HARVESTING INTENSITY EFFECTS ON SOIL DYNAMICS AND EARLY GROWTH OF SITKA SPRUCE

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To my parents

and

Laurence.

'I have made a heap of all that I have found'

Nennius, Historia Brittonum.
In, Roman Britain and the English Settlements, p. 329.
The Oxford History of England, Oxford, 1963.

Declaration

I have compiled this thesis from my own research, except where otherwise stated and acknowledged. No part has been presented for a higher degree.

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Abstract

The influence of conventional (stem only) and whole tree (all above ground biomass) harvesting on soil characteristics and second rotation Sitka spruce (*Picea sitchensis* (Bong.) Carr.) growth was investigated on a peaty gley soil in Kielder Forest, Northumberland. One site was intensively studied in the third and fourth years after restocking. The full factorial experiment (established by the Forestry Commission and the Macaulay Land Use Research Institute) included three treatments; retention of harvest (± R), herbicide application (± H) and fertiliser additions (± F), giving eight treatments which were replicated in three randomised blocks. Of the treatments, the effects of ± R, ± H and their interaction were observed. Confounding effects of soil compaction resulting from the passage of machinery were reduced by driving harvesters between treatment assessment plots.

The total nutrient capital (N, P, K, Mg and Ca) and physical characteristics including bulk density, horizon depth and oven dried weight of the soil (LFH and upper O horizons) were determined annually. *In situ* mineralisation of inorganic nitrogen, fluctuations in soil moisture content, organic matter, and pH were recorded throughout the third growing season using capped corers. A vegetation survey (species type, biomass and nutrient content) was performed in August of the third growing season. Phenological and morphological characteristics measured in spruce included timing of bud flush, occurrence and length of lammas, duration and length of the leader extension and tree height. Foliar nutrient concentrations (N, P, K, Mg and Ca) were analysed throughout both growing seasons. At the end of the fourth growing season root depth and distribution were observed in relation to waterlogging and anaerobic soil depth.

Treatment did not consistently alter soil nutrient capital or annually measured soil physical properties. Compared to - R plots, residue retention reduced seasonal fluctuations in mean soil temperatures and moisture content, especially in the litter layer. Differences were greatest in the summer when temperatures were warmer and precipitation low. Net ammonification (88 kg N ha^{-1}) and total nitrogen mineralisation (90 kg N ha^{-1}) during the third growing season were not significantly affected by treatment. However, significantly greater nitrate was released in the LFH horizon of + R and + RH plots ($P < 0.039$). The presence of woody residue (which may trap downy seed) and increased availability of nitrate possibly explain the greater occurrence of *Chamerion angustifolium* (L.) in + R treatments. Net nitrogen mineralisation in

the organic horizons occurred in the order L > FH> O. The potential for nutrient uptake by spruce in the more nutrient rich areas was favoured by the high proportion of fine root (83.5 %) sampled in the LFH horizon. The results were followed by a series of laboratory incubations and controlled condition birch (*Betula pendula* Roth) bioassays.

Spruce growing in residue retained plots demonstrated significantly longer periods of shoot extension ($P = 0.046$) and greater leader lengths attributable to lammas ($P < 0.002$) during the third growing season. More favourable physical conditions afforded by the residue and greater nutrient availability may enhance initial growth. Similar differences were not observed the following year suggesting that the sheltering influence of residue had diminished. Tree height was not significantly affected by treatment throughout the experimental period. However, leader extension was significantly greater throughout the third growing season in + H treatments ($P = 0.020$). Foliar calcium concentration and content were significantly higher in + R treatments at the end of both growing seasons ($P \leq 0.041$ and $P \leq 0.015$, respectively). Consistent treatment effects were not observed for foliar N, P, K or Mg..

The initial results suggested that the growth of Sitka spruce was not affected detrimentally by whole tree harvesting. However, implications for long term productivity of spruce plantations growing on poor sites cannot be predicted. Reduced levels of foliar calcium and the absence of nutrient release from decaying above ground biomass found after whole tree harvesting may affect future yields.

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Abbreviations and Chemical Symbols

WT	Whole tree (with respect to harvesting)
CON	Conventional (with respect to harvesting)
FC	Forestry Commission
MLURI	Macaulay Land Use Research Institute
AET	Actual evapotranspiration
G.S.	Growing season
d.b.h	Diameter at breast height (1.3 m)
a.s.l.	Above sea level
n	Sample number
N	Nitrogen or Normal (with respect to solution strength)
P	Phosphorus
$K^{(+)}$	Potassium (ion)
$Mg^{(2+)}$	Magnesium (ion)
$Ca^{(2+)}$	Calcium (ion)
$Mn^{(2+)}$	Manganese (ion)
$Fe^{(2+)}$	Iron (ion)
$Al^{(3+)}$	Aluminium (ion)
$Zn^{(2+)}$	Zinc (ion)
$SO_4^{(2-)}$	Sulphate (ion)
H^+	Hydrogen ion
NH_3	Ammonia
NH_4^+	Ammonium ion
NO_3^-	Nitrate ion
C	Carbon
CO_2	Carbon dioxide
KCl	Potassium chloride
H_2SO_4	Sulphuric acid

Chapter 1

INTRODUCTION

1

1.1 Introduction

In 1992, over 150 countries signed the UN Framework Convention on Climate Change. This committed the United Kingdom to return its carbon dioxide (CO_2) emissions to the 1990 level by the year 2000. Consequently, alternative and efficient sources of energy are required to replace that proportion supplied by the combustion of fossil fuels. The use of biofuels, such as logging debris (foliage and small branches), provides a potential option (Alexander 1991; Olsson *et al.* 1996) which is already practised in some countries, including Sweden, Denmark and some areas of Canada.

Removal of all aboveground residue during harvesting and thinning may be associated with additional benefits. For example, sites cleared of debris are perceived to be easier to restock (Low 1985; Nelson and Dutch 1991) and the economics of some silvicultural operations, such as thinning, may be improved in the presence of suitable markets. Despite the silvicultural and financial advantages associated with total biomass removal, various proportions of residue are exported during current felling practises. The least amount of organic material is taken during conventional felling (CON) in which only stems are removed, leaving foliage, branches, stumps and roots on site. Depending on site conditions and management, the logging debris may be piled into rows, heaped and burnt or left where it falls. Removal of all aboveground material occurs during whole-tree harvesting (WT). Only stumps and roots remain at the site, while the branch and foliar biomass is chipped and removed. Similar site conditions result when whole trees are skidded to a fixed point for delimbing (Hendrickson *et al.* 1986). Complete removal of trees (above and below ground material) may also be practised for forest health reasons. For example, extraction of stumps and roots of Scots pine (*Pinus sylvestris* L.) and Corsican pine (*Pinus nigra* var. *maritima* Ait. Melville) sometimes occurs at Thetford Forest (East England). This procedure reduces the impact of the fungus, *Heterobasidion annosum*, which spreads through root contact (Greig 1984). However, the technique is uncommon and will not be discussed further.

In Britain, the cost efficiency of using modern felling machinery is increased by operating throughout the year (Greacen and Sands 1980). However, the harvesters apply heavy loads which can damage soft soils, especially when wet. Therefore the trees are often felled in a 'herring bone' fashion so that the crowns fall into bands (*Plate 1.1*). After snedding

(debranching or limbing), the stems are crosscut to timber specifications before extraction. The resulting swathes of logging debris form roadbeds which help to prevent machinery from sinking into the peat, causing soil damage, compaction and mixing. Banking the residue clears between approximately 40 (Titus and Malcolm 1991) and 90 % (Rosen and Lundmark-Thelin 1987) of the felled site of debris. Initially, these strips are akin to WT harvested areas and experience similar localised conditions.

Plate 1.1: The distribution of logging residue and cut stems shortly after clearfelling a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stand within Kielder Forest.

Harvesting and the removal of residue at clearfelling poses a potential threat to the sustained growth of successive rotations of conifers at some sites. In order to predict which areas will be detrimentally affected, it is important to understand the system dynamics after felling.

Nutrient cycling in forest ecosystems was first studied at the end of the last century. At the time, the exploitation of timber was generally perceived to be a negligible threat to nutrient losses and subsequent productivity (Ericsson 1994). It was not until the second half of the twentieth century that evidence was discovered in Sweden and Germany of decreasing forest growth following harvesting (Rennie 1955; Kostler 1956). Rennie (1955) and Kostler (1956) observed reductions in subsequent yields when repeated annual litter raking and removal of the forest floor for use in cow sheds and stables were performed in combination with timber production. Consequently, concerns for the long term productivity of forests increased. The policy of clearcutting and biomass removal was questioned again at the end of the 1960's when Likens *et al.* (1969) highlighted the potential effects of harvesting on water quality as well as nutrient losses via leaching. The results obtained from the Hubbard Brook catchment in New Hampshire, USA, (Likens *et al.* 1969) contrasted sharply with the low nitrate (NO_3^-) losses recorded by Cole and Gessel (1965) from nitrogen (N) poor Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in Washington. Further studies (Carey 1980; Proe and Dutch 1994) demonstrated that the export of above ground residue during WT harvesting accounted for large removals of nutrients from clearfelled sites. Advances in silviculture and the use of genetically improved stock with faster growth rates (Bowen and Nambiar 1984), are recognised as additional threats to the sustained productivity of forests as rotation lengths are reduced and harvesting frequency increases.

Immediate and long term changes in soil physical characteristics, nutrient availability and vegetation regrowth occur following harvesting and tree removal. The nature and duration of responses depends on site quality, tree species, intensity of residue retention and climate. Long term studies measuring tree growth and nutrient availability after different harvesting regimes are scarce but have been carried out in Sweden (Lundkvist 1988), New Zealand (Dyck and Skinner 1990) and North America (Cole 1988). To counter the paucity of data, experiments have been established over the past two decades. The following sections briefly describe nutrient dynamics occurring in mature forests and detail processes acting in temperate plantations during harvesting, re-establishment and growth of successive rotations. The literature reviewed includes results from studies performed in the temperate forests of Europe, North America, Australia and New Zealand.

1.2 Forest soil nutrient dynamics prior to felling

Rates of forest soil nutrient dynamics are determined by properties such as soil temperature, moisture (Gadgil and Gadgil 1978; Vitousek 1981; Waring and Schlesinger 1985), acidity, substrate quality (Gadgil and Gadgil 1978; Vitousek 1981; Smethurst and Nambiar 1990b)

and geology. The influence of each factor varies with soil depth and horizon, resulting in corresponding changes in rates of nutrient mineralisation and immobilisation (Boone 1992).

Forest soils represent an important pool of nutrients and contain at least 85 % of the total N capital in most temperate forest ecosystems (Cole and Rapp 1981). Yet the majority of this resource is inert and unavailable for uptake or leaching. In natural forests and unfertilised forest systems, the main source of actively mineralisable N originates from within the litter and organic matter (Aber and Melillo 1980; Jurgensen *et al.* 1992). Therefore, disturbances and changes in management practice which remove the forest floor can have drastic implications for N availability.

The timing and quantity of net N mineralisation in relation to plant requirements is a key process governing the successional development and the climax productivity of the system (Clark and Rosswall 1981; Melillo and Gosz 1983). The factors controlling N dynamics within closed canopy forest ecosystems include successional stage (Rice and Pancholy 1972; Vitousek and Reiners 1975), stand age (Johnson 1992; Emmett *et al.* 1993) and species composition). The role of these factors has been extensively reviewed (Cole 1981; Gosz 1981; Berg 1986; Carlyle 1986) and will not be discussed further.

1.3 Mechanical disturbance and physical site modifications during harvesting

Clearfelling a stand of trees upsets the ecosystem dynamics. For example, Ryan *et al.* (1992) observed that up to 65 % of a watershed area was disturbed and 25 % of the forest floor was removed during WT harvesting of a hardwood forest in North America. However, the extent and impact of the mechanical disturbance are affected by soil type and time of felling. For example, heavy machinery is unlikely to damage frozen soils and has little influence on sands (Cortina and Vallejo 1994) or very dry material. The greatest effects are sustained on soft wet sites, especially within the surface horizons (top 10 cm depth) under skidder trails (Hatchell *et al.* 1970). Modifications resulting from the passage of heavy machinery include soil compaction (Greacen and Sands 1980; Skinner *et al.* 1989; Johnson *et al.* 1991), substantial increases in bulk density (Skinner *et al.* 1989; Johnson *et al.* 1991) decreases in organic horizon thickness (Johnson *et al.* 1991), and mixing of organic and mineral horizons (Huntingdon and Ryan 1990; Ryan *et al* 1992). Lateral movement and dislocation of soil horizons may lead to declines in site quality, as organic matter and nutrient pools are redistributed and access by roots is reduced (Skinner *et al.* 1989).

Felling of standing trees changes the soil microclimate, especially within the upper organic horizons. Prior to harvesting closed forest canopies intercept precipitation and solar radiation, reduce wind speed above the soil surface and modify air temperatures. Moisture inputs to the forest floor occur largely as stemflow or throughfall, while evapotranspiration accounts for some of the losses. During clearfelling, the tree canopy is removed and ground vegetation is crushed or damaged resulting in a bare restock site subject to different climatic conditions. Exposure of the forest floor to direct precipitation inputs is likely to increase nutrient leaching to the ground water, surface runoff (Likens *et al.* 1977; Bormann and Likens 1979; Rosen 1984; Adamson *et al.* 1987; Adamson and Hornung 1990) and soil erosion (Likens *et al.* 1977; Bormann and Likens 1979; Mahendrappa and Kingston 1994). Cessation of evapotranspiration and interception losses may cause the watertable to rise on poorly drained soils, and increase forest floor moisture levels (Bormann *et al.* 1974; Rosen 1984; Pyatt and Anderson 1986) by up to 50 % compared to uncut plantations (Smethurst and Nambiar 1990b).

Fluctuations in soil moisture content are partly influenced by the intensity of biomass removal. After WT harvesting, moisture levels in the bare surface horizons vary depending on precipitation inputs and evaporation following warming of the forest floor by direct sunlight (Smethurst and Nambiar 1990b; Cortina and Vallejo 1994). At Kielder Forest, Titus and Malcolm (1991) recovered considerably greater volumes of leachate from bare soils than from CON felled areas. The reductions in volume collected under residue were attributed to interception of precipitation by logging debris and the greater water holding capacity of the litter present under residue mats (Titus and Malcolm 1991). In addition, evaporative losses from the upper soil horizons are mediated by the presence of a logging debris mulch (Ballard and Will 1981; Farrell *et al.* 1981; Squire *et al.* 1985; Titus and Malcolm 1991) resulting in decreased diurnal and seasonal fluctuations.

Modifications in soil temperature occur post felling and are mediated by the degree of residue retention. Although the differences in mean values between standing and cut forests may be minor (Smethurst and Nambiar 1990b), a wider range of temperatures has been recorded in the upper soil horizons of harvested areas (Cortina and Vallejo 1994). The seasonal and diurnal fluctuations are moderated by residue retention and increasing soil depth (Smethurst and Nambiar 1990b) resulting in a more stable temperature environment in CON harvested areas (Farrell *et al.* 1981; Smethurst and Nambiar 1990b). In bare soils actual hourly mean temperatures during July and August have been recorded to increase by 6 to 8 °C, while the peak temperatures were attained 2 hours later than under logging debris (Mahendrappa and

Kingston 1994). Mahendrappa and Kingston (1994) recognised consistently similar trends at lower depths which they considered to have the potential to enhance weathering in the subsoil.

In exposed areas, the removal of the tree canopy and ground vegetation at felling increases the wind speed above the soil surface. However, the extent of this change is influenced by the harvesting method. Where residue is retained the wind speed decreases, compared to bare soils, and the level of shelter afforded by the debris increases with increasing wind speed (Proe and Dutch 1994).

Temporal changes in the thickness of the logging debris result in reductions in visible cover from, for example, 40 to 10 % within 6 years after felling (Kardell 1992). Consequently, the physical or barrier effect resulting from the residue will be most important during the early regeneration phase after clearfelling. Physical differences within the forest floor between CON and WT harvested areas will also diminish as ground vegetation cover increases and the crown diameter of second rotation trees expands.

1.4 Modifications in soil chemistry and site nutrients following clearfelling

Prior to harvesting closed canopy stands, low levels of nutrients are added to the soil continuously. The inputs are present in throughfall, stemflow, litterfall, root turnover and root exudates. However, the source of nutrients is removed after felling, and replaced by a single quantity of logging residue. Depending on the intensity of harvesting, the biomass of residue retained at the site, the nutrient capital and subsequent timing and rate of nutrient release from the logging debris differ.

