in both pure and mixed stands. Much of the reason-

ing in this investigation is based on the assumption that biomass N capital is greater in mixture stands, when this was only estimated in a rather crude manner. However, the study did not aim to quantify all the different pools and N fluxes involved in the cycling of N in pure spruce and larch spruce systems; but to identify key points, or processes, in the cycle where differences could occur, which could explain the observed differences in spruce growth and N status. In this, the study has been largely successful.

12:2 Conclusions

Improved spruce growth and N status in association with larch appears to result from greater mineralization of native organic matter. Causal mechanisms are uncertain but microclimatic differences do not seem to be important; possible explanations probably pertain to the larch root/mycorrhizosphere complex and/or a stimulatory effect of larch litter and the associated decomposer community. Further work is required to a) corroborate the findings of this study, and b) to examine areas which have been neglected.

12:3 Further research

Basic information required as a foundation by any future study is an accurate determination of the N capital of pure and mixed stands.

The area most neglected in this study has been a consideration of below ground processes; there is a need to assess the contribution of fine root turnover together with quantitative and qualitative differences in mycorrhizas; the suggestion that the larch rhizosphere can mineralize N fractions unavailable to spruce should be further investigated, perhaps using seedling mixtures; rooting morphology and intensity should also be investigated.

N fixation has been largely discounted, but sequential measurements still require to be carried out on a seasonal basis. If possible, it might be revealing to follow the phenology of N uptake in pure and mixed stands, and to follow the mixture effect through an age sequence.

Finally, there is an alternative view which may be taken regarding the enhanced growth and N status of spruce in larch

mixtures. Not that larch increases N availability but that Sitka spruce decreases it, conceivably this could result through mycorrhizal antagonism (Gadgil and Gadgil, 1975).

12:4 Silvicultural implications

The use of larch/spruce mixtures as a means of obtaining good spruce growth on N deficient sites, without the need for N fertilizer, is clearly very attractive. Additional benefits include weed suppression by the larch and a probable self-thinning effect which could enhance stability on otherwise unstable sites. At present, however, it is not certain whether the effect will continue to meet spruce N requirements throughout the rotation, although it still appears to be in operation at Inchnacardoch 18 years from planting. It is probable that once canopy closure is achieved on these sites N: cycling should be able to maintain rates of growth.

Both the experiments investigated in this study had mixtures which were 75% larch and 25% spruce, arranged as alternate triplets in alternate rows. It seems improbable that many of the larch present in pure larch rows have any effect on the growth of the triplet spruce. These will be most influenced by the adjacent larch triplets and larch immediately contiguous in the pure larch rows. Consequently the proportion of larch could probably be reduced, an obvious alternative being a 50:50 mixture consisting of alternate pairs of larch and Sitka spruce. However if the stimulatory effect were in any way litter related the proportion of larch may be critical.

Limited visual observations of mixtures planted on more fertile mineral soils, where N availability is unlikely to limit spruce growth, indicate no mixture effect with spruce growth rapidly suppressing the larch.

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APPENDICES .

Appendix 1A.

Values of F for the comparison of treatment (F_t) and block (Fb) means, using a 2-way analysis of variance, for Mabie 7 data.

F_t, $V_1=1$, $V_2=114$; Fb, $V_1=2$, $V_2=114$ (V = degrees of freedom)

	F_t/Fb
ODW	35.64/1.18
%N	225.40/4.52
%P	22.73/1.27
%K	100.54/2.43

Appendix 1B.

Values of F for the comparison of treatment (F_t) and block (Fb) means, using a 2-way analysis of variance, for Inchnacardoch 164 data.

F_t, V_1=1, V_2=92; Fb, V_1=4, V_2=92 (V = degrees of freedom).

F_t/Fb.

ODW	SS-N	SS+N	JL/SS-N	JL/SS+N
SS-N	-	144.90/3.94	149.16/4.31	167.82/2.35
SS+N	-	-	2.55/1.94	8.29/0.47
JL/SS-N	-	-	-	1.53/1.32
JL/SS+N	-	-	-	-
%N				
SS-N	-	298.52/7.54	314.40/6.09	799.93/2.20
SS+N	-	-	0.95/1.69	26.87/6.00
JL/SS-N	-	-	-	48.98/6.40
JL/SS+N	-	-	-	-
%P				
SS-N	-	154.67/4.01	161.64/4.00	234.07/2.52
SS+N	-	-	0.44/3.31	14.31/1.17
JL/SS-N	-	-	-	12.26/7.79
JL/SS+N	-	-	-	-
%K				
SS-N	-	26.05/6.72	170.42/0.75	67.76/2.46
SS+N	-	-	35.99/1.38	4.04/4.01
JL/SS-N	-	-	-	25.50/3.11
JL/SS+N	-	-	-	-

Appendix 2A.

Change in foliar nutrient concentrations and the weight of 100 needles (g) during senescence. Mean values (n=15) and (95% confidence limits).

Sampling date	%N	%P	%K	Weight
16.8.81	1.82	0.48	1.50	0.754
	(0.27)	(0.03)	(0.32)	(0.068)
6.9.81	1.66	0.47	1.15	0.656
	(0.29	(0.04)	(0.31)	(0.100)
27.9.81	1.62	0.49	1.76	0.720
	(0.16)	(0.01)	(0.24)	(0.050)
19.10.81	1.43	0.49	1.40	0.594
	(0.17)	(0.01)	(0.19)	(0.060)
9.11.81	0.68	0.49	1.10	0.546
	(0.16)	(0.01	(0.24)	(0.078)

Appendix 2B.

Change in the nutrient content of 100 needles (mg) during senescence. Mean values (n=15) and (95% confidence limits).

Sampling date	N	P	K
16.8.81	13.82	3.64	11.26
	(2.66)	(0.41)	(2.54)
6.9.81	11.16	3.34	7.22
	(2.93)	(0.45)	(2.13)
27.9.81	11.66	3.50	12.78
	(1.42)	(0.23)	(2.17)
19.10.81	8.54	2.92	8.42
	(1.50)	(0.28)	(1.54)
9.11.81	3.68	2.68	6.06
	(0.98)	(0.34)	(1.54)

Appendix 3A.

Change in component nutrient concentrations. Mean values (n=10) and (95% confidence limits).

%N

Component	Harvest 1 (22.9.82)	Harvest 2 (27.10.82)	Harvest 3 (22.11.82)	Harvest 4 (24.12.82)
Needles	2.11	1.79	0.53	-
	(0.257)	(0.193)	(0.044)	-
Twigs	0.93	1.15	1.38	1.69
	(0.137)	(0.130)	(0.094)	(0.208)
Bark	0.93	1.43	1.77	2.12
	(0.107)	(0.137)	(0.188)	(0.3130
Wood	0.44	0.52	0.77	0.85
	(0.047)	(0.085)	(0.067)	(0.092)
Woody Root	0.73	1.00	1.21	1.36
	(0.063)	(0.108)	(0.100)	(0.231)
Non-woody Root	1.49	1.55	1.57	1.91
	(0.154)	(0.184)	(0.176)	(0.219)

%P

Needles	0.46	0.42	0.33	-
	(0.056)	(0.076)	(0.065)	-
Twigs	0.19	0.20	0.23	0.25
	(0.024)	(0.024)	(0.025)	(0.012)
Bark	0.17	0.19	0.21	0.22
	(0.025)	(0.021)	(0.026)	(0.020)
Wood	0.11	0.10	0.17	0.17
	(0.013)	(0.019)	(0.016)	(0.020)
Woody Root	0.18	0.17	0.28	0.24
	(0.023)	(0.020)	(0.019)	(0.020)
Non-woody Root	0.61	0.32	0.41	0.30
	(0.084)	(0.044)	(0.034)	(0.029)

Appendix 3A cont:-

%K

Needles	0.71	0.68	0.66	-
	(0.070)	(0.125)	(0.082)	-
Twigs	0.49	0.44	0.46	0.50
	(0.078)	(0.060)	(0.037)	(0.056)
Bark	0.49	0.52	0.70	0.76
	(0.063)	(0.061)	(0.059)	(0.046)
Wood	0.23	0.19	0.26	0.25
	(0.28)	(0.20)	(0.045)	(0.024)
Woody Root	0.31	0.33	0.37	0.39
	(0.054)	(0.030)	(0.057)	(0.042)
Non-woody Root	0.71	0.57	0.48	0.46
	(0.101)	(0.089)	(0.032)	(0.046)

Appendix 3B

Change in component oven dry weight (g). Mean values (n=10) and (95% confidence limits).

Component	Harvest 1 (22.9.82)	Harvest 2 (27.10.82)	Harvest 3 (22.11.82)	Harvest 4 (24.12.82)
Needles	10.96	8.13	1.90	-
	(1.728)	(1.080)	(0.895)	-
Twigs	8.61	6.77	7.39	5.92
	(1.912)	(1.442)	(1.776)	(0.959)
Bark	3.93	3.88	3.80	3.32
	(0.507)	(0.817)	(1.141)	(0.517)
Wood	4.44	5.70	6.39	5.92
	(0.853)	(0.777)	(2.042)	(1.266)
Woody Root	5.00	4.76	4.74	4.26
	(0.978)	(1.225)	(1.141)	(0.955)
Non-woody Root	5.37	6.22	6.10	7.21
	(1.211)	(1.513)	(1.085)	(1.011)
Total weight	38.31	35.58	30.67	26.22
	(4.916)	(4.079)	(5.935)	(2.204)
Total weight (- needles)	27.35	27.45	28.77	-
	(3.219)	(3.554)	(5.438)	-

Appendix 3C.

Change in component nutrient content (mg). Mean values (n=10) and (95% confidence limits).

N

Component	Harvest 1	Harvest 2	Harvest 3	Harvest 4
Needles	229.68	145.09	10.69	-
	(37.05)	(30.19)	(2.45)	-
Twigs	78.51	73.48	102.84	101.91
	(12.21)	(11.17)	(16.75)	(17.13)
Bark	36.30	54.20	70.31	70.69
	(6.69)	(12.09)	(12.05)	(16.48)
Wood	19.15	30.43	49.80	51.15
	(3.00)	(9.23)	(18.17)	(16.93)
Woody Root	37.13	46.55	55.15	58.49
	(6.28)	(10.97)	(8.52)	(17.34)
Non-woody	76.94	93.58	95.19	137.03
Root	(13.61)	(23.13)	(16.13)	(33.03)
Total	477.71	443.33	383.98	419.27
	(61.46)	(74.23)	(72.81)	(97.23)
Total	248.03	298.24	373.29	-
(- needles)	(35.13)	(43.70)	(70.85)	-

Appendix 3C cont:-

P

Component	Harvest 1	Harvest 2	Harvest 3	Harvest 4
Needles	48.80	34.30	5.90	-
	(8.91)	(8.13)	(2.92)	-
Twigs	16.60	12.81	14.97	14.56
	(2.82)	(1.98)	(3.25)	(2.66)
Bark	6.55	7.21	8.40	7.38
	(0.85)	(1.76)	(2.88)	(2.02)
Wood	4.59	5.48	10.89	9.96
	(0.72)	(1.83)	(2.29)	(2.43)
Woody Root	9.24	8.05	12.38	10.55
	(2.41)	(2.74)	(3.51)	(4.17)
Non-woody Root	32.10	18.39	24.53	21.36
	(11.32)	(5.64)	(7.89)	(5.04)
Total	117.88	86.24	77.07	63.81
	(15.29)	(15.54)	(19.36)	(12.48)
Total	69.08	51.94	71.17	-
(-Needles)	(15.39)	(9.76)	(17.92)	-

K

Needles	78.60	54.99	11.39	-
	(11.33)	(9.52)	(3.71)	-
Twigs	41.24	28.84	33.90	29.98
	(8.38)	(7.07)	(7.89)	(6.70)
Bark	19.24	20.00	27.50	25.36
	(3.56)	(4.84)	(8.15)	(4.66)
Wood	10.21	11.08	16.95	14.68
	(2.43)	(2.81)	(7.24)	(4.73)
Woody Root	16.09	15.51	17.34	16.48
	(5.50)	(3.87)	(4.81)	(4.00)
Non-woody Root	36.76	32.60	29.39	32.94
	(9.83)	(5.97)	(5.54)	(5.82)
Total	202.14	163.02	136.47	119.44
	(73.00)	(30.71)	(28.04)	(23.64)
Total	123.54	108.33	125.08	-
(-Needles)	(26.58)	(15.07)	(25.16)	-

Appendix 4A.