1.4.1 Soil acidity and cation exchange capacity

The acidity of most forest soils differs considerably between each horizon but fluctuates only slightly (seldom more than 1 pH unit) with seasonal changes (Pritchett 1979). Following clearfelling of forests rapid and significant increases in pH usually occur within the upper soil horizons (Nyvkist and Rosen 1985), although slight drops have been recorded (Adamson and Hornung 1990). The decreases in acidity are thought to arise through two processes. The first is the combination of free hydrogen ions (H^+) with ammonia (NH_3), produced during the mineralisation of organic N, to form ammonium ions (NH_4^+). Secondly, potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}) ions and other cations released during the decomposition of organic debris neutralise soil acids (Nyvkist and Rosen 1985). The cations are taken up by growing trees in exchange for H^+ ions and become concentrated in the foliage. Consequently the acidification and neutralising processes which occur during conventional forestry practice (including CON harvesting) more or less balance each other for each stand

rotation. In contrast, removal of base rich needles during WT harvesting depletes the source of cations which may result in soil acidification (Nilsson *et al.* 1982). Of the two processes outlined above, Nyvkist and Rosen (1985) emphasised that the increases in pH recorded after clearfelling were too high and too rapid to result merely from the release of base cations. It was suggested that transformations of humic substances were probably more important in determining soil acidity.

Exchange sites are generated when organic matter undergoes decomposition to form fulvic and humic acids which have much higher exchange capacity than the original material (Williams *et al.* 1978). Base cations join to the exchange sites, but are displaced by H^+ ions produced during nitrification of NH_4^+ (Krause 1982). Consequently, in soils where NO_3^- is produced after clearcutting of forests, there is a potential for NO_3^- and base cation losses through leaching. This appears to be related to the rate of nitrification (Likens *et al.* 1969). In addition, H^+ ions increase the solubility and mobility of acid cations such as aluminium (Al^{3+}), iron (Fe^{2+}), manganese (Mn^{2+}) and zinc (Zn^{2+}) (Maliondo 1989; Maliondo *et al.* 1990). However, the leaching of a given cation is strongly controlled by the amount of that cation on soil exchange sites, the selectivity coefficients governing the exchange of the cation with other cations (Reuss 1983) and the total cation (or anion) concentration in the soil.

1.4.2 Removal of nutrients and organic matter in logging residue

Removal of biomass at harvesting is accompanied by associated losses of nutrients. The export of nutrients is disproportionately greater during WT compared to CON harvesting (Weetman and Webber 1972; Nyvkist 1977; Alban *et al.* 1978; Carey 1980; Maliondo *et al.* 1990; Fahey *et al.* 1991a; Miller *et al.* 1993) due to the occurrence of higher concentrations in the small twigs and foliage (Hendrickson *et al.* 1986; Titus and Malcolm 1991). Although the removal of nutrients at harvesting can adversely affect the fertility of some forest soils, the influence on total ecosystem nutrients is considered to be minimal at some sites (Miller *et al.* 1980). A review by Dutch (1993) summarises the quantities of biomass and nutrients removed after CON and WT harvesting of broadleaf and conifer tree species.

In addition to the losses of nutrients at clearfelling, soil organic matter may be greatly affected by harvesting and the intensity of residue removal. Berg and Staaf (1983) measured reductions in organic matter content and horizon depth 3.5 years after WT harvesting a 120 year old Scots pine stand compared to conventionally felled areas and similar modifications were observed by Hendrickson *et al.* (1986). The soil organic matter was predicted to decrease to a minimum (about 50 % of the original content) approximately 15 years after clearfelling, before accumulating slowly (Covington 1981). The reduction was thought to

result from loss of litter inputs and accelerated decomposition following harvesting (Bormann and Likens 1979; Covington 1981). However, during a review by Johnson (1992) the link between losses of soil organic matter and harvesting is questioned, as there was little firm evidence of decreases following disturbance. In addition, Huntingdon and Ryan (1990) found no detectable change in N or C content in the forest flooor of mineral soil 3 years after harvesting. As organic matter is important as a source of C for microbial immobilisation of nutrients (Vitousek and Matson 1985) and in regulating the soil cation exchange capacity and the ability to retain water (Brady 1990), the potential for removals during WT harvesting may modify soil processes. For example, removal of Radiata pine (*Pinus radiata* D. Don) litter by raking significantly lowered cation exchange capacity and levels of exchangeable soil Ca, Mg and K (Ballard and Will 1981).

Localised reductions in nutrient capital and organic matter may follow CON harvesting where piling or banking is practised. Redistribution of biomass concentrates logging residue into areas representing between 10 to 15 % (Rosen and Lundmark-Thelin 1987) and 66 % (Titus and Malcolm 1991) of the total clearfelled area, depending on management regime. During the harvesting of Sitka spruce plantations in upland Britain, Titus and Malcolm (1991) observed that the residue was systematically distributed at a rate of 49 t ha^{-1} over 66 % of the site, and contained 219, 20 and 71 kg ha^{-1} N, P and K, respectively.

1.5 Decomposition of residue and nutrient dynamics after clearfelling

The method and timing of nutrient release from residue depends on the element, its source and the microclimate. Rapid inputs of nutrients to the soil occur through leaching from aboveground logging debris, whereas decomposition and mineralisation within the residue provides further nutrients through time. Differences in nutrient availability after CON or WT harvesting arise due to the varying quantities of organic matter substrate present and modifications in microclimatic conditions.

1.5.1 Leaching from residue

Emmett *et al.* (1991a) recorded enhanced inputs of soluble organic N, P and K in throughfall under residue relative to incoming rain. The amount of N leached is generally small (although losses of 10 to 25 % of the total N have been recorded in some litters) and the duration of this stage is short (Berg and Staaf 1981). In contrast, Rosen and Lundmark-Thelin (1987) recorded decreased concentrations of inorganic N in precipitation passing through the woody debris during the first two years after clearfelling. This was considered to be a consequence of the high C/N ratio (> 75) of residue leading to a large demand for N by microbes during decomposition (Staaf and Berg 1982).

1.5.2 Decomposition of foliage and woody material

The decomposition of woody material and foliage present after harvesting involves the breakdown of residue into smaller particles by an abundance of soil animals, ranging from microscopic nematodes to large earthworms. The resulting fragmentation and mixing of litter into the upper layers of the soil occurs during the first year after abscission in most forests types (Waring and Schlesinger 1985). Once incorporated into the deeper organic horizons the litter is inoculated with bacteria and fungi (Swift *et al.* 1979) and decomposition rates may increase (Binkley 1984). The fungal hyphae penetrate the cell structure of plant tissues, while the bacteria predominantly colonise the litter surface (Waring and Schlesinger 1985). Unfortunately, the activity and population size of soil organisms cannot be accurately determined as proportions may be inactive, large seasonal variations may occur depending on the microclimate and it is difficult to distinguish between live and dead fungal hyphae (Baath and Soderstrom 1982). However in the conifer forests of northern Europe, 95 % of the decomposition is considered to be dominated by microbes (Persson 1993).

The rate of breakdown is influenced by many factors including climate (Meentemeyer 1978; Abbot and Crossley 1982; Attiwill 1986), nutrient availability (Berg and Staaf 1980; Harmer and Alexander 1985; Woods and Raison 1983; Hendrickson *et al.* 1985), tissue chemistry (Meentemeyer 1978) and concentrations of organic fractions in the litter (Fogel and Cromack 1977; Berg and Staaf 1981). Additional variables considered important in the decay of branch and stem material include the activity of colonising fungi and invertebrates (Rayner and Boddy 1988), density of the substrate (Yoneda 1985), moisture content of the wood (Ericsson *et al.* 1985), diameter of the woody tissue and the position relative to the ground surface (Harmon *et al.* 1986; O'Connell 1997). Of these factors, early research indicated that actual evapotranspiration (AET) was several orders of magnitude more important in predicting the rate of litter decomposition than substrate quality (Meentemeyer 1978). In agreement with this observation, decay rates of foliar and woody litter from a clearcut in the southern Appalachians reduced considerably in excessively dry conditions (Abbott and Crossley 1982). However as the AET increased, the influence of litter quality was thought to become more important (Meentemeyer 1978).

The rate of litter decomposition can be explained by a double exponential model (Louisier and Parkinson 1976; O'Connell 1997) with two distinct phases of mass loss. Initial losses of labile components are rapid (O'Connell 1997) and are influenced by nutrient availability and the presence of light organic fractions. For example, higher nutrient concentrations initially stimulated mass loss in Scots pine litter (Berg and Staaf 1980), and positive linear

relationships have been recorded between weight loss and initial concentrations of N and P in leaves of three *Eucalyptus* species (Woods and Raison 1983). In Radiata pine litter, the first 3 months decomposition were attributed to the degree of sclerophylly and lignification, which were in turn related to the nutrient concentrations within the substrate (Maheswaran and Attiwill 1987). Similarly, the removal of nutrients (N, P, K and Mg) available for decomposer organisms during WT harvesting has been recorded to reduce decay rates of litter (Hendrickson *et al.* 1985). As decay proceeds and the extractable substances are lost, structural constituents such as non-cellulose polysaccharides (hemicelluloses), celluloses, and lignins remain (Berg and Staaf 1980; Berg *et al.* 1982a). The relative increases in the heavier organic fractions influence subsequent immobilisation and release of nutrients (Berg and Staaf 1981). Compounds such as lignin inhibit decomposition and N mineralisation (Melillo *et al.* 1982; Berg *et al.* 1984) by forming stable nitrogenous compounds, reducing N availability to decomposer organisms (Berg *et al.* 1984). The low decomposition rates of the structural constituents, becomes the factor controlling the second stage of breakdown (McClaugherty *et al.* 1985; Maheswaren and Attiwill 1987).

Differences between the decomposition rates of needle litter present after CON and WT harvesting result from the retention of green foliage during stem only removal. The fresh needles have a higher specific weight than senesced brown foliage and the intact cuticles of green needles are expected to decrease nutrient leaching losses (Tukey 1970) and retard the attack of decomposers lowering short term decomposition rates. However, Ballard and Will (1981) recorded faster decomposition in green Radiata pine litter than in brown needles after incubation for one year, which was probably due to the completion of the initial breakdown of needles and the greater availability of nutrients for microbial action. As applications of fertiliser greatly modify the nutrient balance within the forest floor, decomposition rates of litter may change accordingly. Titus and Malcolm (1987) measured decreases in mass loss of 2 year old Sitka spruce litter after fertiliser application which was explained as the response to a lack of available C as an energy source. At Kielder Forest, available C was considered to be a greater limitation to decomposition than N, P and K levels in litter (Titus and Malcolm 1987).

Decomposition of branches is delayed as diameter increases (or as surface area/volume ratio decreases) (Fahey *et al.* 1991b; O'Connell 1997). The reduced decay rate arises due to the slow colonisation of the substrate and is most prominent in the early stages of decomposition (Abbot and Crossley 1982; Yoneda 1985; Harmon *et al.* 1986). However, the low density of bole wood and probably low extractive contents in the tissue (i.e. resins) favour rapid decay of very large diameter substrates and negate the surface to volume effect (Fahey *et al.* 1991b).

The pattern of decay and nutrient release in woody residues in contact with the ground and those suspended above the soil surface differ. Fahey *et al.* (1991b) recorded that N concentrations in ground residue increased during the first 4 years of decay, whereas decreases were recorded for suspended branches. Ten years after felling, nutrient release from the woody residues generally followed the order K>Ca=P>N while net N accumulation was observed except in the smallest size class (<0.5 cm) (Fahey *et al.* 1991b). After 10 years N and P begin to be released from the woody parts and branches (Staaf 1984).

The invasion of ground vegetation after harvesting may inhibit decomposition processes through the suppression of biological activity following plant uptake of moisture (Fisher and Gosz 1985) and nutrients (Gadgil and Gadgil 1971) or the production of allelopathic chemicals by mycorrhizal fungi (Gadgil and Gadgil 1971; 1975).

1.5.3 Mineralisation and immobilisation of nitrogen

Many techniques have been devised to measure field rates of mineralisation and immobilisation (see *Chapter 3.1*). However, it is difficult to test the reliability of the results obtained due to the unknown effects of the assay conditions in various soils (Raison *et al.* 1987). Disturbance during sampling and analysis causes alterations of physical structure, moisture content and/or rhizosphere processes. As all the procedures used to determine nutrient release are associated with different artefacts, comparison of absolute quantities of mineralised nutrient should be made with caution (Raison *et al.* 1987). The processes thought to control mineralisation of nutrients in the forest floor (including soil temperature, moisture and substrate quality) have been extensively reviewed (Cole and Rapp 1981; Waring and Schlesinger 1985; Carlyle 1986). In the following section, changes in nutrient release rate resulting from physical and chemical modifications to the forest floor after CON and WT harvesting have been detailed with an emphasis towards N dynamics.

Laboratory and *in situ* incubations indicate that positive relationships exist between N mineralisation, and substrate temperature and moisture content within certain ranges (Matson and Vitousek 1981; Tietema *et al.* 1989; see *Chapters 4.3.1*). Therefore, following harvesting changes in field rates of inorganic N release might be expected to respond to fluctuations in microclimate accordingly. However, *in situ* studies have revealed increased (Johnson *et al.* 1985; Vitousek and Matson 1985; Frazer *et al.* 1990; Smethurst and Nambiar 1990b), unchanged (Burger and Pritchett 1984; Hendrickson *et al.* 1985; Rosen and Lundmark-Thelin 1987) and decreased (Bird and Chatarpaul 1988) rates of soil organic matter decomposition, ammonification and nitrification depending on climate, soil type and species of tree felled. The environmental conditions resulting after harvesting can increase

total bacterial populations (Lungren 1982) and numbers of nitrifying bacteria (Todd *et al.* 1975), reduce total and active fungal biomass and cause possible changes in fungal species composition (Baath 1980). In response to the greater numbers of bacteria, nematode populations grow (Sohlenius 1982) and the numbers of litter feeding enchytraeids rise dramatically with inputs of organic matter. However, Clarholm *et al.* (1981) recorded no obvious relationship between standing biomass of bacteria and substrate temperature or moisture content implying that the enhanced mineralisation rates recorded were not caused by greater microbial populations. In this case, microbial activity probably alters in response to changes in substrate chemistry. An additional modification which arises after tree removal and the cessation of photosynthetically derived inputs in root exudates, is the reduction of available C (Fisher and Gosz 1985). Several studies (Gadgil and Gadgil 1975; Bäath 1980; Hendrickson and Robinson 1984) have indicated that this may have as great an impact on microbial populations as surface litter inputs. Where increased bacterial populations were observed they were short lived, and numbers returned to pre-felling levels within 3 years (Edwards and Ross-Todd 1983; Lundkvist 1983).

In addition to microclimatic factors, the activity of the soil microorganisms responsible for N mineralisation is thought to be regulated by decomposition of the substrate (Berg and Staaf 1981) and subsequent availability of N and an energy source (C). However, additions of mineral N do not necessarily increase microbial activity (Williams 1972). Interactions between C and N in controlling inorganic N release have resulted in various parameters being used to predict mineralisation. These include initial N concentrations (Berg and Ekbohm 1983; Van Cleve *et al.* 1986; Ross *et al.* 1995), the total C/N ratio (Berg and Staaf 1981; Adams and Attiwill 1982; Vitousek 1982; Vitousek and Matson 1985), the C/N ratio of a particular fraction of the litter (Burger and Pritchett 1984), available C/available N ratio (Flanagan and Van Cleve 1983), total C (Ross *et al.* 1995) and labile organic C (Riha *et al.* 1986). In addition, N mineralisation has been found to be more closely correlated to C/N ratio when expressed as a proportion of the total N (N mineralised/N total ratio) (Sollins *et al.* 1984). As decomposition proceeds the quantity of the substrate and the quality of the contents change. Over a period of 15-16 years after harvesting Scots pine and Norway spruce (*Picea abies* (L.) Karst) forests in Sweden, C and N in the humus layer decreased markedly and were associated with a fall in the C/N ratio (Olsson *et al.* 1996). Similarly, studies at sites of different ages in the northern hardwood forests of America indicated reductions in forest floor mass and N content of between 30 and 50 % within 5 to 20 years of harvesting (Covington 1981; Federer 1984). Therefore, management practices which influence the quantity or composition of organic matter retained at the site are expected to affect subsequent mineralisation potential.

Both NH_4^+ and NO_3^- are produced within the forest floor during mineralisation post harvesting. However the proportions of each species of inorganic N are not significantly correlated (Hart *et al.* 1994) and vary depending on site factors. A number of studies have shown that NH_4^+ is the dominant form of dissolved inorganic N in the soils of British conifer plantations (Carey *et al.* 1981; Williams 1983; Adams 1986; Carlyle and Malcolm 1986; Harmer and Alexander 1986). The presence of NO_3^- in conifer forest soils is generally considered to be low due to the acidic nature of the peat which limits nitrifier activity (Williams 1995), low soil temperatures, high moisture contents (Heal *et al.* 1982), intense microbial competition for NH_4^+ (Heal *et al.* 1982; Carlyle 1986), inhibitory organic compounds (Olsson and Reiners 1983) and allelochemicals (Rice and Pancholy 1972), uptake of NO_3^- by vegetation (Carlyle 1986) and possibly NO_3^- adsorption (Heal *et al.* 1982). Furthermore, the availability of C energy sources may determine N uptake by ammonifying heterotrophs (Alexander 1977) so that additions of C in logging residue increase competition for N and reduce nitrification rates (Van Miegroet *et al.* 1990). As the C source becomes limiting heterotrophic competition for NH_4^+ declines and nitrification rates increase.