Initial oven dry weights (g) and nutrient contents (mg) of litter mixtures.

Oven dry weight. g(% of total).

Treatment	Larch litter	Spruce litter	Total
L_0S_{10}	0.00 (0)	7.38 (100)	7.38
L_2S_8	1.62 (22)	5.90 (78)	7.52
L_4S_6	3.24 (42)	4.43 (58)	7.67
L_6S_4	4.86 (62)	2.95 (38)	7.81
L_8S_2	6.48 (81)	1.48 (19)	7.96
$L_{10}S_0$	8.10 (100)	0.00 (0)	8.10
N. mg (% of total)			
L_0S_{10}	0.00 (0)	59.78 (100)	59.78
L_2S_8	27.86 (37)	47.79 (63)	75.65
L_4S_6	55.73 (61)	35.88 (39)	91.61
L_6S_4	83.59 (78)	23.90 (22)	107.49
L_8S_2	111.46 (90)	11.99 (10)	123.45
$L_{10}S_0$	139.32 (100)	0.00 (0)	139.32
P. mg (% of total)			
L_0S_{10}	0.00 (0)	6.64 (100)	6.64
L_2S_8	2.11 (28)	5.31 (72)	7.42
L_4S_6	4.21 (51)	3.99 (49)	8.20
L_6S_4	6.32 (70)	2.66 (30)	8.98
L_8S_2	8.42 (86)	1.33 (14)	9.75
$L_{10}S_0$	10.53 (100)	0.00 (0)	10.53

Appendix 4B.

Final oven dry weights (g) and nutrient contents (mg) of litter mixtures. Mean values (n=4) ± 95% confidence limits.

Oven dry weights, g (% weight loss).

Treatment	Total (Larch + Spruce)
L_0S_{10}	2.38 ± 0.02 (68)
L_2S_8	2.48 ± 0.39 (67)
L_4S_6	3.11 ± 0.25 (59)
L_6S_4	3.71 ± 0.09 (52)
L_8S_2	3.98 ± 0.19 (50)
$L_{10}S_0$	4.40 ± 0.01 (46)
N mg (% loss)	
L_0S_{10}	28.91 ± 1.74 (52)
L_2S_8	33.43 ± 10.38(56)
L_4S_6	45.96 ± 5.60 (50)
L_6S_4	55.98 ± 3.17 (48)
L_8S_2	56.21 ± 8.38 (56)
$L_{10}S_0$	64.52 ± 5.99 (54)
P mg (% loss)	
L_0S_{10}	2.17 ± 0.12 (67)
L_2S_8	2.43 ± 0.68 (67)
L_4S_6	3.04 ± 0.32 (63)
L_6S_4	3.12 ± 0.24 (65)
L_8S_2	2.81 ± 0.84 (71)
$L_{10}S_0$	3.02 ± 0.20 (71)

Appendix 4C.

Nutrient release (mg) and pH of leachate over the incubation period. Mean values (n=4) and (95% confidence limits).

Treatment	Ammonium	Nitrate	Phosphate	pH
Day 30				
L_0S_{10}	0.05(0.01)	0.00(0.00)	0.21(0.03)	5.92(0.03)
L_2S_8	0.07(0.01)	0.00(0.00)	0.23(0.05)	6.15(0.28)
L_4S_6	0.07(0.02)	0.00(0.00)	0.31(0.03)	6.06(0.26)
L_6S_4	0.08(0.01)	0.00(0.00)	0.32(0.01)	6.30(0.18)
L_8S_2	0.14(0.03)	0.01(0.01)	0.54(0.05)	6.38(0.17)
$L_{10}S_0$	0.17(0.02)	0.03(0.01)	0.60(0.01)	6.44(0.19)
Day 60				
L_0S_{10}	0.03(0.00)	0.00(0.00)	0.07(0.00)	5.35(0.09)
L_2S_8	0.06(0.00)	0.00(0.00)	0.10(0.00)	5.55(0.09)
L_4S_6	0.11(0.02)	0.01(0.00)	0.17(0.01)	5.40(0.18)
L_6S_4	0.14(0.03)	0.28(0.03)	0.23(0.00)	5.40(0.00)
L_8S_2	0.39(0.08)	0.97(0.04)	0.52(0.02)	5.25(0.09)
$L_{10}S_0$	0.61(0.07)	0.92(0.03)	0.69(0.04)	5.20(0.00)
Day 90				
L_0S_{10}	0.00(0.00)	0.00(0.00)	0.03(0.01)	5.60(0.18)
L_2S_8	0.05(0.00)	0.03(0.04)	0.07(0.00)	5.50(0.00)
L_4S_6	0.08(0.01)	0.10(0.04)	0.14(0.01)	5.25(0.28)
L_6S_4	0.07(0.01)	0.31(0.06)	0.19(0.02)	5.40(0.00)
L_8S_2	0.16(0.00)	0.80(0.00)	0.37(0.07)	5.15(0.09)
$L_{10}S_0$	0.30(0.05)	1.06(0.19)	0.40(0.04)	4.80(0.00)
Day 120				
L_0S_{10}	0.02(0.00)	0.00(0.00)	0.08(0.03)	5.35(0.09)
L_2S_8	0.02(0.00)	0.01(0.01)	0.12(0.02)	5.65(0.09)
L_4S_6	0.04(0.01)	0.13(0.02)	0.16(0.03)	5.10(1.72)
L_6S_4	0.09(0.01)	0.46(0.05)	0.25(0.02)	5.20(0.18)
L_8S_2	0.40(0.13)	1.26(0.32)	0.45(0.07)	4.40(0.18)
$L_{10}S_0$	0.49(0.22)	1.65(0.49)	0.45(0.07)	4.05(0.09)