Although early results suggested that nitrification does not occur in acid peaty forest soils of the British uplands, more recent evidence disputes this (Harmer and Alexander 1985; Adamson *et al.* 1987; Stevens and Hornung 1988; Williams 1995). At Beddgelert Forest in north Wales, inorganic N in leachates following clearfelling was dominated by NO_3^- (Stevens and Hornung 1988). The small NH_4^+ concentrations probably arose due to the retention of cations by the soil exchange complex, fixation by clay minerals, root uptake or nitrification. Preferential uptake of NH_4^+ by species such as Sitka spruce is also possible. However, this is unlikely as the proportion of NH_4^+ to NO_3^- does not change after felling as might be expected if the trees were taking up more NH_4^+ than NO_3^- (Gosz 1981). Williams (1995) detected levels of NO_3^- which were significantly correlated with the pH in soils after felling Sitka spruce in South Wales. It was suggested that the ability to nitrify in acid condition arose from the adaptation of bacteria to the slow depressions in pH which develop as the tree crop becomes established. Alternatively, Emmett *et al.* (1991a) proposed that acid tolerant nitrifiers were responsible at Beddgelert Forest, whereas a heterotrophic nitrification pathway may be present in some soils which allows nitrifiers to convert dissolved organic N directly to NO_3^- (Adams 1986; Killham 1987). As organic N is an important component of the total dissolved N (Harmer and Alexander 1985; Rosen and Lundmark-Thelin 1987), this pathway could be very important in some forest soils (Stevens and Wannop 1987). In some peat soils (Afan, southern Wales), the small levels of NO_3^- (2 kg N ha^{-1}) may have been derived from atmospheric inputs (Williams 1995).

Harvesting changes the inorganic N content of the forest floor and underlying soil, generally increasing inorganic N availability (Vitousek and Matson 1985; Frazer *et al.* 1990; Smethurst and Nambiar 1990b; Stevens and Hornung 1990) to soil microorganisms and plants. However, the duration of stimulated mineralisation varies. Stevens and Hornung (1990) recorded higher concentrations of inorganic N for up to 14 months after harvesting, whereas Frazer *et al.* (1990) measured increased annual rates of mineralisation for 5 and 17 years after clearfelling a mixed conifer stand (49 and 31 kg ha^{-1}, respectively) compared to uncut areas (12 kg ha^{-1}). After clearfelling a Radiata pine plantation, Smethurst and Nambiar (1990b) noted higher mineralisation rates for 3 years post harvesting. However, mineralisation was preceded by a 4 month lag period in the litter layer and 12 months in the mineral soil. Delays in nitrification after harvesting have been noted by Davidson *et al.* (1992) and have been interpreted as a response to increases in nitrifier population sizes that were small initially (Vitousek and Matson 1985; Van Miegroet *et al.* 1990) or the inactivation of allelopathic compounds (Vitousek and Matson 1985).

The intensity of residue retention influences soil ammonification and nitrification. The favourable microenvironment and increased substrate availability experienced under residue increases microbial activity, accelerates turnover of inorganic N (Squire 1983; Rosen 1986; Frazer *et al.* 1990; Smethurst and Nambiar 1990b; Stevens and Hornung 1990), stimulates nitrification (Stevens and Hornung 1990; Emmett *et al.* 1991a) and alters the duration of response (Stevens and Hornung 1990). In contrast, increased turnover of N (Vitousek and Andariese 1986) or larger NO_3^- pool sizes and losses from the soil (Vitousek and Matson 1985) may be recorded after the removal of surface organic material during intensive site preparation. However, the enhanced mineralisation rates in forest soils following different harvesting procedures may be short lived. For example, Smethurst and Nambiar (1990b) observed no significant differences between mineralisation rates in soils experiencing different management of residue and litter three years after felling Radiata pine. Additional evidence collected 5 years after harvesting demonstrated that there were no differences in inorganic N release from the organic horizons of Radiata pine stands experiencing WT, CON harvesting and CON harvesting with added logging residue (Ross *et al.* 1995).

1.6 Short term nutrient losses from the site/soil after clearfelling

Depending on the timing and quantities of nutrient becoming available, N released from decaying above and below ground residue could be lost from the site through leaching, erosion, volatilisation or denitrification. These processes can be reduced if nutrients are

taken up by ground vegetation, retained in the logging residue until later stages of stand development or translocated vertically downwards to the mineral soil.

1.6.1 Leaching

Hydrologic losses of nutrients from the soil, including dissolved organic N, NH_4^+, NO_3^-, K, P, Fe, Ca, Mg and Al (Kimmins and Feller 1976; Vitousek and Melillo 1979; Adamson *et al.* 1987; Mann *et al.* 1988; Stevens and Hornung 1988; Adamson and Hornung 1990; Stevens *et al.* 1995) have been recorded to increase immediately after forest harvesting. The rise in exports results from enhanced volumes of water leaving the site (Adamson *et al.* 1987) and higher concentrations of mobile ions in the soil (Adamson and Hornung 1990). Depending on the site and the nutrient, losses from clearfelled sites differ through time. For example, Adamson and Hornung (1990) and Stevens *et al.* (1995) recorded peaks in NO_3^- concentrations one year after felling whereas K and P were highest during the second year. Although NO_3^- levels returned to unharvested forest values in the fourth year, K and P did not return to initial levels during the six year period (Adamson and Hornung 1990). In contrast, results from sites across America demonstrated that the increased leaching losses were short lived and that levels returned to undisturbed stand values within 3 years (Mann *et al.* 1988). As the duration of elevated nutrient export is relatively brief at many sites, hydrologic losses are expected to be minor compared to removals in harvest biomass (with the possible exceptions of Ca and K) (Mann *et al.* 1988).

Of the nutrients lost after harvesting, the leaching of large quantities of NO_3^- from some sites has caused concern, as stream water quality declines, causing the survival and viability of populations of fish and aquatic invertebrates to fall. Modern felling practices have been adapted to reduce changes in water chemistry, by clearcutting small blocks or strips and retaining buffer strips at least 10 m wide by the side of water courses. However, the NO_3^- ion is highly mobile due to its large diffusivity, low buffer power and lack of adsorption onto the solid phase of the soil (Van Miegroet and Cole 1984). Therefore, NO_3^- losses are often recorded following harvesting despite the precautions adopted during felling. Losses are maximised where;

- excess mineralisation occurs,
- mineralised N is rapidly converted to nitrate,
- water availability in the soil is sufficient to move nitrate to streams or ground water without causing waterlogging (Vitousek 1981), and
- root uptake is low in the presence of nitrification, for example, at low soil temperatures (< 7°C) (Stevens *et al.* 1993) or after removal of vegetation using herbicide (Vitousek and Matson 1985).

Losses of NO_3^- from conifer forest soils of the British uplands were considered to be low as nitrification was minimal (Williams 1983; Miller *et al.* 1990). However, measurements recorded in Wales (Stevens and Hornung 1988, 1990; Williams 1995) (see *Chapter 1.5.3*) demonstrated nitrification and a potential for leaching losses. In addition, results from Kershope Forest (Cumbria) demonstrated rapid increases of NO_3^- during the first 3 years after forest disturbance (Adamson and Hornung 1990). Despite these observations, several factors are thought to mitigate leaching of nitrate from clearfelled sites including low net N mineralisation rates (caused by either N immobilisation or low gross N mineralisation), lags in nitrification (probably caused by low initial populations of nitrifying bacteria or the allelochemic inhibition of nitrification) (Vitousek *et al.* 1982) and competition for NH_4^+ among heterotrophs, plants and nitrifiers (Riha *et al.* 1986). In addition, Vitousek *et al.* (1982) observed that the presence and length of lags in nitrification were inversely correlated with the mean concentration of mineral N in the soil. Therefore, N retention within disturbed forest ecosystems may increase where available N is low prior to disturbance (Vitousek *et al.* 1982).

Leaching losses of NO_3^- following harvesting are also influenced by the intensity of residue retention. At some sites, the modified soil moisture, temperature and available substrate afforded by residue promotes mineralisation and leaching compared to that in bare soils (Rosen and Lundmark-Thelin 1987; Stevens and Hornung 1988; Emmett *et al.* 1991a). Emmett *et al.* (1991a) isolated the effects of microclimatic factors from the changes in substrate quality by applying an inert artificial residue cover to the forest floor. An increase in NO_3^- loss demonstrated that the improved environmental conditions experienced beneath the residue were critical in enhancing nitrification. Inputs of residue during harvesting can reduce the potential for accelerated mineralisation and leaching of N by immobilising NH_4^+ and NO_3^- (Meentemeyer and Berg 1986). The organic matter of the soil has a large potential to retain inorganic N by means of biotic (microbially mediated) and abiotic (chemical) reactions (Johnson 1992). The abiotic process incorporates NO_3^- by condensation reactions which occur between phenols and derivatives, originating from partially degraded lignin and fungal products with either amino acids or NH_4^+. In contrast, Mann *et al.* (1988) did not record any major effects of harvesting procedure on leaching of nutrients or volumes of runoff from a range of hardwood and softwood forests in the U.S.

1.6.2 Denitrification and volatilisation

Leaching from the forest floor accounts for only a proportion of the annual losses of N. Despite this, few studies have considered denitrification and volatilisation of N from forest

soils, largely because relatively low nitrification rates (perceived for acid soils) and acid soils do not favour these processes, respectively. However at Kershope Forest in Northumberland, loss of N from the soil through denitrification was of approximately the same order as that lost through leaching (Adamson *et al.* 1987) and are of comparable magnitude to pollutant inputs (Ineson *et al.* 1991).

Denitrification is the loss of N_2 and nitrous oxide (N_2O) gases from the soil after the reduction of NO_3^- and nitrite (NO_2^-) anions by microbes. It occurs under wet conditions when all or part of the soil is anaerobic (Rowell 1994). As the process is driven by the availability of NO_3^-, any disturbance to the soil which enhances nitrification may increase denitrification. In addition, changes in substrate quality alter microbial activity and rates of N_2 and N_2O loss. For example, Bormann and Likens (1979) suggested that root and litter material retained after harvesting acts as an energy source for the heterotrophs responsible for denitrification. Consequently, large losses of gaseous N_2O and N_2 can occur following harvesting compared to that from an undisturbed forest. Dutch and Ineson (1990) and Ineson *et al.* (1991) estimated annual losses of 1 to 3.2 kg N ha^{-1} y^{-1} for a standing Sitka spruce forest in Northumberland, whereas losses form clearfelled sites increased to between 9 and 40 kg N ha^{-1} y^{-1} during the first 2 years after harvesting. The losses returned to pre-felling levels 4 years after felling. Competition for nitrate between heterotrophs and plant roots can reduce denitrification losses. Therefore, reductions in vegetation re-establishment by herbicide application eliminates a nitrate sink and increases denitrification (Vitousek and Matson 1985).

Loss of N through volatilisation is common under alkaline conditions when NH_4^+ ions are converted to ammonia (NH_3) in solution, which can then be released into the soil atmosphere (Rowell 1994). In the wet climate of Britain volatilisation losses are likely to be less than in a more continental climate, while the acid forest floor found in conifer forests does not encourage conversion to NH_3.

1.6.3 Prevention of nutrient losses by trees and ground vegetation

Invasion of clearfelled sites by ground vegetation can be beneficial as the potential for available nutrients to be lost from the site is reduced by plant uptake. However, the regrowing vegetation offers newly planted or regenerating trees competition for resources which may result in nutrient deficiencies or reduced growth. As the successive tree crop grows and canopy closure is attained the ground vegetation is slowly suppressed by reduced light availability. The following section outlines patterns of vegetation establishment following clearfelling, the quantities of nutrients accounted for by plant uptake and the detrimental

effects to trees resulting from competition. Long term nutrient availability, growth and productivity are detailed in *Chapter 1.7.*

Establishment of ground vegetation on clearfelled sites and the species diversity are influenced by the intensity of residue retention. In the absence of residue, the bare soils are suitable for colonising vegetation (Weetman and Webber 1972; Nyvkist 1977), whereas logging debris can alter the seedbed and radiation environment. Fahey *et al.* (1991a) recorded twice the accumulation of biomass on WT harvested sites compared to CON felled areas. During the same study, Stevens and Hornung (1990) recorded a negative correlation, 2 to 3 years after felling between vegetation regrowth and the level of residue retention. The differences were attributed to the suppression of vegetative regrowth by residue present on the forest floor. However 4 years after felling, the physical barrier effect of the residue had diminished allowing vegetation to become established. The presence of logging debris at a site in North Wales also influenced species diversity by impeding the growth of grasses and sedges so that mosses constituted a higher proportion of total biomass in the CON harvested areas (Fahey *et al.* 1991a). However, the higher nutrient concentrations of plants grown in CON felled plots suggested that the fertility in these soils was greater. Similarly, the greater abundance of ruderals and tall herbs in CON harvested areas shortly after felling, indicated higher soil nutrient availability with residue retention (Kardell 1992).

Some of the nutrients released following clearfelling accumulate in trees and ground vegetation (Emmett *et al.* 1991b; Fahey *et al.* 1991a) resulting in a negative correlation between inorganic N concentration in soil water samples and vegetation cover in WT harvested plots (Stevens and Hornung 1990). The relationship was attributed to the rapid re-establishment of vegetation and the lack of a N source in felling debris. As the biomass of the plants increases, retention of nutrients at the site becomes more efficient and losses through leaching, denitrification and volatilisation are reduced. Emmett *et al.* (1991b) identified grasses as the major sink for N with uptake over a 15 month period equivalent to 2.66 g N m^{-2} at 50-75 % cover. Uptake by Sitka spruce planted at the site was also significant with net uptake ranging from 0.6 g N m^{-2} when growing with the grass to 1.74 g N m^{-2} when planted within a pile of residue. In contrast, the elimination of plant growth by herbicide application or the retention of residue might be expected to prevent uptake and increase losses (Bormann and Likens 1970). This was demonstrated at the Hubbard Brook Experimental Forest in New Hampshire, where the application of herbicide for three years following clearfelling of hardwoods resulted in the loss of base cations and NO_3^- ions (Likens *et al.* 1970). However, in areas where normal vegetation recovery was permitted, loss of ions was much lower (Likens *et al.* 1978).

The benefits associated with regrowth of vegetation are accompanied by the adverse effects of competition with trees for nutrients (Cox and Van Lear 1985; Emmett *et al.* 1991b), soil moisture (Squire 1983; Flint and Childs 1987) and incoming solar radiation. Weeds compete strongly for nutrients resulting in tree biomass being halved (Smethurst and Nambiar 1989; Emmett *et al.* 1991b), chlorotic foliage and reduced foliar P concentrations compared with Sitka spruce grown in weed free environments. The residue present in CON felled areas, reduces the establishment of competing vegetation, enhances tree growth (Proe *et al.* 1996) and significantly increases concentrations of N and Mn in the foliage of Sitka spruce trees (Fahey *et al.* 1991a).

1.7 Long term nutrient availability and tree growth following CON and WT harvesting

Depending on site characteristics and the intensity of biomass removed during harvesting, long term nutrient availability and productivity of subsequent crops of trees may be adversely affected. The following section summarises literature reporting C and macronutrient (N, P, K, Mg and Ca) dynamics, and the response of tree growth to CON and WT harvesting.

1.7.1. Macronutrients and carbon

A decline in the total N capital of the organic horizons generally occurs during the first 4 to 5 year after clearfelling. In Australia, a reduction of 20 % was measured after 4 years (Smethurst and Nambiar 1990a), whereas losses in Britain of 32 % were recorded over 5 years (Titus and Malcolm 1991). Covington (1981) performed studies in New Hampshire, USA., using a sequence of different aged hardwood stands to determine C and N pools during the 15 years following harvesting of stems only. Reductions of approximately 50 % occurred in the forest floor compared to pre harvest levels. Although large N losses are reported, atmospheric inputs of N occur in many forested regions of continental Europe. In these areas, inputs counterbalance outputs and little long term change in total N capital results (Federer *et al.* 1989).

Quantities of P, K, Mg and Ca in the forest floor also decrease following clearfelling. During the first 5 years after harvesting a Sitka spruce stand, Titus and Malcolm (1991) measured reductions of 41 and 62 % for P and K respectively. Long term predictions of elemental losses (from the organic and mineral soil to the bottom of the rooting zone) through leaching and harvest removals, estimate decreases of between 2 and 10 % for P, K and Mg in the 120 years following harvesting of spruce-fir and hardwood forests in eastern USA (Federer *et al.* 1989). However, the greatest depletion was predicted for Ca which could be reduced by 20 to

60 % during the same period of time (Federer *et al.* 1989). Inputs to the soil through rock breakdown and dry deposition were not thought to balance the deficit. Although Ca deficiencies are currently scarce in acid forest soils, Stevens *et al.* (1988) observed that the Ca removals during harvesting (WT and CON) were greater than the extractable cations available in the soil to rooting depth. In addition, Mann *et al.* (1988) stressed that continued intensive harvest removal of Ca could pose problems within a few harvest rotations.