Appendix 4C cont:-

Day 150

L_0S_{10}	0.00(0.00)	0.00(0.00)	0.07(0.01)	5.20(0.00)
L_2S_8	0.02(0.01)	0.00(0.00)	0.11(0.02)	5.40(0.00)
L_4S_6	0.03(0.01)	0.27(0.11)	0.13(0.01)	5.10(1.72)
L_6S_4	0.10(0.07)	1.01(0.13)	0.30(0.07)	4.95(0.09)
L_8S_2	0.27(0.08)	1.85(0.60)	0.45(0.13)	3.95(0.09)
$L_{10}S_0$	0.65(0.05)	1.28(0.17)	0.53(0.06)	4.00(0.00)

Day 180

L_0S_{10}	0.00(0.00)	0.00(0.00)	0.09(0.02)	5.20(0.00)
L_2S_8	0.00(0.00)	0.00(0.00)	0.12(0.03)	5.25(0.09)
L_4S_6	0.04(0.01)	0.37(0.11)	0.16(0.01)	5.10(0.18)
L_6S_4	0.15(0.09)	1.13(0.03)	0.26(0.01)	5.10(0.18)
L_8S_2	0.50(0.15)	1.82(0.04)	0.41(0.12)	4.05(0.28)
$L_{10}S_0$	0.74(0.06)	1.69(0.25)	0.49(0.08)	3.80(0.00)

Appendix 5A.

Treatment bulk densities and conversion of mineral N concentrations to $kgha^{-1}$.

1. Bulk densities ($g\ cm^{-3}$).

   (a) Mabie 7: based on 6 composite samples per treatment, plough position and depth. Each composite sample made up of 10 individual samples. Mean values (n=6) and (95% confidence limits).

	Ridge			Flat		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
OW	0.14 (0.01)	0.15 (0.01)	0.16 (0.01)	0.10 (0.01)	0.14 (0.01)	0.15 (0.01)
H	0.13 (0.01)	0.16 (0.01)	0.17 (0.01)	0.11 (0.01)	0.14 (0.01)	0.16 (0.01)
OW/H* (n=12)	0.14 (0.01)	0.16 (0.01)	0.17 (0.01)	0.11 (0.01)	0.14 (0.01)	0.16 (0.01)

*Treatment means were not significantly different therefore values were combined.

Appendix 5A cont:-

(b) Inchnacardoch 164: based on 5 composite samples per treatment, plough position and depth. Each composite sample made up of 5 individual samples. Mean values (n=5) and (95% confidence limits).

	Ridge			Flat		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
SS-N	0.09 (0.01)	0.17 (0.02)	0.16 (0.01)	0.04 (0.01)	0.08 (0.01)	0.06 (0.01)
JL/SS-N	0.10 (0.01)	0.17 (0.01)	0.16 (0.01)	0.04 (0.01)	0.08 (0.01)	0.07 (0.01)
JL/SS-N* +SS-N	0.09 (0.01)	0.17 (0.01)	0.16 (0.01)	0.04 (0.01)	0.08 (0.01)	0.07 (0.01)

* Treatment means were not significantly different therefore values were combined.

2. Conversion of mineral N concentrations to $kgha^{-1}$.

(a) Field incubations.

Corer Ring Volume (CRV) = 103 cm^3.

No Rings ha^{-1} = 3.21×10^6

Mineral N concentration (MNC) = mgg^{-1}.

CRV x bulk density = g sample $Ring^{-1}$ (G)

G x MNC = mg Mineral N $Ring^{-1}$

mg Mineral N $Ring^{-1}$ x 3.21 = kg Mineral N ha^{-1}.

(b) Laboratory incubations

As (a) but first must determine the proportion of G represented by the 10g fresh weight sample.

3. Summing monthly ridge and flat mineralization values to obtain an annual estimate.

Assumptions, ridge position contributes 0.33 land surface,
flat position contributes 0.67 land surface.

(Mineral N Ridge x 0.33) + (Mineral N Flat x 0.67) =
Mineral N Total $kgha^{-1}$

Appendix 5B.

Net N mineralization ($kgha^{-1}$) for 0-9 cm depth. Mean values (n=6) and (95% confidence limits).

OWOW = OW material incubated under OW conditions.
OWH = OW material incubated under H conditions.
HH = H material incubated under H conditions.
HOW = H material incubated under OW conditions.

1. July - August 1981.

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
6.14	7.79	4.91	7.92	5.06	12.34	5.86	13.31
(0.44)	(0.61)	(0.67)	(0.60)	(0.39)	(5.14)	(0.92)	(3.29)
*1		*2	NS[3]	*1		NS[2]	NS[3]
*4	NS[5]						

2. August - September 1981.

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
6.31	8.54	6.66	7.97	5.44	15.31	6.10	16.60
(1.27)	(0.33)	(0.89)	(1.28)	(0.77)	(1.12)	(0.42)	(2.57)
*		NS	NS	*		NS	NS
NS	*						

* means significantly different, NS not significantly different at P = 0.05 in Cochrane's approximation for a Fisher-Behrens test. 1 = OWOW vs. HH, 2 = OWOW vs. OWH, 3 = HH vs. HOW, 4 = OWOW (ridge) vs. OWOW (flat). 5 = HH (ridge) vs. HH (flat).