1.7.2 Tree growth

Although the retention of residue reduces the impacts of harvesting, clearfelling is a catastrophic disturbance which affects soil processes. Therefore the frequency of felling is likely to play a greater role in retention of organic matter at the site and the productivity of successive rotations than the intensity of biomass removal. This idea was supported by the computer simulation of Aber *et al.* (1978), who predicted that short rotations (30 years) would reduce the average forest floor biomass to roughly one half of that under a 90 year rotation. Unfortunately, field experiments to investigate the effects of rotation length on the growth of subsequent rotations of trees are scarce due to their long term nature and will not be discussed below.

The productivity and growth of second and third rotation crops of trees is variable. In Denmark, comparisons of three consecutive spruce rotations demonstrated lower growth in the second and third rotations than during the first (Holmsgaard *et al.* 1961). However, after correction for differences in soil conditions no significant change in yield could be documented (Holmsgaard *et al.* 1961). Studies performed by Keeves (1966) in Australia to determine growth of Radiata pine plantations demonstrated that the second rotation frequently produced lower yields than that of the first crop. The poor growth was attributed to a loss of N (Stone and Will 1965; Flinn *et al.* 1980) and organic matter (Flinn *et al.* 1980) during site preparation. However, during the past two to three decades, yields from European forests are reported to have increased (Becker *et al.* 1990; Eriksson and Johansson 1993; Nilsson *et al.* 1995; see *Chapter 7.4*) and enhanced growth after WT harvesting has been recorded by Hendrickson (1988) and Dyck *et al.* (1990).

Declines in productivity may be alleviated if the forest floor and residue are retained, as decomposition and mineralisation of foliage and small branches can release sufficient nutrients to meet tree uptake requirements for approximately 8 years (Carey 1980). Regular foliar sampling by Proe and Dutch (1994) supported the work of Carey (1980), and indicated that P and K were unlikely to limit tree growth during the first 10 years of the second rotation after WT or CON harvesting. However foliar N declined to marginal levels from age 7

onwards in unfertilised trees and may restrict growth until canopy closure. Despite the lack of differences in nutrient concentrations present in spruce 9 years after planting, trees grown in WT harvested plots contained 50, 5 and 20 kg ha^{-1} less N, P and K respectively, compared to CON treatments due to the smaller biomass attained. Further to the nutritional benefits afforded by the residue, modifications in the microclimate provide an environment more suitable for root growth (Farrell *et al.* 1981) and aboveground shelter which significantly reduces wind speed and may favour tree growth (Proe *et al.* 1994). Consequently greater tree biomass and height were recorded 10 years after planting in CON areas compared to WT harvested sites (Proe and Dutch 1994; Proe *et al.* 1996). Despite the more favourable conditions experienced after CON felling, measurements of tree growth have also demonstrated negative or unchanged responses following residue retention. Bjorkroth (1983) reported higher growth and survival of Scots pine in WT harvested plots during the first 10 years. However, from years 10 to 20 growth was positively influenced by the residues, and the initial poor response was negated resulting in little difference in total growth for the 20 year period. The effects of WT harvesting of early thinnings on the growth Scots pine and Norway spruce yielded variable results during the first 5 years and no significant influence of residue retention (Jacobson *et al.* 1996).

1.8 The natural range of Sitka spruce and growth in the UK

Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is the largest of the native spruces of North America (Mitchell 1996). It has a natural range restricted to a narrow strip (200 km wide) along the coastal fog belt of the Pacific Ocean, from California to Alaska (approximately 2000 km). The trees have adapted to a maritime climate and demand relatively high amounts of Ca, Mg and P (Mitchell 1996). Growth is improved in deep moist well aerated soils and the trees commonly occupy alluvial soils along streams, sandy coarse textured soils or soils having a thick accumulation of organic material.

The Sitka spruce grown in the British Isles originates from the Queen Charlotte Islands, Washington and Oregon. The climate in Britain favours vigorous growth from 1 to 1.3 m a year and generally yields a greater volume of timber than other crop trees (Mitchell 1985). Before planting in the field, seedlings typically spend 1 to 2 years in seedbeds followed by 1 to 2 years in transplant lines (Crowther *et al.* 1991). Provided the plants are treated with care, the survival after outplanting is expected to be high (approximately 90 %) (Crowther *et al.* 1991). Plantation forests are not generally considered to be N limited unless the trees are planted on unflushed peats, heathlands dominated by *Calluna vulgaris* (McIntosh 1983), deep peats or nutrient poor sands (Miller and Miller 1987). However, small growth responses to N fertiliser additions may occur if trees are at a mature stage of the rotation and N becomes

immobilised in the humus and biomass (Miller 1981). Phosphorus and K commonly limit the growth of Sitka spruce (McIntosh 1980), although K is normally only a problem where peat depths are greater than 30 cm. Deficiency symptoms can be avoided with the application of rock phosphate and muriate of potash at recommended rates of 450 kg ha^{-1} (60 kg P ha^{-1}) and 200 kg ha^{-1} (100 kg K ha^{-1}), respectively (Taylor 1991).

Second and third rotation crops are commonly established by planting with seedlings, although natural regeneration may be employed in suitable areas. The advantages associated with restocking include exact spacing of trees, use of selected provenances or genetically improved material and the control of timing of re-establishment. In comparison the use of natural regeneration can be problematic. Firstly, good mast years are intermittent and unpredictable (Crowther *et al.* 1991) and distribution and growth may be patchy, depending on the suitability of the seed bed. Secondly, no opportunity is provided for a change of species or the introduction of improved genetic stock. Where natural regeneration is favoured, establishment costs are small. Dense thickets result which should be respaced at an early stage to prevent damage from early snowfall (Crowther *et al.* 1991). Responses to nutrient additions in second rotation trees are generally lower than those experienced in the first crop (Taylor 1990; Proe and Dutch 1994; Proe *et al.* 1996). On peatland soils, the increased P and K availability during the second rotation (Taylor 1986) eliminates the requirement for fertilisers during the early years. However, there does not appear to be major differences in N availability between the first and second rotations of Sitka spruce grown on heaths or peatlands (Taylor and Tabbush 1990).

1.9 Aims and Objectives

In November 1979, a 40 year old plantation of Sitka spruce was felled in Kielder Forest, the residue banked into swathes and the subsequent growth of Sitka spruce seedlings monitored. Within 3 years, differences in height indicated that WT harvesting was detrimental to growth compared to CON felling (Proe and Dutch 1994). However, the height of trees grown in bare soils present between the residue swathes of CON harvested plots were not significantly reduced after 3 years from planting. In order to ascertain the mechanisms responsible for the enhanced height increments and higher nutrient contents of trees planted in logging debris, three experiments were set up in the North of England and Scotland.

In 1992, the first of the research sites was established in Kielder Forest. This area was selected as it was proximal to the original experiment and was considered to experience similar climatic conditions and soil type. Two different intensities of biomass were exported (stems only and all above ground material), and fertiliser and herbicide were applied to assess

the viability of silvicultural techniques in alleviating problems associated with harvesting regime. The confounding effects of soil compaction were avoided by driving machinery between plots. Unfortunately the long term effects of biomass removal cannot be investigated at present due to the short period of time elapsed since restocking. However, early growth of trees and soil nutrient dynamics have been reported. Continued observations at these sites will allow the formation of a management plan which integrates the harvesting method employed with site type.

In conjunction with the Forestry Commission (FC) and the Macaulay Land Use Research Institute (MLURI), the site within Kielder Forest was comprehensively studied. Measures of tree and vegetation growth, edaphic factors and microclimate were collected, in order to;

- *determine whether the presence of logging residue influenced environmental factors, nutrient availability and the early growth of Sitka spruce and ground vegetation.*

The experiments reported in this thesis were performed during the third and fourth growing seasons (throughout 1994 and 1995), and focused on characterising soil nutrient dynamics, and growth and nutrient content of trees and ground vegetation. To address the principle objective, there were a number of subsidiary aims;

- *to evaluate whether logging debris influenced the physical and chemical characteristics of the soil in the absence of differences in physical damage,*

  Harvesting closed canopy stands results in drastic modifications to the soil. Furthermore, the retention of logging debris influences environmental conditions and alters the nutrient capital available, compared to that of bare soils. *In situ* studies were used to evaluate the nutrient status and physical characteristics of the soil with respect to seasonal fluctuations and treatment differences (*Chapter 3*). Rates of N mineralisation were determined at different temperatures using laboratory incubations, and differences in the quality of litter remaining after CON and WT harvesting were ascertained with a bioassay performed under controlled conditions (*Chapter 4*).

- *to assess whether any changes in soil chemistry following different intensities of harvesting influenced the nutrient content and height attained by Sitka spruce,*

  Trees growing at the site acted as an *in situ* bioassay and could be used to detect changes in nutrient availability within the rooting zone of the forest floor. However, to ensure that nutrients being mineralised could be taken up by trees, it was necessary to determine the depth of rooting and identify the soil horizons in which proliferation of root tips occurred (*Chapter 5*). Assuming that the Sitka

spruce accessed mineralised nutrients, tree height, biomass and foliar nutrient analysis could be used to determine differences in soil nutrient availability between treatments (*Chapter 6*).

- *to quantify whether changes in nutrient availability and physical factors influence shoot phenology,*

  The timing of bud burst, duration of leader growth and occurrence of lammas shoots are thought to be influenced by microenvironment and nutrient availability. Therefore, differences in these variables may indicate an effect of treatment (*Chapter 6*).

- *and to detect differences in the species, biomass and nutrient content of ground vegetation growing with different quantities of logging residue.*

  The species diversity, biomass and nutrient content of ground vegetation are good indicators of soil characteristics. Differences in nutrient availability and the suitability of the forest floor in the establishment of vegetation may be demonstrated by species composition and plant cover or biomass (*Chapter 3*).

The results obtained during this research will be used to give suggestions and guidelines for the restocking of upland clearfell sites after consideration of economic and silvicultural factors and market demand for logging residue.

Chapter 2

DESCRIPTION OF STUDY SITES

2.1 Introduction

With the exception of one study, all field experiments and sample collections occurred at the same location (*Site 1*). A neighbouring, clearfelled area (*Site 2*) was visited to gather needle litter for use in a birch bioassay detailed in *Chapter 4* and referred to in *Chapter 3*. Both sites are within Kielder Forest District, Northumberland, England (*Figure 2.1*).

Detailed macro- and micro-climatic measurements were recorded by M.F. Proe and J Griffiths of the Macaulay Land Use Research Institute (MLURI) at *Site 1* only. As macro-climate is largely independent of recent site history and the two areas are proximal, *Site 1* data is used to describe both locations. Other variables, such as topography and soil characteristics vary little between sites. Therefore the two areas will be treated as one and attention drawn to the factors that differ at *Site 2* considered important to the reported experiments.

Figure 2.1: The location of Kielder Forest (■) within Great Britain.

2.2 Location

Owned by the Forest Enterprise (an Agency within the Forestry Commission), Kielder Forest covers approximately 60 000 ha. *Sites 1* and *2* are positioned due East of Kielder village, approximately 2 and 3 km overland, respectively (55° 10' N, 2° 30' W) (*Figure 2.2*). *Site 1* has an elevation of 300 m above sea level (a.s.l.) and a westerly aspect, whereas *Site 2* has a south easterly aspect and an elevation of 380 m a.s.l.

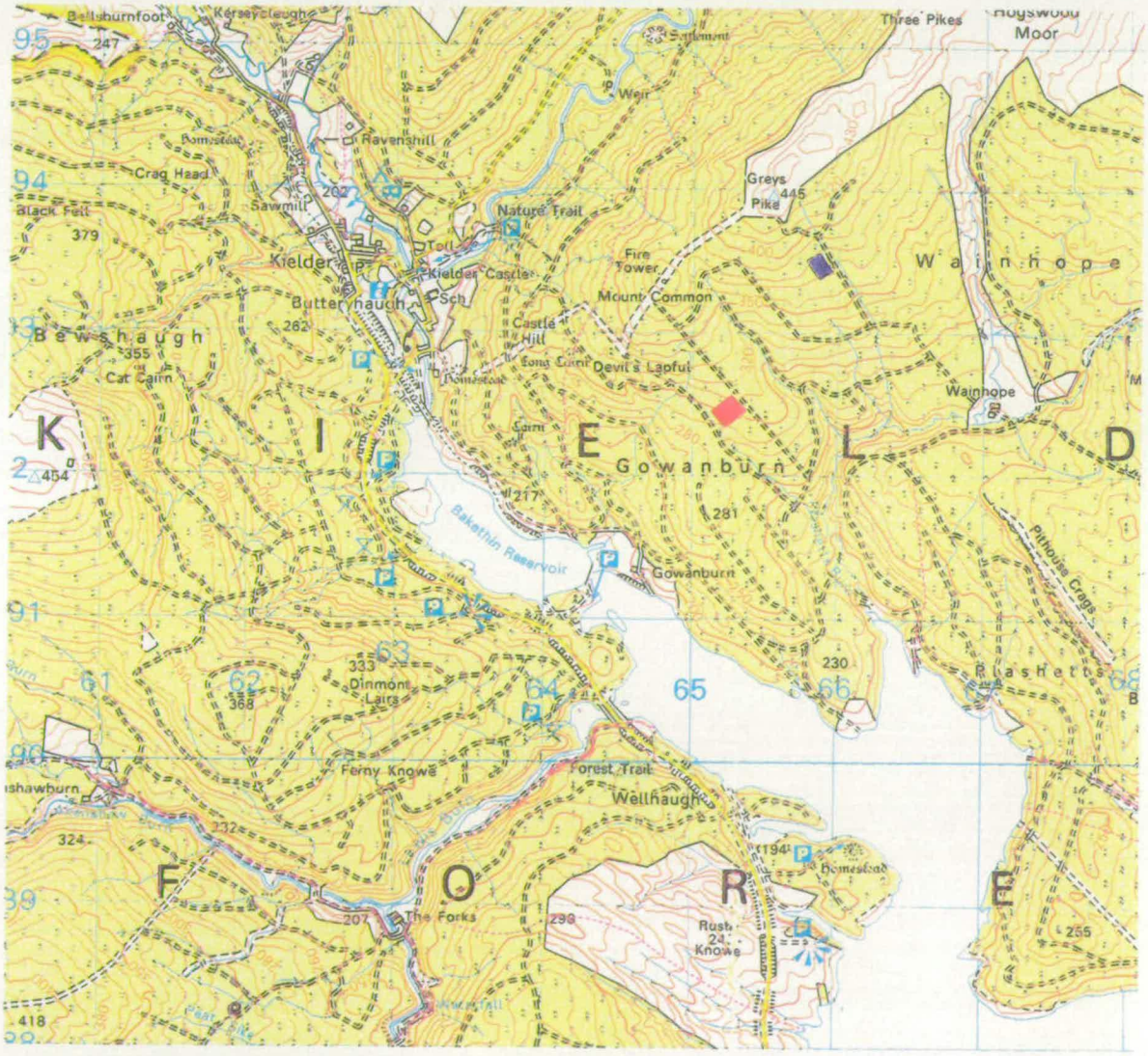


Figure 2.2: The position of *Sites 1* (■) and *2* (■) within Kielder Forest.

2.3 Geology and Soils

The soil is a uniform peaty gley (Pyatt 1970) (a cambic stagnohumic gley (Avery 1980)), which has developed post glacially on Scremerston Coal Group Sandstones overlying Carboniferous limestone (Proe *et al.* 1994). These soils are characterised by a shallow organic horizon (5 to 45 cm thick) consisting of amorphous peat of low hydraulic conductivity (Boggie and Knight 1980). The pore size distribution of the underlying mineral horizon minimises vertical water movement (Titus and Malcolm 1992) and results in a water table which frequently lies near the soil surface. During the first rotation a deep litter layer or LFH horizon (Kubiena 1953) develops above the O horizon. The gradually decomposing needle litter in the surface layers gives rise to a litter layer on top ('L' horizon), a decomposition or fermentation layer immediately below ('F' horizon) and a humus layer ('H' horizon), where plant remains are no longer recognisable (Trudgill 1989). Soil acidity increases with depth, with pH decreasing from 4.5 in the litter layer to 3.5 in the underlying organic horizon.

2.4 Climate

The climate is cool and moist, with approximately 1300 mm rainfall per year and mean monthly air temperatures range from 0 to 15 °C (Proe *et al.* 1994). *Site 1* is protected from exposure by the neighbouring stands of pole and thicket stage Sitka spruce (*Figure 2.7*) and experiences mean monthly wind speeds of 0.17 m s^{-1} (Proe *et al.* 1994).

2.5 Site history

Site 1

Site 1 represents approximately 2.6 ha of an area first planted with Sitka spruce in 1940. In 1991, the unthinned crop had attained a top height of approximately 23.5 m and a basal area of 67 m^2 ha^{-1} of which about 13 % was dead wood (Proe *et al.* 1994). The general yield class (Edwards and Christie 1981) was estimated to be 14 m^3 ha^{-1} y^{-1}. In the autumn of 1991, the stand was felled using a mechanical harvester. To prevent soil compaction, the harvester did not traverse the assessment plots and was used only minimally within the buffer zones of treatment plots (see *Figure 2.7a*)

The site was replanted with Sitka spruce of Queen Charlotte Island origin in May 1992. Occasionally it was necessary to cut through residue using a chain saw to permit access to planting positions. Tree seedlings were spaced at approximately 1.6 m (4 100 trees per hectare). However, assessment plots were planted at double density to allow destructive harvesting of spruce. No other site preparation was performed, although all trees were treated

with permethrin to minimise damage by weevils (*Hylobius abietis* L.). The insecticide was applied on three occasions; prior to planting, and during the first and second growing seasons.

Site 2

The first rotation of Sitka spruce (Queen Charlotte Island origin) was planted in 1940 and exhibited an estimated general yield class of 10 to 12 m^3 ha^{-1} y^{-1} (D.C. Malcolm *pers. comm.*). It was harvested in autumn 1995 using a 'bench' felling technique, whereby all the logging residue was banked into strips and acted as a road bed for extraction machinery. No other site preparation or tree planting occurred before needle litter collection (see *Chapter 4*).

2.6 Vegetation

Originally the sites were mixed grasslands, dominated by a mixture of *Molinia caerulea* (purple moor grass) and *Calluna vulgaris* (heather). However, at the time of felling and planting there was no ground vegetation (Proe and Dutch 1994), due to the lack of light penetrating the closed canopy and the accumulation of needle litter (Titus 1985).

During the summer of 1994 a vegetation survey was performed at *Site 1* (see *Chapter* 3 for detailed methodology and results). The species present were; *Agrostis capillaris* (common bent grass), *Agrostis stolonifera* (white bent), *Betula pendula* (birch), *C. vulgaris*, *Carex* spp. (sedges), *Deschampsia flexuosa* (wavy hair grass), *Digitalis purpurea* (foxglove), *Dryopteris dilatata* (broad buckler fern), *Chamerion angustifolium* (rosebay willowherb), *Epilobium montanum* (broad-leaved willowherb), *Erica cinerea* (bell heather), *E. tetralix* (cross-leaved heath), *Eriophorum vaginatum* (cotton grass), *Galium saxatile* (heath bedstraw), *Holcus lanatus* (Yorkshire fog), *Juncus effusus* (common rush), *J. squarrosus* (heath rush), *Luzula multiflora* (woodrush), *M. caerulea*, *Poa annua* (annual meadow grass), *Polytrichum* spp. (moss), *Potentilla erecta* (tormentil), *Rubus fructicosus* (blackberry), *Rumex acetosa* (common sorrel), *R. acetosella* (sheep's sorrel), *Sorbus aucuparia* (rowan), *Vaccinium myrtillus* (whortleberry), other mosses and naturally regenerating Sitka spruce.

In addition, fungal fruiting bodies from residue retained and clear treatment plots at *Site 1* (+ R and - R, respectively; see *Chapter 2.7*) were surveyed in autumn 1995. Due to the low frequency of fungi, whole treatment plots were observed and all samples identified. The following species were present; *Maramius androsaceus* (horse hair fungus), *Hypholoma capnoides*, *Hypholoma marginatum*, *Hygrophoropsis aurantiaca* (false chanterelle), *Mycena galericulata* (bonnet mycena), *Clitocybe* sp., *Gloeophyllum sepiarium* (bracket), *Russula emetica* (emetic russula) and *Calocera viscosa* (jelly antler fungus).

2.7 *Site 1 Experimental design*

The experiment had three treatments (logging residue, herbicide and fertiliser), at two levels (present or absent), in a full factorial design (*Table 2.7*). This resulted in eight treatment combination plots, each separated by a minimum of 2 m. The plots measured 20 m by 20 m, contained an internal assessment plot of 10 m square and an outer buffer zone of 300 m^2. The majority of micro-climatic measurements were recorded within the assessment areas, whereas most of the analyses reported in this thesis were performed on data collected from the buffer zone (*Figure 2.7a*). Use of the outer area allowed experimentation and destructive harvesting without compromising the long-term experiments continuing within the assessment plots. The blocks were replicated three times and treatment combinations allocated randomly to each plot (*Figure 2.7b* and *Table 2.7*).

Table 2.7: A table summarising; the presence (✓) or absence (-) of treatments applied at *Site 1*, the abbreviated nomenclature and whether or not the plot was studied in the experiments detailed in this thesis (n = 3 for each treatment).

			Treatment		
Treatment combination	*Abbreviated form*	*Studied*	*Residue retention*	*Herbicide application*	*Fertiliser application*
Residue	+ R	✓	✓	-	-
Residue and herbicide	+ RH	✓	✓	✓	-
Residue and fertiliser	+ RF	-	✓	-	✓
Residue and herbicide and fertiliser	+ RHF	-	✓	✓	✓
Clear	- R	✓	-	-	-
Clear and herbicide	+ H	✓	-	✓	-
Clear and fertiliser	+ F	-	-	-	✓
Clear and herbicide and fertiliser	+ HF	-	-	✓	✓

The specific objectives of this study (see *Chapter 1.9*) were to investigate the influences of logging residue and competing vegetation on site conditions and tree growth. Consequently, all experimentation occurred within treatment plots with and without residue and herbicide applications (*Table 2.7*). The effect of fertiliser was not investigated, although the treatment details have been summarised below and initial results from the site are reported by Proe *et al.* (1994).

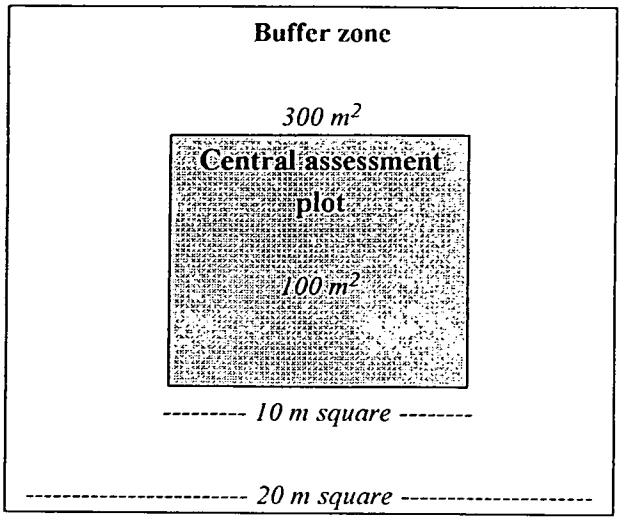


Figure 2.7a: An example of *Site 1* plot layout. Micro-meteorological data was recorded within the central (shaded) zone (by MLURI). The majority of the remaining experiments were performed in the outer (unshaded) area.

Treatments applied at Site 1

Residue remaining from trees growing within each + R plot was evenly redistributed over it. For all - R treatment plots, whole trees were removed from the plot with the branches intact. Herbicide treatments received glyphosate applications in September 1992 and August 1993 at rates recommended by the Forestry Commission's Field Book 8 (Williamson and Lane 1989). Additional applications were made in autumn 1994 and 1995. Any naturally regenerating Sitka spruce which either survived herbicide treatment or grew in plots outwith the + H treatments was pulled up, and retained on site. All fertiliser plots were broadcast with N, P and K in August of 1992 and 1995. Nitrogen was applied as ammonium nitrate at 470 kg ha^{-1} (160 kg N ha^{-1}) in 1992 and as urea at 350 kg ha^{-1} (160kg N ha^{-1}) in 1995, phosphorus as unground rock phosphate at 450 kg ha^{-1} (60 kg P ha^{-1}) and potassium as muriate of potash at 200 kg ha^{-1} (100 kg K ha^{-1}). The treatments will be repeated at three year intervals until canopy closure.

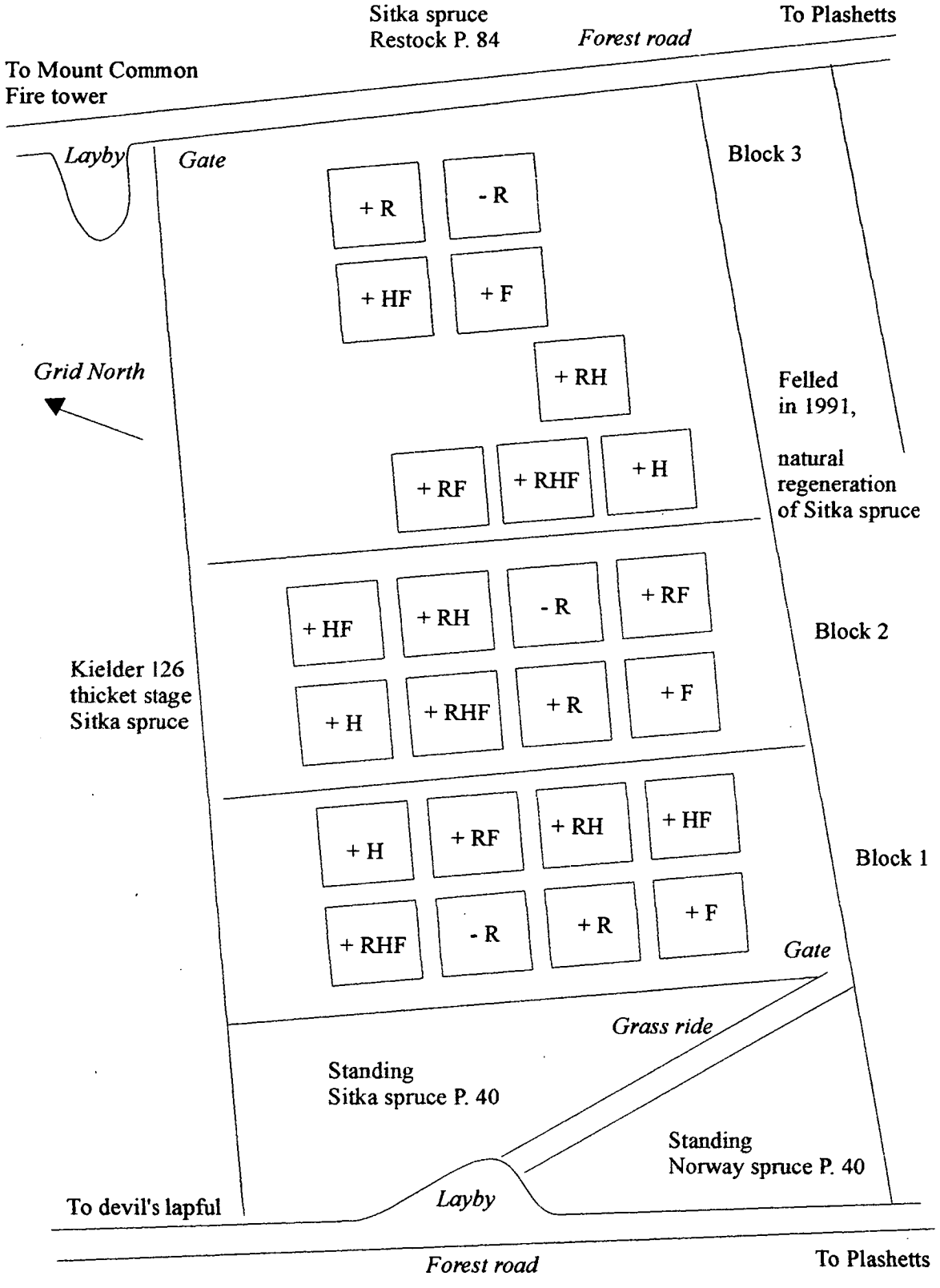


Figure 2.7b: A map of *Site 1*, not to scale. Three blocks and all treatment plots are represented (see *Table 2.7* for abbreviations). Forest roads and surrounding stands are shown.

2.8 Site 1 Micrometeorology

From April 1992, micro-climatic data was recorded within the assessment areas of treatment plots. Variables measured included shoot, soil and air temperatures, wind speed, precipitation, water table depth and photon flux density. Of these, air and soil temperatures, wind speed, water table depth and precipitation are presented. The frequency of data collection, and summary tables and graphs demonstrating climatic trends recorded during 1994 and 1995 are detailed below. (See Proe *et al.* 1994, for apparatus used for data collection.)

In cases where further manipulation of data was required during experimentation, or attention is drawn to specific relationships observed between variables, the procedures and results have been outlined in the appropriate chapters. For example, air temperature and wind speed records are referred to in *Chapter 6*, water table depth, soil temperatures and precipitation discussed in *Chapter 5* and soil temperatures and precipitation data used in *Chapter 3*.

2.8.1a Air and soil temperatures (+ R and - R plots only)

Screened thermistors and temperature probes recorded air and soil temperatures, respectively, in all + R and - R assessment plots. Measurements were taken at 10 cm above and below the soil surface. Values were collected once every 10 minutes, averaged over two hour periods and converted to weekly means using the average of the daily means; (the difference between daily minimum and maximum). Accumulated degree days over 5.6 °C (thermal time, see *Chapter 6*; Cannell and Smith 1983) was calculated as the daily temperature, greater than a threshold of 5.6 °C, summed for the year. A summary of 1994 and 1995 data is tabulated (*Table 2.8.1a*) and the weekly treatment means are plotted (*Figure 2.8.1a*).

Annual trends indicated that mean weekly air temperatures remained below 5 °C from the beginning of each year until early April. During the following 3 to 4 months temperatures increased, attaining maxima between weeks 30 and 35 (late July and August). By week 44 (early November), temperatures had fallen to approximately 5 °C. A further decline was measured towards the end of the year, with temperatures fluctuating between 3 °C and below freezing, until the following spring (*Figure 2.8.1a*). During 1994, the range of air temperatures experienced within + R and - R treatment plots was less extreme than that recorded in the following year. For example, the 1994 maximum weekly means were 2 to 3 °C cooler, while minimum weekly means were at least 6 °C warmer. In addition, lower yearly means and accumulated degree days were recorded in this year. Within each year, the effect of treatment was very small, resulting in identical yearly means and small differences between

values for the other variables summarised in *Table 2.8.1a* (0.1 °C for the maximum weekly mean and 6 to 7 days for accumulated degree days).

Soil temperature data obtained in 1994 and 1995 revealed a close relationship with patterns in air temperature. However, the large fluctuations recorded above ground were dampened by the insulating layer of soil (*Figure 2.8.1a*), resulting in less extreme maximum and minimum weekly means. The greatest buffering effect was observed during periods of low air temperatures, when the water table had risen close to the soil surface. The higher moisture content present in the upper horizons increased the thermal conductivity, allowing more heat to pass from the body of the soil to the surface layers. As a result, soil temperatures below freezing were rarely recorded, despite the occurrence of minimum weekly air means below 0 °C in both treatments and years. Also, yearly mean temperature and accumulated degree days in soil were higher than the associated air temperatures by approximately 0.5 °C and at least 13 days, respectively.

Table 2.8.1a: A summary of air and soil temperatures recorded in + R and - R treatments during 1994 and 1995. The maximum and minimum weekly means, yearly means (± standard errors) and the accumulated degree days above 5.6°C (± standard errors) are presented (n = 3).