Appendix 5B cont:-

3. September - October 1981.

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
3.79	7.73	3.75	7.22	3.89	11.83	4.16	11.84
(0.82)	(1.20)	(0.48)	(0.64)	(0.44)	(1.13)	(1.18)	(2.79)
*		NS	NS	*		NS	NS
NS	*						

4. October - November 1981

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
0.85	3.03	2.16	2.27	0.87	4.30	1.96	3.17
(0.22)	(0.23)	(0.61)	(0.67)	(0.22)	(0.79)	(0.54)	(0.85)
*		*	*	*		*	NS
NS	*						

5. February - March 1982

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
3.67	3.92	2.80	4.73	3.97	4.16	3.59	5.15
(1.03)	(0.56)	(0.32)	(1.59)	(0.63)	(1.62)	(0.67)	(1.10)
NS		NS	NS	NS		NS	NS
NS	NS						

6. March - April 1982

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
-2.69	-0.73	-2.41	-1.13	-3.22	1.72	-2.02	2.70
(0.74)	(0.12)	(0.58)	(0.37)	(0.86)	(0.45)	(0.31)	(0.24)
*		NS	NS	*		*	*
NS	*						

Appendix 5B cont:-

7. April - May 1982

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
3.98	5.12	3.79	4.51	5.74	6.64	4.28	7.50
(0.54)	(0.99)	(0.48)	(0.27)	(2.63)	(0.66)	(0.91)	(2.18)
*		NS	NS	NS		NS	NS
NS	*						

8. May - June 1982

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
6.16	8.49	6.53	7.85	8.15	11.60	8.60	13.06
(1.38)	(0.80)	(1.86)	(0.91)	(1.88)	(2.13)	(1.20)	(1.51)
*		NS	NS	*		NS	NS
NS	*						

9. June - July 1982

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
-1.08	1.35	-1.78	1.01	-1.47	2.26	-2.75	2.31
(0.21)	(0.79)	(0.44)	(0.66)	(1.14)	(0.85)	(0.48)	(1.33)
*		*	NS	*		*	NS
NS	NS						

10. November - December 1982

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
0.05	0.02	-0.32	1.14	1.31	-0.37	-1.15	-0.20
(0.29)	(0.12)	(0.18)	(0.28)	(0.35)	(0.31)	(0.24)	(0.39)
NS		NS	*	*		*	NS
*	*						

Appendix 5B cont:-

11. December - February 1982/3

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
0.28	-1.12	-0.47	-0.78	-0.87	-1.53	-0.65	-1.82
(0.09)	(0.25)	(0.32)	(0.19)	(0.19)	(0.27)	(0.18)	(0.74)
*		*	*	*		NS	NS
*	*						

12. February - March 1983

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
0.65	3.60	0.93	2.48	0.04	3.09	0.53	3.15
(0.26)	(0.84)	(0.26)	(0.81)	(0.11)	(0.71)	(0.25)	(0.54)
*		NS	NS	*		*	NS
*	NS						

13. March - April 1983

Ridge				Flat			
OWOW	HH	OWH	HOW	OWOW	HH	OWH	HOW
1.08	4.46	1.54	5.63	1.00	8.16	1.64	7.25
(0.55)	(0.92)	(0.57)	(1.87)	(0.21)	(2.68)	(0.23)	(2.46)
*		NS	NS	*		NS	NS
NS	*						

Appendix 5C.

Initial mineral N ($kgha^{-1}$) in fresh samples for 0 - 9 cm depth. Mean values (n=6) and (95% confidence limits).

1. July 1981

	RIDGE	FLAT
OW	1.33 (0.01)	1.69 (0.27)
H	0.96 (0.24)	1.79 (0.22)

2. August 1981

OW	2.48 (0.08)	2.75 (0.16)
H	1.74 (0.24)	2.99 (0.29)

3. September 1981

OW	1.52 (0.13)	2.11 (0.22)
H	1.34 (0.33)	1.89 (0.25)

4. October 1981

OW	2.49 (0.76)	2.20 (0.66)
H	1.75 (0.62)	4.16 (0.74)

5. February 1982

OW	1.04 (0.32)	1.77 (0.13)
H	1.40 (0.19)	1.87 (0.38)

6. March 1982

OW	6.60 (0.46)	7.51 (0.46)
H	5.38 (2.10)	6.26 (2.38)

7. April 1982

OW	2.34 (0.50)	2.65 (1.09)
H	2.45 (0.36)	3.60 (1.08)

8. May 1982

OW	4.15 (0.17)	4.72 (0.74)
H	3.43 (0.65)	5.31 (0.81)

9. June 1982

OW	5.21 (1.51)	5.98 (1.51)
H	4.35 (1.20)	5.36 (1.35)

10. November 1982

OW	2.70 (0.49)	3.51 (0.23)
H	3.35 (0.26)	3.77 (0.21)

Appendix 5C cont:-

11. December 1982			
	OW	3.90 (0.71)	4.91 (1.55)
	H	4.48 (0.78)	5.16 (1.56)
12. February 1983			
	OW	2.00 (0.36)	2.21 (0.32)
	H	1.85 (0.20)	2.19 (0.42)
13. March 1983			
	OW	2.06 (0.36)	2.11 (0.05)
	H	1.63 (0.45)	1.99 (0.12)

Appendix 5D

Net N mineralization ($kgha^{-1}$) at different depths. Mean values (n=6) and (95% confidence limits).

1. July - August 1981.

	RIDGE			FLAT		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
OWOW	2.84	1.82	1.48	1.71	1.46	1.89
	(0.38)	(0.50)	(0.39)	(0.67)	(0.39)	(0.49)
HOW	3.96	2.07	1.89	6.70	3.89	2.72
	(0.95)	(0.43)	(0.44)	(3.44)	(0.42)	(0.75)
HH	3.90	1.80	2.09	7.43	3.23	1.68
	(0.60)	(0.49)	(0.11)	(4.76)	(0.60)	(0.20)
OWH	1.86	1.46	1.59	2.48	1.77	1.61
	(0.50)	(0.44)	(0.34)	(0.80)	(0.10)	(0.23)