	Air temperature (°C)			
	1994		***1995***	
	+R	***-R***	***+R***	***-R***
Max. weekly mean	15.4	15.3	17.5	17.8
Min. weekly mean	-1.9	-1.8	-7.4	-7.5
Yearly mean	6.7 (± 0.2)	6.7 (± 0.2)	7.3 (± 0.3)	7.3 (± 0.3)
Degree days (over 5.6 °C)	928 (± 71)	922 (± 69)	1172 (± 60)	1179 (± 81)

	Soil temperature (°C)			
	1994		***1995***	
	+R	***-R***	***+R***	***-R***
Max. weekly mean	14.6	15.0	15.6	16.3
Min. weekly mean	0.9	0.9	1.5	0.91
Yearly mean	7.2 (± 0.2)	7.4 (± 0.3)	8.0 (± 0.2)	8.1(± 0.2)
Degree days (over 5.6 °C)	960 (± 55)	1054 (± 54)	1185 (± 67)	1241 (± 46)

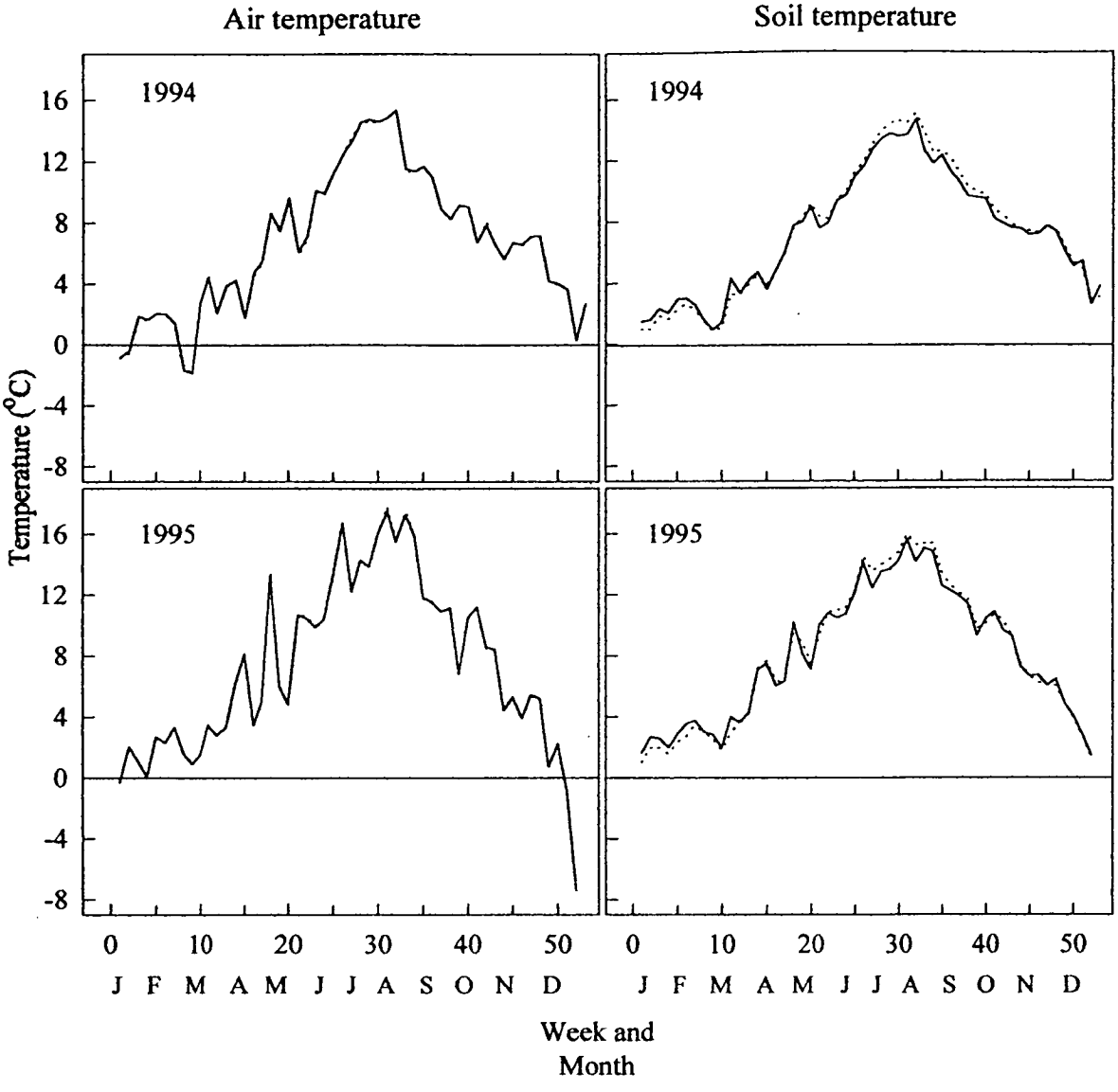


Figure 2.8.1a: Mean weekly air and soil temperatures from + R (solid line) and - R (dotted line) treatments plotted for 1994 and 1995.

Treatment also affected soil temperature at 10 cm depth. The logging residue present in + R plots acted as a mulch above the soil surface, further reducing the influence of air temperature. The greatest effect was observed for accumulated degree days over 5.6 °C in which - R treatment plots experienced an extra 94 and 66 degree days than + R plots during 1994 and 1995, respectively.

In addition to the data collected above, a soil temperature profile was established to observe the influence of soil horizon and depth. Probes were inserted along the line of planting into the middle of the L layer, and directly below this, between the F and H, and the H and O horizons for each replicated profile. Due to the limited number of data loggers available, duplicate measurements occurred in the buffer zones of the + R and - R treatment plots from block 2, only. The depths of each soil horizon varied across the plot and with respect to treatment, therefore the probe depths differed accordingly (*Table 2.8.1b*).

Table 2.8.1b: Temperature probe depth within the + R and - R plots of block 2.

	Depth of soil temperature probe below the soil surface (cm)					
	+ R			***- R***		
Soil horizon	***Rep. 1***	***Rep. 2***	***Mean***	***Rep. 1***	***Rep. 2***	***Mean***
L	7	4	5.5	1	1	1.0
F/H	13	12	12.5	6	4	5.0
H/O	17	14	15.5	10	9	9.5

Table 2.8.1c: Table summarising the weekly means of maximum and minimum soil temperatures recorded within different soil horizons of + R and - R treatment plots during 1994 and 1995 (n = 1).

	Soil temperature (°C)											
	1994						***1995***					
	+ R			***- R***			***+ R***			***- R***		
Soil horizon	*L*	*F/H*	*H/O*	*L*	*F/H*	*H/O*	*L*	*F/H*	*H/O*	*L*	*F/H*	*H/O*
Max. weekly	20.1	22.0	15.0	29.0	21.0	19.2	22.7	19.0	16.0	40.0	26.0	18.5
Min. weekly	1.0	3.1	3.2	-1.8	0.4	1.7	-0.9	0.6	0.4	-2.0	-1.0	0.8
Yearly	9.5	9.9	9.2	10.1	9.6	9.8	8.0	7.9	8.0	9.4	8.5	7.9

Temperatures were recorded every 2 minutes using a Squirrel logger. The readings were averaged for each one hour period, and the data downloaded in the field using Grantwise software. Within each treatment and horizon the duplicated values were meaned, before calculation of the maximum and minimum weekly values and the yearly means (*Table 2.8.1c*; as calculated in *Table 2.8.1a*). A plot of the weekly means is represented in *Figure 2.8.1b*.

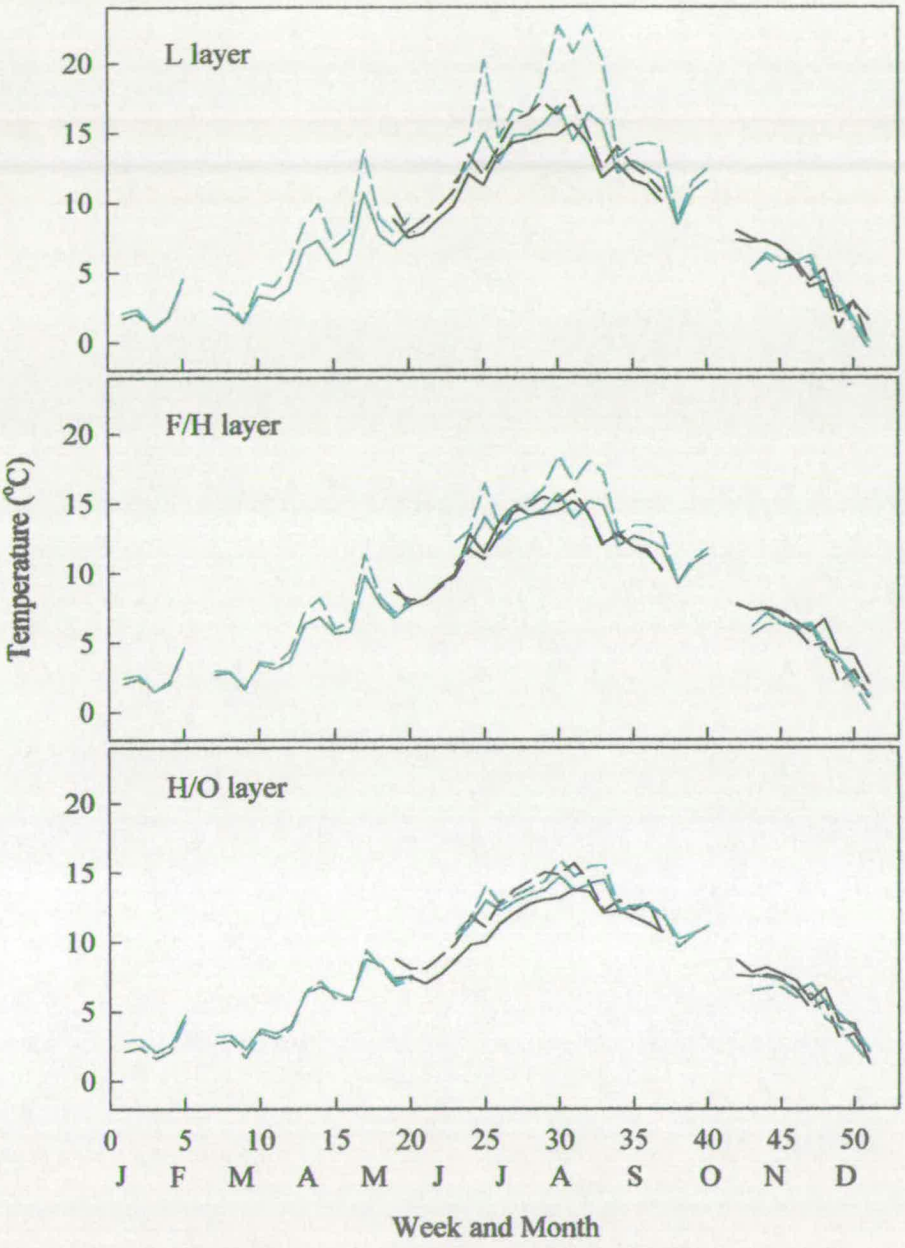


Figure 2.8.1b: Temperature profiles recorded in the L, between the F and H, and H and O soil horizons from May to December 1994 (——) and during 1995 (——). Weekly means from + R (solid line) and - R (broken line) treatment plots within block 2 are presented. Gaps represent missing data.

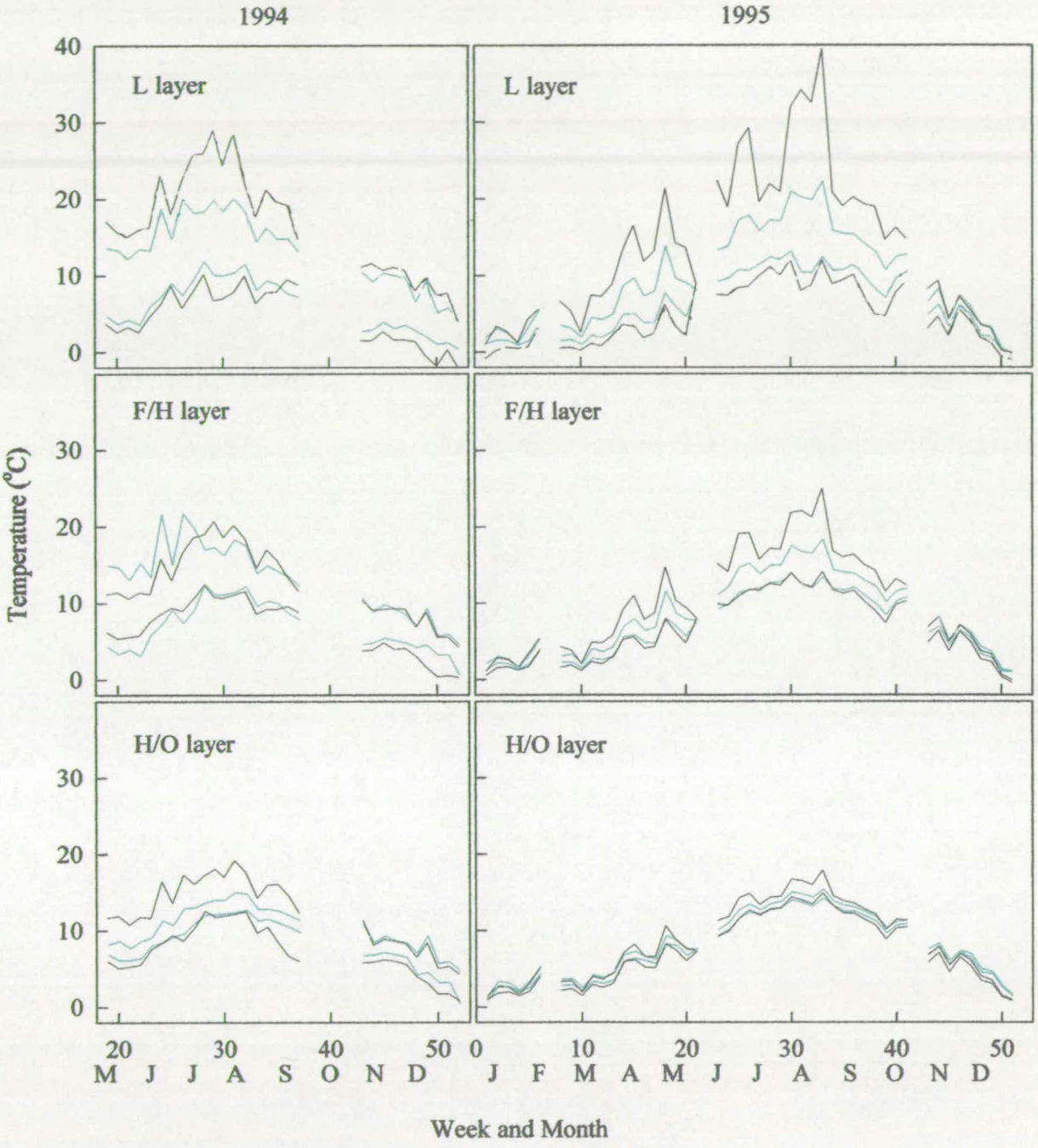


Figure 2.8.1c: Weekly maximum and minimum temperatures experienced in the L, between the F and H, and the H and O soil horizons from May to December 1994 and during 1995. + R (——) and - R (——) treatment plots from block 2 are represented.

Soil temperature was affected by depth and treatment. With increasing depth the influence of air temperature on the soil decreased rapidly, resulting in reduced extremes of temperature lower in the profile. This was especially evident in the - R plot, where the temperature range experienced was greatly reduced from 0.01 m (mid L) to 0.05 m (F/H) depth (*Figure 2.8.1b* and *Table 2.8.1c*). The trend occurs as a result of the low thermal conductivity of soil, which restricts conduction of heat through it. Consequently, the influence of above ground conditions in determining soil temperature greatly reduces with depth.

The reduced range of temperatures recorded in the + R plot can be partly explained due to the increased depth of the soil probes below the surface. However, comparison of temperatures between treatments recorded at similar depths (F/H horizon of the - R, and the L horizon of the + R plot), demonstrated a narrower range within the + R plot, suggesting the occurrence of a treatment effect. In + R plots, the majority of the woody material retained in the logging residue is pale in colour and reflects solar radiation. In addition, the mulch immobilises air within pockets above the soil surface. As air has a very low thermal conductivity, heat is transmitted to and from the soil very slowly. As a result, the residue reduces heating of the soil during periods of sunshine and provides an insulating layer which protects the soil from extreme temperature fluctuations experienced above ground.

2.8.2 Wind speed (+ R and - R plots only)

Wind speed was measured in all + R and - R treatment plots at approximately 0.30 m above ground level using cup anemometers. To cover plot variability, the anemometers were moved each month between five random locations within the assessment area. Wind speed was screened every 5 minutes and the average recorded every two hours. From this data, weekly means were used to derive yearly means (average of weekly values) (*Table 2.8.2* and *Figure 2.8.2*).

Wind speed was generally greater in 1994 than 1995, resulting in higher maximum, minimum and mean values (*Table 2.8.2*). Both years experienced relatively little wind during the period from week 20 to 35 (mid May to the beginning of September) (*Figure 2.8.2*). Whereas, stronger winds were recorded during weeks 1 to 16 (from the start of January to mid April), and weeks 41 to 52 (from mid October to the end of the December).

Table 2.8.2: Maximum and minimum weekly and yearly mean wind speed (± standard errors) recorded for + R and - R treatments during 1994 and 1995 (n = 3).

	Wind speed			
	1994		*1995*	
	+ R	*- R*	*+ R*	*- R*
Max. weekly mean (m s^{-1})	1.97	2.14	1.31	1.31
Min. weekly mean (m s^{-1})	0.17	0.25	0.10	0.08
Yearly mean (m s^{-1})	0.92 (± 0.06)	1.06 (± 0.07)	0.55 (± 0.04)	0.58 (± 0.04)

During 1994 and 1995, the sheltering effect of the logging residue modified the wind speed near the soil surface. Although the extent of this influence above ground is unknown, anemometers positioned at a height of 0.30 m detected differences between treatments. Consequently, the yearly mean wind speed was lower in + R treatment plots than - R plots, for the corresponding time period (*Table 2.8.2*). The greater difference between treatments observed in 1994 occurred in response to the stronger wind speeds. Proe *et al.* (1994) observed the same trends at this site in 1992 and 1993, and suggested that the decrease in wind speed due to sheltering, increased with increasing wind speed. The effect was also evident in 1995, when differences between treatment reduced due to the slower winds experienced. However, the lower wind speeds measured probably arose due to the gradual increase in shelter produced by tree height and basal crown diameter growth, rather than an actual decrease in wind speed above the canopy. Therefore the trend for a decline in wind speed at 0.30 m height, during 1994 and 1995 would be expected to continue until canopy closure.

2.8.3 Site precipitation (1994 and 1995)

Daily precipitation was measured using a rain gauge positioned within block 2. Weekly means are presented in *Figure 2.8.3*.