2. August - September 1981.

OWOW	3.06	2.11	1.14	2.13	1.84	1.47
	(0.70)	(0.42)	(0.20)	(0.33)	(0.12)	(0.40)
HOW	4.50	2.06	1.41	9.85	3.78	2.97
	(0.93)	(0.31)	(0.16)	(2.62)	(0.71)	(0.22)
HH	4.68	2.39	1.47	9.23	3.45	2.63
	(0.54)	(0.21)	(0.20)	(1.15)	(0.45)	(0.29)
OWH	3.39	1.80	1.47	2.75	1.80	1.55
	(0.79)	(0.15)	(0.19)	(0.17)	(0.37)	(0.12)

Appendix 5D cont:-

3. September - October 1981.

OWOW	2.80	0.67	0.32	1.76	1.03	1.10
	(0.58)	(0.13)	(0.06)	(0.27)	(0.66)	(0.50)
HOW	4.36	1.89	0.97	5.85	4.07	1.92
	(0.33)	(0.45)	(0.18)	(1.43)	(1.58)	(0.98)
HH	4.99	1.49	1.25	6.89	3.86	1.08
	(1.05)	(0.27)	(0.38)	(1.34)	(1.42)	(0.44)
OWH	2.53	0.98	0.24	2.00	1.33	0.83
	(0.42)	(0.06)	(0.08)	(0.40)	(0.49)	(0.29)

4. October - November 1981

OWOW	0.52	0.12	0.21	0.35	0.40	0.12
	(0.18)	(0.05)	(0.04)	(0.11)	(0.10)	(0.03)
HOW	1.70	0.19	0.38	2.59	0.46	0.12
	(0.76)	(0.05)	(0.16)	(0.85)	(0.05)	(0.03)
HH	2.56	0.12	0.35	3.34	0.82	0.14
	(0.36)	(0.06)	(0.13)	(0.69)	(0.28)	(0.05)
OWH	1.14	0.67	0.35	1.04	0.76	0.16
	(0.58)	(0.29)	(0.07)	(0.65)	(0.17)	(0.04)

5. February - March 1982.

OWOW	1.11	1.39	1.17	1.04	1.39	1.54
	(0.32)	(0.55)	(0.31)	(0.32)	(0.32)	(0.26)
HOW	1.76	1.55	1.42	1.52	1.40	2.23
	(0.74)	(0.31)	(0.37)	(0.45)	(0.27)	(0.62)
HH	2.18	0.69	1.05	1.67	1.22	1.27
	(0.42)	(0.05)	(0.29)	(0.53)	(0.51)	(0.63)
OWH	0.69	1.04	1.07	0.83	1.19	1.57
	(0.08)	(0.22)	(0.33)	(0.31)	(0.29)	(0.42)

Appendix 5D cont:-

6. March - April 1982

OWOW	-0.66	-0.87	- 1.16	-0.53	-1.39	-1.30
	(0.37)	(0.11)	(0.56)	(0.18)	(0.38)	(0.45)
HOW	-0.30	-0.31	-0.52	1.44	1.09	0.17
	(0.05)	(0.08)	(0.13)	(0.23)	(0.16)	(0.16)
HH	-0.13	-0.26	-0.34	1.42	0.31	-0.01
	(0.04)	(0.14)	(0.13)	(0.49)	(0.07)	(0.02)
OWH	-0.48	-0.86	-1.07	-0.25	-0.80	-0.97
	(0.10)	(0.47)	(0.26)	(0.10)	(0.29)	(0.31)

7. April - May 1982

OWOW	1.07	1.52	1.39	1.39	2.00	2.35
	(0.31)	(0.37)	(0.25)	(0.62)	(0.79)	(1.31)
HOW	1.43	1.55	1.53	2.32	2.68	2.50
	(0.10)	(0.30)	(0.19)	(0.81)	(0.25)	(1.53)
HH	1.63	1.53	1.96	2.51	2.69	1.44
	(0.18)	(0.17)	(0.80)	(0.47)	(0.42)	(0.38)
OWH	1.25	1.28	1.26	1.08	1.36	1.84
	(0.44)	(0.22)	(0.42)	(0.49)	(0.24)	(0.81)

8. May - June 1982

OWOW	1.67	2.08	2.41	1.36	3.17	3.62
	(0.40)	(0.57)	(0.65)	(0.41)	(1.04)	(0.78)
HOW	2.37	2.57	2.91	3.88	4.82	4.36
	(0.61)	(0.58)	(0.54)	(0.43)	(1.05)	(0.78)
HH	3.09	2.67	2.73	3.46	4.02	4.12
	(0.94)	(0.55)	(0.87)	(0.40)	(0.93)	(0.96)
OWH	2.00	2.07	2.46	1.44	3.06	4.10
	(0.37)	(0.73)	(0.92)	(0.33)	(0.68)	(0.78)

Appendix 5D cont:-

9. June - July 1982

OWOW	0.38	-0.61	-0.85	-0.03	-0.55	-0.89
	(0.06)	(0.10)	(0.15)	(0.21)	(0.69)	(0.96)
HOW	1.40	-0.28	-0.11	0.34	1.61	0.36
	(0.68)	(0.06)	(0.08)	(0.24)	(1.23)	(0.51)
HH	1.50	-0.12	-0.03	0.65	1.04	0.57
	(0.78)	(0.09)	(0.07)	(0.45)	(0.42)	(0.72)
OWH	0.07	-0.94	-0.91	-0.33	-1.12	-1.30
	(0.04)	(0.29)	(0.31)	(0.20)	(0.41)	(0.21)

10. November - December 1982

OWOW	0.33	-0.18	-0.20	0.81	0.46	0.04
	(0.11)	(0.09)	(0.10)	(0.22)	(0.12)	(0.06)
HOW	1.10	0.15	-0.11	0.36	-0.30	-0.26
	(0.18)	(0.09)	(0.07)	(0.12)	(0.13)	(0.05)
HH	0.75	-0.24	-0.49	0.48	-0.26	-0.59
	(0.19)	(0.27)	(0.11)	(0.08)	(0.16)	(0.20)
OWH	-0.05	-0.12	-0.15	0.25	-0.53	-0.87
	(0.06)	(0.11)	(0.05)	(0.07)	(0.24)	(0.18)

11. December - February 1982/3

OWOW	0.13	-0.15	0.30	0.22	-0.86	-0.23
	(0.07)	(0.10)	(0.11)	(0.03)	(0.18)	(0.07)
HOW	0.47	-0.59	-0.66	-0.47	-0.60	-0.75
	(0.07)	(0.16)	(0.11)	(0.06)	(0.26)	(0.35)
HH	0.09	-0.66	-0.55	-0.32	-0.67	-0.54
	(0.06)	(0.12)	(0.14)	(0.04)	(0.15)	(0.18)
OWH	0.22	-0.47	-0.22	0.26	-0.52	-0.39
	(0.15)	(0.20)	(0.11)	(0.08)	(0.06)	(0.08)

Appendix 5D cont:-

12. February - March 1983.

OWOW	0.08	0.30	0.27	0.04	-0.02	0.02
	(0.02)	(0.16)	(0.13)	(0.04)	(0.06)	(0.03)
HOW	1.87	0.50	0.11	2.53	0.33	0.29
	(0.84)	(0.03)	(0.14)	(0.65)	(0.16)	(0.13)
HH	1.44	0.88	1.28	1.53	0.82	0.74
	(0.79)	(0.19)	(0.97)	(0.47)	(0.22)	(0.28)
OWH	0.25	0.25	0.43	0.39	0.09	0.05
	(0.12)	(0.22)	(0.16)	(0.19)	(0.74)	(0.05)

13. March - April 1983

OWOW	0.56	0.31	0.21	0.41	0.12	0.47
	(0.31)	(0.18)	(0.17)	(0.11)	(0.06)	(0.09)
HOW	2.68	1.32	1.63	2.24	2.86	2.15
	(1.04)	(0.52)	(0.58)	(0.65)	(1.00)	(0.84)
HH	1.61	1.26	1.59	3.07	2.60	2.49
	(0.35)	(0.16)	(0.52)	(0.75)	(0.89)	(1.14)
OWH	0.57	0.73	0.24	0.57	0.50	0.57
	(0.10)	(0.27)	(0.27)	(0.16)	(0.21)	(0.18)

Appendix 5E.

Net N mineralization ($kgha^{-1}$) for intact cores (0-3 cm depth). Mean values (n=6) and (95% confidence limits).

1. November - December 1982

	Ridge	Flat
OWOW	0.14	0.39
	(0.45)	(0.33)
HOW	0.96	2.11
	(1.21)	(2.91)
HH	0.05	2.43
	(0.79)	(3.75)
OWH	-0.25	0.08
	(0.73)	(0.28)

2. December - February 1982/3

OWOW	0.15	-0.12
	(0.19)	(0.50)
HOW	1.30	0.35
	(1.25)	(0.92)
HH	0.83	0.80
	(0.53)	(0.38)
OWH	0.15	0.00
	(0.41)	(0.48)

3. February - March 1983

OWOW	0.32	0.07
	(0.27)	(0.31)
HOW	0.38	0.33
	(0.31)	(0.17)
HH	0.26	0.78
	(0.15)	(1.00)
OWH	0.49	0.27
	(0.45)	(0.22)

Appendix 5E cont:-

4. March - April 1983

OWOW	0.84	0.31
	(0.71)	(0.47)
HOW	2.71	1.93
	(1.44)	(1.03)
HH	2.31	2.79
	(1.78)	(1.54)
OWH	0.46	0.86
	(0.24)	(0.50)

Appendix 5F.

Net N mineralization ($kgha^{-1}$) for 0-9 cm depth in OW and H treatment material incubated under laboratory conditions. Mean values (n=4) and (95% confidence limits).

	RIDGE		FLAT
1. July - August 1981			
OW	14.82	*	11.36
	(0.36)		(0.50)
	*		*
H	19.61	*	23.02
	(0.33)		(1.41)
2. February - March 1982			
OW	9.09	NS	9.61
	(0.20)		(0.95)
	*		*
H	13.07	NS	13.86
	(0.69)		(0.67)
3. April - May 1982			
OW	6.44	*	7.59
	(0.33)		(0.29)
	*		*
H	7.31	*	18.39
	(0.73)		(0.53)
4. May - June 1982			
OW	8.18	*	7.35
	(0.16)		(0.40)
	*		*
H	9.11	*	9.89
	(0.39)		(0.38)

* Means significantly different, NS not significantly different at P = 0.05 in Cochrane's approximation for a Fisher-Behrens test.

Appendix 5G.

Cumulative N mineralization ($kgha^{-1}$) at different depths, and summed for 0-9 cm after 30 and 60 days. Material from Inch-nacardoch 164, incubated under laboratory conditions. Mean values (n=4) and (95% confidence limits). Material collected December 1982.

30 days	Ridge			Flat		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
SS-N	1.19	1.46	1.90	1.75	0.90	1.06
	(0.86)	(0.11)	(0.05)	(0.11)	(0.05)	(0.02)
JL/SS-N	2.47	6.63	3.44	0.40	0.77	1.55
	(3.39)	(0.90)	(0.63)	(0.32)	(0.13)	(0.12)
60 days						
SS-N	2.20	2.08	3.07	1.75	1.27	1.30
	(0.12)	(0.17)	(0.37)	(0.21)	(0.37)	(0.21)
JL/SS-N	4.79	14.84	10.95	6.76	1.22	3.59
	(2.26)	(0.62)	(0.74)	(1.30)	(0.63)	(0.62)

0 - 9 cm

30 days	Ridge		Flat
SS-N	4.55	*	3.71
	(0.50)		(0.07)
	*		NS
JL/SS-N	12.54	*	2.72
	(2.06)		(1.03)
60 days			
SS-N	7.35	*	4.32
	(0.25)		(0.27)
	*		*
JL/SS-N	30.58	*	11.57
	(1.42)		(0.91)

* Means significantly different, NS not significantly different at P = 0.05 in Cochrane's approximation for a Fisher-Behrens test.

Appendix 5H

Initial moisture content (% Fresh weight) and pH of material used in the Inchnacardoch laboratory incubation. Mean values (n=4) and (95% confidence limits).