Total annual precipitation at *Site 1* was greater in 1994 (1460 mm) compared to the following year (1025 mm). The pattern of rainfall between years was generally consistent. In 1994, large amounts of precipitation were received between late November and the end of December, with reduced amounts from the beginning of April to the end of July. During 1995 the wet periods at the start and end of the year were separated by a longer period of dry weather (< 30 mm per week) from the beginning of March to September.

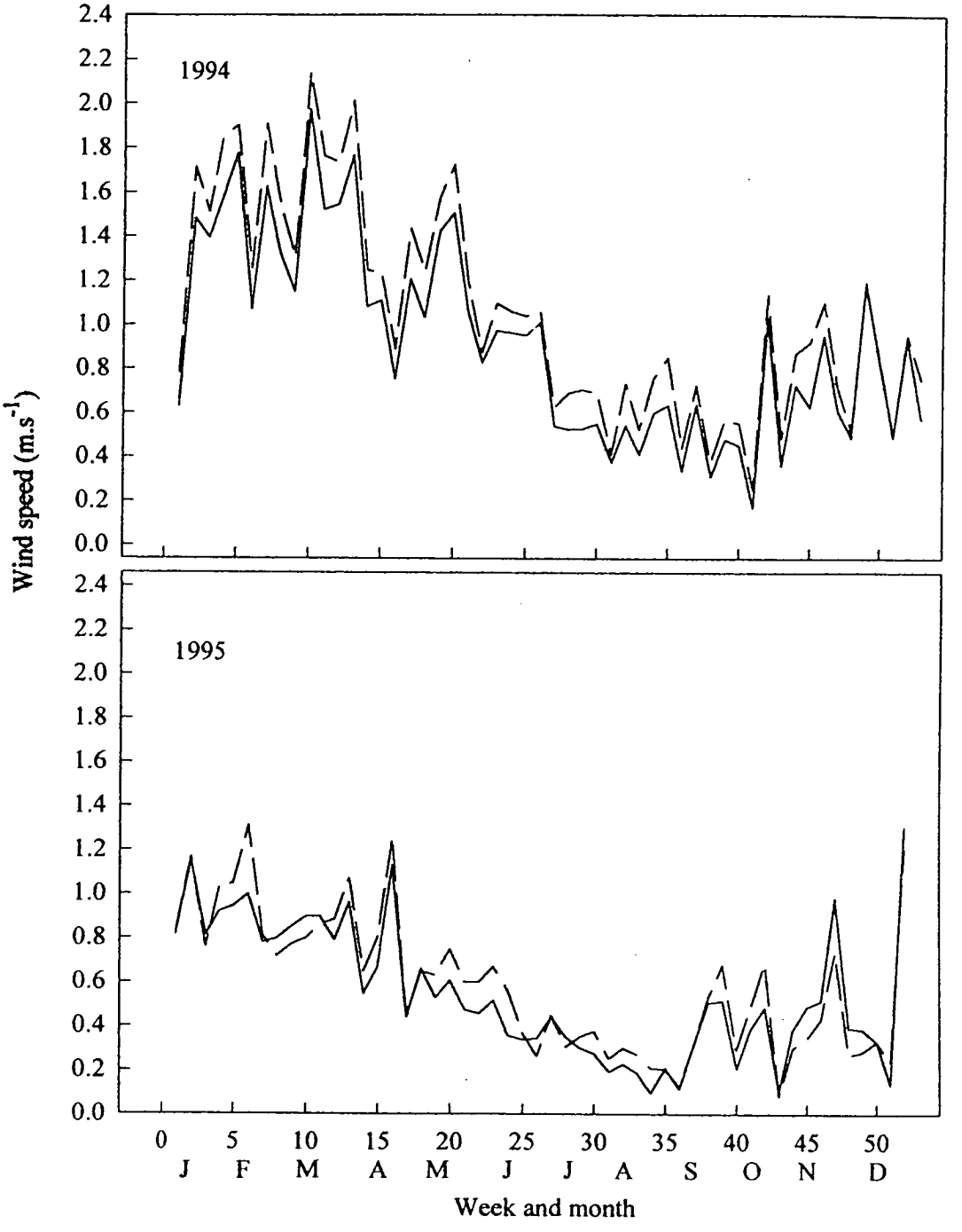


Figure 2.8.2: Mean weekly wind speed plotted for + R (solid line) and - R (dotted line), recorded during 1994 and 1995 (n = 3).

2.8.4 Water table depth (+ R, + RH, - R and + H treatment plots).

A 0.1 m diameter by 0.8 m depth vertical hole was bored in each + R, + RH, - R and + H treatment plot and lined with perforated plastic tubing. At fortnightly intervals the water table depth inside the tube was recorded using a rule and float. The results recorded from April 1994 to the end of 1995 are discussed in relation to soil temperature (at 0.10 m depth) and precipitation received at the site. Sample means and standard errors are summarised in *Table 2.8.4* and presented in *Figure 2.8.4.*

From April to December 1994, the water table fluctuated between 0.08 and 0.71 m depth. Levels were shallowest (from 0.08 and 0.4 m), during and shortly after periods of high precipitation (between 10 and 100 mm per week). Consequently, waterlogging close to the soil surface was recorded in April, at the end of June and from mid September to the end of the year. In May, early June and August, precipitation inputs decreased to less than 20 mm per week resulting in a drop in the water table to between 0.38 and 0.71 m. During summer, periods of drier weather are accompanied by warmer soil temperatures and greater solar radiation. These factors modify soil moisture and water table depth by increasing evaporative losses and evapotranspiration from spruce and other vegetation.

At the beginning of 1995, the precipitation received at the site was high (between 20 to 80 mm per week) resulting in the mean water table level remaining within 0.10 to 0.32 m of the soil surface. However, at the end of March two months of drier, warmer weather occurred. During this period precipitation inputs reduced, soil moisture loss through evaporation and evapotranspiration increased and the water table dropped to between 0.45 and 0.75 m. In June, the level increased rapidly by approximately 0.25 m in response to increased precipitation. However, after another dry period during July and August accompanied by high soil temperatures (between 12 to 16 °C), the water table dropped to deeper than 0.75 m. Within a fortnight, precipitation increased and the water table had risen towards the soil surface. Depth remained constant at between 0.15 and 0.4 m to the end of the year.

From spring 1994 to the end of 1995, the water table was consistently deeper in the herbicide treated plots. However, analysis of variance using repeated measures (procedure outlined in *Appendix 1*) demonstrated that differences during 1995 were not significant. The effect of treatment appeared greatest and experienced least fluctuation when the water table lay close to the soil surface. During these periods, the shallowest plot mean was recorded for the + R treatment, followed by the - R, and herbicide treatments. Depending on the year, + RH or + H

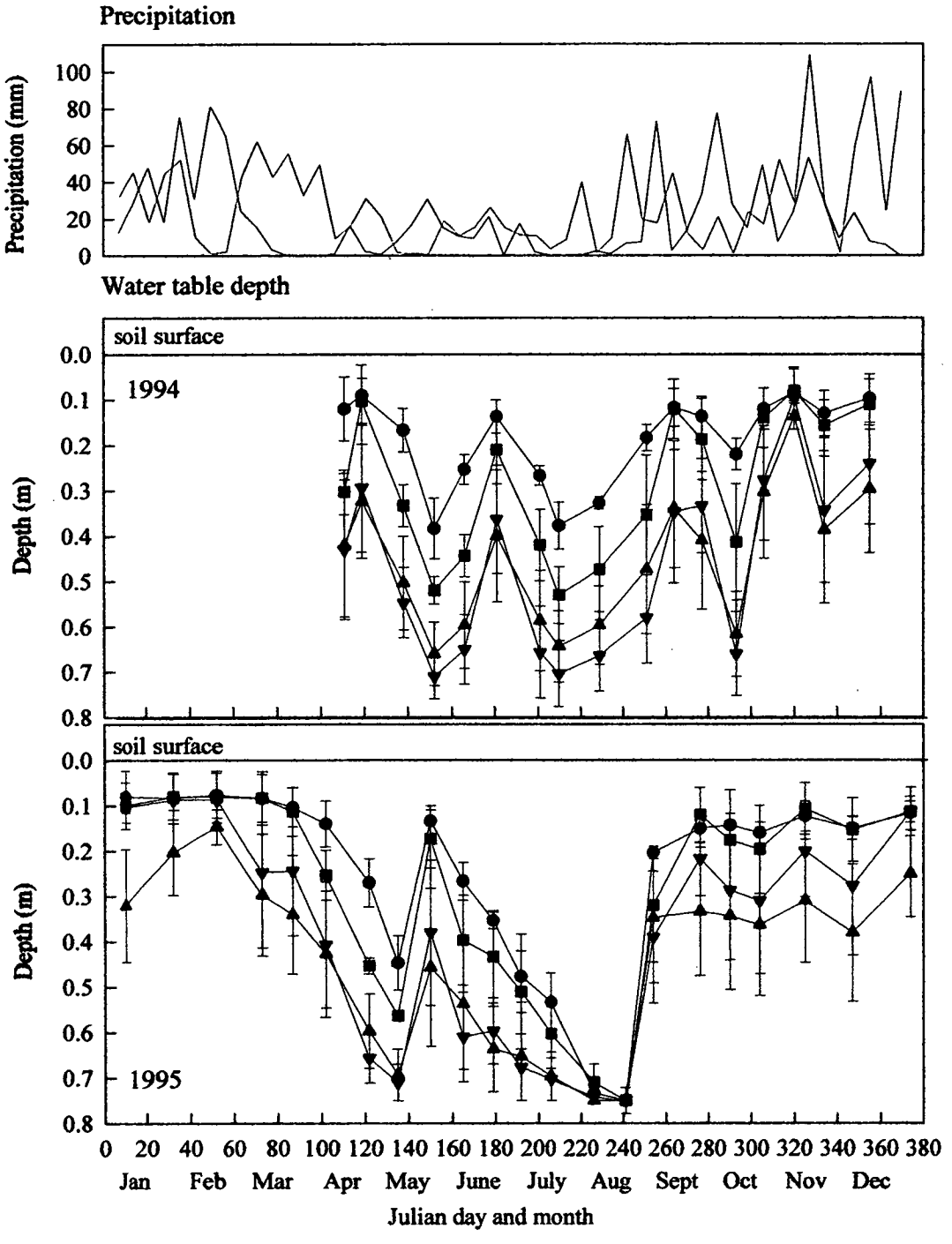
means were shallower. From April to December 1994, + H plots recorded deeper water tables, whereas mean + RH were lower thereafter.

Table 2.8.4: Summary of the sample mean (± standard errors) for water table data recorded during 1994 and 1995 in + R, + RH, - R and + H treatment plots (n = 3). Note: 1995 mean maximum values do not have an associated standard error, as the water table depth was below the level at which accurate measurements could be made.

	Water table depth (m)							
	1994 (April to December)				***1995 (all year)***			
Treatment	***+ R***	***+ RH***	***- R***	***+ H***	***+ R***	***+ RH***	***- R***	***+ H***
Maximum mean	0.38	0.66	0.53	0.71	> 0.75	> 0.75	> 0.75	> 0.75
	(± 0.05)	(± 0.01)	(± 0.06)	(± 0.05)				
Minimum mean	0.09	0.14	0.08	0.10	0.08	0.25	0.08	0.10
	(± 0.07)	(± 0.03)	(± 0.05)	(± 0.07)	(± 0.06)	(± 0.10)	(± 0.05)	(± 0.12)
Mean	0.14	0.23	0.14	0.22	0.25	0.45	0.30	0.40
	(± 0.05)	(± 0.12)	(± 0.07)	(± 0.12)	(± 0.03)	(± 0.10)	(± 0.06)	(± 0.08)

As the water table dropped, levels within - R and + H treatments appeared to increase in depth more rapidly. This suggests that during periods of little rainfall, the lack of a residue mulch allows greater evaporation from the soil surface. However, as precipitation increased the difference between treatments is expected to narrow. This is because the loss of moisture from evaporation in the clear plots is replaced, and the precipitation reaching the soil surface of the residue retained plots is reduced due to losses by interception. Therefore, although residue retained treatments retain moisture more efficiently, the amount of precipitation reaching the soil would be less than that in clear plots.

Although water table depth fluctuated with changes in precipitation, the responses recorded were dampened and slightly delayed. This may result due to the buffering nature of the soil, the intervals between discrete measurements or a combination of both factors.



Figures 2.8.3 and *2.8.4*: Weekly mean precipitation during 1994 (▬) and 1995 (—) at *Site 1* (n = 1) and water table depth throughout 1994 and 1995, recorded in + R (●), + RH (▲), - R (■) and + H (▼) treatment plots. Sample means (± standard error bars) are represented (n = 3).

2.9 *Growth of Sitka spruce at Kielder Forest*

Within Kielder Forest, 72% of the land area is covered by Sitka spruce which is the most productive species grown in the area (mean GYC = 12) (McIntosh 1995). The remaining planted area is covered with four main conifers and various broadleaves (*Table 2.9*).

Trees within the forest experience harsh growing conditions, including waterlogged soils, low nutrient availability and exposure. High winter water tables, low soil hydraulic conductivity and the occurrence of anaerobic peds in the organic horizons restrict rooting depth to the upper 45 cm (Mason and Quine 1995). These limitations render the trees susceptible to windthrow. At Eskdalemuir (20 km west of Kielder Forest), the return period of wind gusts likely to cause extensive damage (over 40 m s^{-1}) is approximately once every 60 years (Mason and Quine 1995). However, the return period will be influenced by elevation and on higher ground at Kielder (over 300 m) the interval might be 30 years or less (Mason and Quine 1995). Reductions in the planting density from between 3 500 and 5 000 trees ha^{-1} during the early development of the forest, to 2 500 trees ha^{-1} in the 1980's have increased the soil available to each tree. A wider root spread (Fraser and Gardiner 1967) and a lower tree height/diameter ratio develop which are better able to withstand the overturning moment exerted be the wind (Quine *et al.* 1995). Despite this, in exposed areas felling of vulnerable stands was suggested at a top height of 15 - 20 m (Godwin 1968).

Table 2.9: Land use in Kielder Forest in 1995 (McIntosh 1995).

Land use	***Area***	***Mean GYC[a]***
Sitka spruce (*Picea sitchensis* (Bong.) Carr.)	72 %	12
Norway spruce (*Picea abies* (L.) Karst.)	12 %	9
Scots pine (*Pinus sylvestris* (L.)	2 %	8
Lodgepole pine (*Pinus contorta* var. *latifolia* (Wats.))	9 %	6
Larch (*Larix* spp.)	1 %	8
Other conifers	3 %	8 - 10
Broadleaves	1 %	0 - 2
Total planted area	42 500 ha	
Open space intimately linked with plantations (roads, rides, deer glades)	7 500 ha	
Discrete areas of open space (raised bogs, agricultural areas, unplanted heather moorland)	12 000 ha	
Total area	62 000 ha	

[a] General Yield Class

Wind is also an important factor influencing tree growth in Britain (Worrell and Malcolm 1987). Direct effects include the abrasion of needles (Pitcairn and Grace 1985) and stunting of tree stem elongation through mechanical stimulation (Telewski 1995). Reductions in boundary layer resistance may lower needle temperatures and the chemical reaction rates associated with plant growth (van Gardingen and Grace 1991), while transpiration rates increase especially in warm conditions (van Gardingen *et al.* 1991).

At *Site 1* the removal of residue significantly reduced height growth during the first two seasons after restocking (Proe *et al.* 1994). This difference was attributed to the sheltering effect (measured at 30 cm aboveground) afforded by residue in reducing wind speed and the detrimental effects associated with it. However, as tree height and crown diameter increase, reductions in wind speed will be influenced less by the residue and governed more strongly by the neighbouring trees.

Residue removal at harvesting modifies soil temperature by increasing the means recorded during the summer months. This should favour the production of new root tips during the growing season as increases in soil temperature result in greater numbers of roots initiated per Sitka spruce plant (Tabbush 1986). Root tip diameter and length of the main lateral root also increase with increasing soil temperature between 5 and 25 ^{o}C in young Sitka spruce (Coutts and Philipson 1987). As air temperatures fall in the autumn, decreases in soil temperature are more rapid in the absence of residue. Therefore the duration of annual root growth may be shorter in the clear areas, despite higher mean temperatures being attained.

The major factor controlling vertical growth of Sitka spruce roots at *Site 1* is the frequently high water table which occurs during the autumn and winter months. Consequently, the enhanced summer growth of tree roots in the absence of residue may be offset by damage due to water logging (see *Chapter 5*). A critical period for root injury is during the autumn when the soil temperature still maintains active growth rendering the root sensitive to anaerobic conditions (Coutts and Philipson 1987). The insulation experienced under residue may be detrimental to root growth as warmer soil temperatures are sustained later in the season with the potential to cause greater root death than experienced in bare soil.