Moisture content (% Fresh weight)

	Ridge			Flat		
	0-3 cm	3-6 cm	6-9 cm	0-3 cm	3-6 cm	6-9 cm
SS-N	79.0	76.0	77.8	84.0	81.6	84.8
	(6.8)	(6.4)	(4.6)	(7.7)	(3.7)	(4.6)
JL/SS-N	77.0	70.9	76.4	85.0	83.6	87.6
	(6.0)	(4.3)	(4.0)	(3.7)	(7.3)	(2.1)
pH						
SS-N	3.87	3.73	3.67	4.17	3.83	3.62
	(0.04)	(0.03)	(0.02)	(0.06)	(0.06)	(0.00)
JL/SS-N	3.98	3.50	3.58	4.04	3.86	3.59
	(0.05)	(0.05)	(0.05)	(0.11)	(0.03)	(0.04)

Appendix 51.

Net N mineralization ($kgha^{-1}$) at different depths in OW and H treatment material incubated under laboratory conditions. Mean values (n=4) and (95% confidence limits).

1. July-August 1981.

	RIDGE			FLAT		
	0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
OW	9.49	2.01	3.32	4.73	2.82	3.81
	(0.46)	(0.32)	(0.28)	(0.84)	(0.23)	(0.05)
H	14.67	1.96	2.98	15.86	4.30	2.86
	(0.46)	(0.05)	(0.34)	(2.40)	(0.42)	(0.26)

2. February-March 1982.

OW	5.60	1.75	1.74	4.11	2.22	3.28
	(0.19)	(0.26)	(0.11)	(1.42)	(0.83)	(0.16)
H	6.94	2.70	3.43	6.76	2.92	4.18
	(0.69)	(0.74)	(0.62)	(1.02)	(0.56)	(0.11)

3. April-May 1982.

OW	2.87	2.33	1.24	3.64	1.99	1.96
	(0.19)	(0.42)	(0.34)	(0.04)	(0.42)	(0.26)
H	4.35	2.17	0.79	15.02	1.57	1.80
	(1.25)	(0.16)	(0.00)	(0.91)	(0.00)	(0.00)

4. May-June 1982.

OW	4.03	1.90	2.25	1.67	3.19	2.49
	(0.19)	(0.16)	(0.11)	(0.33)	(0.28)	(0.53)
H	4.44	1.69	2.98	3.27	3.29	3.33
	(0.56)	(0.32)	(0.22)	(0.22)	(0.56)	(0.26)

Appendix 6A

Oven dry weight (g) and nutrient content (mg) of birch seedlings grown in Mabie 7 material. Mean values (n=10) and (95% confidence limits).

Oven dry weight (g).

Ridge Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
0.355	0.170	0.119	0.584	0.152	0.231
(0.110)	(0.044)	(0.046)	(0.171)	(0.031)	(0.037)

Flat Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
0.304	0.334	0.265	0.559	0.419	0.223
(0.119)	(0.070)	(0.058)	(0.133)	(0.088)	(0.061)

N content (mg).

Ridge Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
6.65	2.47	1.70	9.97	2.11	2.98
(1.89)	(0.28)	(0.47)	(2.50)	(0.39)	(0.19)

Flat Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
5.25	4.34	3.30	10.51	7.80	3.35
(1.77)	(0.46)	(0.46)	(4.15)	(2.74)	(0.61)

Appendix 6A cont:-

P content (mg).

Ridge Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
0.95	0.47	0.26	2.35	0.41	0.57
(0.34)	(0.08)	(0.09)	(0.77)	(0.11)	(0.08)

Flat Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
0.88	0.84	0.47	1.90	0.94	0.44
(0.38)	(0.18)	(0.09)	(0.48)	(0.35)	(0.12)

K content (mg).

Ridge Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
4.60	2.88	2.01	5.89	2.51	3.73
(1.72)	(0.66)	(0.67)	(1.50)	(0.53)	(0.42)

Flat Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
4.61	3.85	2.60	7.24	5.06	2.88
(2.14)	(3.85)	(2.60)	(7.24)	(5.06)	(2.88)

Appendix 6B.

N mineralization (mgg^{-1}) calculated from plant uptake. Mean values (n=10) and (95% confidence limits).

Ridge Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
0.46	0.24	0.19	0.72	0.18	0.29
(0.13)	(0.03)	(0.05)	(0.18)	(0.03)	(0.02)

Flat Material

OW			H		
0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm
0.54	0.54	0.43	1.04	0.98	0.44
(0.18)	(0.06)	(0.06)	(0.41)	(0.34)	(0.08)

Appendix 6C.

Cumulative net N mineralization (mgg^{-1}) after 120 days. Mean values (n=4) and (95% confidence limits).

		Ammonium	
		OW	H
Ridge	0-3cm	0.45 (0.09)	0.61 (0.09)
	3-6	0.21 (0.02)	0.15 (0.06)
	6-9	0.16 (0.04)	0.17 (0.02)
Flat	0-3	0.43 (0.11)	1.05 (0.20)
	3-6	0.19 (0.11)	0.41 (0.14)
	6-9	0.11 (0.11)	0.22 (0.07)
		Nitrate	
Ridge	0-3cm	0.023 (0.009)	0.027 (0.005)
	3-6	0.021 (0.000)	0.024 (0.003)
	6-9	0.022 (0.003)	0.029 (0.006)
Flat	0-3cm	0.022 (0.002)	0.031 (0.007)
	3-6	0.024 (0.011)	0.031 (0.010)
	6-9	0.028 (0.011)	0.035 (0.014)
		Nitrate + Ammonium	
Ridge	0-3cm	0.48 (0.08)	0.63 (0.08)
	3-6	0.23 (0.02)	0.18 (0.03)
	6-9	0.18 (0.04)	0.20 (0.02)
Flat	0-3	0.45 (0.11)	1.08 (0.20)
	3-6	0.21 (0.10)	0.44 (0.14)
	6-9	0.14 (0.10)	0.26 (0.07)