Differences in root distribution between the herbicide and non-herbicide treated plots can be explained as a direct response to the availability of aerobic soil. However, the effects of treatment on the dynamics of water table depth are unknown. Vegetation growing at the site would be expected to lower the water table slightly, due to losses of moisture through

evapotranspiration and interception. Additional losses would result from interception by residue. However, at *Site 1* neither mechanism is evident. Differences in incoming precipitation are unlikely to cause such trends, as observations of plot position in relation to surrounding stands with high interception potential and their associated water table depths did not demonstrate any trends. Therefore, despite the random allocation of plots across the site, the water table depths observed probably result due to chance and within site variability.

Growth at *Site 1* is determined by physical conditions and nutrition, which may be modified by the presence of logging residue. Physical factors affecting above and below ground growth will be investigated in *Chapter 5* and *6*. Soil nutrient availability is discussed in *Chapters 3* and *4*, while the nutrient status of the trees is reported in *Chapter 6*.

Chapter 3

THE INFLUENCE OF HARVESTING INTENSITY ON PHYSICAL AND CHEMICAL SOIL CHARACTERISTICS AND GROUND VEGETATION SHORTLY AFTER FELLING

3.1 INTRODUCTION

Physical and chemical properties of soils can be affected greatly by clearcutting (see *Chapter 1*). However the impact of felling depends on many factors including harvest intensity, soil type, climate and tree species. It is important to identify the changes in nutrient dynamics and physical characteristics occurring shortly after clearfelling in order that patterns of tree growth during the successive rotation may be understood.

Various soil organisms contribute to site productivity by influencing;

- the input of nutrients to the soil,
- the release of nutrients via organic matter decomposition,
- root uptake rates (mycorrhizal),
- changes in the chemical environment associated with their activity and
- changes in physical soil properties associated with their movement (soil mixing) (Van Miegroet *et al.* 1994). The importance of these processes can be determined using the methods summarised in *Table 3.1.1.* However, tree growth and productivity respond primarily to nutrient availability and the rate of release. Therefore, factors controlling accessibility of nutrients including mineralisation potential and mineralisation in the field (see *Table 3.1.1*) may be the most valuable indicators of tree growth. *Chapters 3* and *4* detail results from *in situ* and laboratory incubations, respectively. The experiments performed assessed the availability of inorganic N during the third and fourth years after clearfelling *Site 1*.

Laboratory incubations provide useful indices of substrate quality and quantity, but do not integrate short or long term changes or the effects of the physical, chemical and biological environments in the field (Keeney 1980). In addition, soil incubation in the laboratory favours continuous mineralisation over extended periods, which is unlikely to arise within the forest floor. In the field, inputs of large amounts of carbon to the soil surface are often sufficient to negate net mineralisation in the soil due to increased immobilisation, making the measurement of net mineralisation by laboratory methods difficult (Paul and Juma 1981; Adams and Attiwill 1986).

Table 3.1.1: Some important soil biological processes, indicator measurements, and methods used in site productivity studies (taken from Van Miegroet *et al.* 1994)

Measurement	*Key Processes*	*Methods*
Abundance of soil fauna	Fragmentation Soil aeration Soil mixing	Soil extraction and counts
Abundance of microflora	Decomposition Nutrient transformation	Dilution Plate Incubation/Fumigation (lab)
Mycorrhizal abundance	Nutrient uptake	Root tip counts
Microbial activity	Decomposition Nutrient transformations Respiration	ATP assays Enzyme assays CO_2 evolution (field)
Litter decomposition	Decomposition Nutrient release	Forest floor thickness Litterbag study Stable isotopes Radioactive tracers
Mineralisation potential	Nutrient release Nutrient transformation	Aerobic and anaerobic incubations (lab)
Mineralisation	Nutrient release Nutrient transformations	Exchange resins Soil incubations (field)

It is generally considered that field incubation techniques provide better estimates of mineralisation, as physical conditions in the sample reflect those in the surrounding bulk soil (Adams *et al.* 1989). These procedures gained in popularity during the 1970's (Ellenberg 1977; Rapp *et al.* 1979) and were considered to be good for quantifying annual rates of net mineralisation. However the validity of the measurements rests on the assumptions that isolating soil does not significantly alter the naturally occurring rate of mineralisation (Adams *et al.* 1989). It is difficult to test this theory due to the unknown effects of the assay conditions on various soils (Raison *et al.* 1987). However, all *in situ* methods change the soil environment through;

- cessation of the carbon input from decomposing litter and fine root turnover,
- increases in carbon input from severed roots,
- modification of the moisture and temperature regimes relative to the bulk soil
- accumulation of inorganic nitrogen (Adams *et al.* 1989), and

- alterations of the physical soil structure and rhizosphere processes (Raison *et al.* 1987).

Despite such drawbacks, *in situ* incubations are frequently used because there are no other readily applied methods for assessing net mineralisation and nitrogen availability in a quantitative manner.

Many field incubation techniques have been designed. For example, Nadelhoffer *et al.* (1984) and Eno (1960) buried soil samples in bags. While Carlyle (1984), homogenised root free soil and repacked it to its original bulk density, before wrapping in cling film and returning to the soil. Although this method allows reciprocal transplanting of samples and removal of carbon substrate (such as severed roots), the disturbance occurring during preparation tends to overestimate nutrient release. More commonly, samples are separated from the bulk soil with minimal disturbance, by the insertion of plastic or metal corers. Adams and Attiwill (1986) isolated intact soil surface cores (0 to 5 cm) with capped plastic corers. Perforations around the perimeter of the corer permitted the moisture to equilibrate within the sample. Similar methods were adopted by Adams *et al.* (1989) during which perforated plastic corers, 10 cm length and 5 cm diameter, were driven into the soil and either covered or left open. Whereas, Raison *et al.* (1987) used unperforated steel corers (capped and uncapped) to sample to a depth of 20 cm.

Duration of *in situ* incubation is usually about four weeks. Although periods from 30 to 90 days have been found to be appropriate (Raison *et al.* 1987). It is important that the soil is incubated long enough to allow significant and measurable change in the concentration of inorganic nitrogen concentration (Raison *et al.* 1987). However, Adams *et al.* (1989) observed decreases in the average rate of net nitrogen mineralisation as the period of incubation increased. Therefore longer containment periods may underestimate soil mineralisation rates. Raison *et al.* (1987) also considered flexibility of incubation duration to be important, in order that changes in the environment, including temperature, wetting and drying cycles, may be accounted for. Estimates of net mineralisation are obtained by subtracting the initial quantity of inorganic nitrogen in the bulk soil from that extractable in contained samples. Annual rates of mineralisation may be derived by summation of the individual amounts of nitrogen mineralised or immobilised during each incubation period.

Available inorganic nitrogen can be estimated using methods including ion exchange resin bags (Binkley and Matson 1983; Binkley 1984; Carlyle 1984; Wiklander and Nommik 1987), tension lysimeters (Tschaplinski *et al.* 1991) and zero tension lysimeters (Titus and Malcolm 1991). Ion exchange resin bags provide a measure of nutrient supply which is repeatable, does not involve considerable disturbance of the soil profile (Carlyle 1984; Gibson 1986) and

may be left for long time intervals before collection (Carlyle 1984). However, as ions from mass flow and diffusion from the surrounding soil replace those of lesser exchange affinity on the resin, a quantitative measure of the soil solution ion concentration is obtained (Gibson 1986) rather than an estimate of mineralisation (Carlyle 1984). Measures of soil water inorganic nitrogen are also obtained from lysimeters placed below the soil rooting depth. Tension lysimeters (in which soil water is drawn in when the tension of the lysimeter is greater than that of the surrounding soil matrix) and zero tension lysimeters (into which soil water only enters as saturated flow) require constant or frequent suction and solutions collection.

The growth responses of vegetation can also be viewed as a biological indicator of site processes and quality which may be manifested at the cellular, whole plant or plant community level (Van Miegroet *et al.* 1994). Trees may demonstrate changes in nutrient uptake rates, physiological functions, foliar surface area and mass, carbon allocation patterns and productivity per plant and unit area (Van Miegroet *et al.* 1994). However after clearfelling, regrowth of ground vegetation may act as a more sensitive indicator of site characteristics. On bare sites, seedling establishment is dependent on the viability of the existing seed bank, the influx of new seed and suitability of the growing conditions. Many factors determine the species type present and biomass accumulated, including the N status of the humus and upper soil horizons (Tolle and Hofmann 1970), soil moisture content and acidity (see Ellenberg 1988; Hawkes *et al.* 1997).

3.1.1 Objectives

The objective of the experiments performed below was to determine the influence of clearfelling on the physical and chemical characteristics of the organic soil horizons, and to assess the potential to support future tree and vegetation growth. Whole-tree and CON (conventional) harvesting effects were observed during the third growing season (GS) at *Site 1*. Net mineralisation of inorganic N was measured using *in situ* incubations of soils contained within disposable steel corers (see *Chapter 3.2*). From these samples, additional physical and chemical measurements could be obtained including;

- horizon depth, bulk density, moisture and organic matter content,
- pH, and total nutrients (N, P, K, Mg and Ca).

In addition, a vegetation survey performed in August 1994 allowed the role of vegetation as a potential competitor for nutrients to be assessed. The species composition and biomass could be used as an indicator of nutrient availability and to compare differences between treatments.

Seasonally high water tables and anaerobic soil peds (*Chapter 2* and *5*) limit Sitka spruce root growth to the top 15 to 40 cm, where forest soil mineralisation rates are documented as being

highest (Adams *et al.* 1972). Therefore all measurements were restricted to the surface organic layers. It was considered important to separate the samples when analysing soil characteristics, in order that changes in substrate quality and physical properties resulting from the input of organic material at felling may be determined. Measurements were performed in the litter (L), fermentation and humified (FH) and organic (O) horizons. In some cases, characteristics within the O horizon could not be determined as the sample was incomplete or absent. Where appropriate, soil properties were expressed per hectare. However, as the total depth of the O layer was not measured, this was calculated for the L and FH horizons only.

In the discussion annual net mineralisation has been estimated using results from laboratory incubations at various temperatures (reported in *Chapter 4*).

3.2 METHODS

Due to the large number of soil samples required, all cores were taken from the buffer zones of + R, + RH, - R and + H treatments (*Chapter 2*). Avoidance of the central assessment plots minimised damage to tree root systems used for continuous physiological measurements and biomass studies, and reduced soil compaction during access. However, the outer buffer areas may have experienced some soil disturbance during passage of machinery at harvesting.

In situ net mineralisation was determined using a sequential coring procedure with field incubations running for 3 to 7 weeks, depending on the time of the growing season. From these, nutrient release was calculated as the difference between the initial and final quantities measured. The method was repeated seven times throughout the growing season from May to November 1994. In addition, soil moisture, pH and loss on ignition were measured on each occasion. Total soil nutrients (N, P, K, Mg and Ca), horizon depth and dry weight bulk density were assessed on two occasions, at the end of the 1994 and 1995 growing seasons.

A vegetation survey was performed by the Forestry Commission in August 1994. All treatment plots, except those with herbicide applications, were assessed. Results from + R and - R treatments are reported.

3.2.1 Soil sampling procedure

Disposable cylindrical steel cans (provided by Carnaud Metalbox, Carlisle) were used throughout the study. Each measured 65 mm diameter x 165 mm depth and was capped to prevent leaching of nutrients from the sample. On each sampling occasion, four cores were taken from each treatment plot for immediate analysis while another four cores remained in the soil to incubate under field conditions. From this, net mineralization for the period of containment in the bulk soil could be estimated. However, leaching losses and atmospheric inputs were not represented. Two 7 mm diameter holes were present in the side wall of each can (capped end). These reduced soil compaction during insertion of the can by allowing air to escape and permitted gaseous exchange in the head space of the can above the litter layer during incubation. The thin can walls (0.2 mm thick) eased insertion to the peaty gley soil and caused minimal soil compaction during sampling.

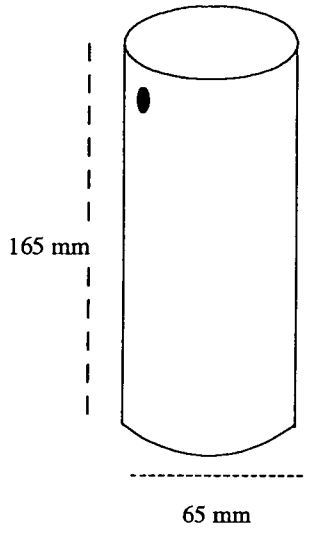


Figure 3.2: Stainless steel soil corer with capped top, open bottom and walls 0.2 mm thick (not to scale). The holes at the top allow exchange of air during insertion and *in situ* incubation.

Roots less than approximately 3 mm diameter were cleanly severed by the cores, however removal of woody debris from the litter surface was required to avoid crumpling of the can. Where this proved difficult or thick woody root prevented insertion of the core, the nearest suitable position was selected. The area of coring within the buffer zone of the plot was allocated randomly. However, each sample (immediate and *in situ*) was taken along the line of planting, and equidistant between trees. Where the remnants of plough furrows remained after the first rotation, cores were taken from the slightly raised areas. It was hoped that some variability within each plot would be avoided by standardising coring location, while reflecting soil nutrients available to the tree roots.

3.2.2 Soil sample preparation

Undisturbed cores were stored in plastic bags for a maximum period of 10 weeks at 2 to 4 °C until analysis. (The effect of storage on the soil within intact cores was investigated. Results are reported in the *Appendix 3.1*) To prevent soil compaction and facilitate access during removal of the sample, the can was sliced open using a blade. The soil surface adjacent to the can was discarded before separating each core into the L (including small fractions of F), FH and O (including all soil below the H layer) horizons for analysis. Within treatment plots and sample dates the soil horizons were bulked together, and live and dead roots removed before homogenising by hand. On two occasions estimates of bulk density were obtained by recording the depth of each horizon before bulking. Duplicate physical and chemical measurements were performed on each horizon from every sample.

3.2.3 *Physical and chemical soil analyses*

Moisture contents were determined gravimetrically. Ten gram subsamples from each treatment plot were dried to constant weight at 85 °C. Loss on ignition of oven dried soil was measured after heating samples to 400 °C for 6 to 8 hours. The pH of fresh soil was derived potentiometrically by adding 25 ml of distilled water to a 10 ± 0.05 g sample and mixing. After 30 minutes standing the pH was measured using a combination electrode. Soil moisture and loss on ignition were expressed as percentages of fresh and oven dried soil, respectively. Bulk density of the soil horizons was calculated from estimates of undisturbed soil volume within the core (horizon depth x 32.22 cm ^{2}) and oven dried weight of the soil.

Measures of available NH_4^+ and NO_3^- were obtained by extracting soil with one normal potassium chloride solution (1N KCl). Fresh soil samples were mixed thoroughly and passed through a 2 mm mesh. From this two 10 ± 0.05 g subsamples were mixed with 200 ml 1N KCl solution and orbitally shaken for 2 hours. Samples were left to settle before collection of a 14 ml measure which was centrifuged at 6 000 rev min^{-1} for 20 minutes and stored at 2 °C until determination of inorganic nitrogen. Ammonium and NO_3^- were measured colorimetrically using a Tecator Flow Injection Analyser or a Perstop Continuous Flow Analyser.

Total soil nutrients (N, P, K, Mg and Ca) were derived using a modified wet digestion micro-Kjeldahl procedure (Allen *et al.* 1974). Samples were oven dried and ground to pass through a 0.5 mm sheath using a centrifuge mill. Two 0.1g subsamples of ground material were weighed (to 3 decimal places) into Pyrex digest tubes. Additions of 2 ml of concentrated H_2SO_4 and two volumes of 0.75 ml of H_2O_2 (30v/v) were made to each replicate. Samples were placed in a heating block at 350°C for 6 hours, or until all organic material had digested and the solution had cleared. After cooling, the digests were transferred to 100 ml volumetric flasks. One 0.5 ml measure of 10 % lanthanum solution was added to each, before making up the solution to 100 ml using distilled water. Blanks and standards were run with each set to allow calibration. Total N and P were determined using a Perstop Analytical Continuous Flow Analyser. Total K, Mg and Ca were assessed using a Pye Unicam SP9 Atomic Absorption Spectrometer.

Percentage organic carbon was estimated from organic matter values derived during loss on ignition (*Equation 3.2.3*). The van Bemmelen conversion factor of 1.724 was used, as organic matter contains approximately 58 % carbon. Total C/N ratios were calculated from percentage organic carbon and total nitrogen.

Organic C (%) = organic matter (%) / 1.724 (van Bemmelen factor) Equation 3.2.3

3.2.4 Vegetation survey and harvest

Five 1 m^2 quadrats were randomly distributed throughout the assessment plots of + R and - R treatments at the beginning of August 1994. Within each quadrat, all vegetation was identified, percentage cover was estimated and above ground material harvested. The occurrence of planted spruce was noted, but remained at the site, while naturally regenerating trees were included in the harvest. All vegetation collected within a plot was bulked, oven dried at 80 °C until constant weight, weighed and analysed for total nutrients (N, P, K, Mg and Ca) using a micro-Kjeldahl wet digestion procedure (*Chapter 6.2.4*). Nutrients accumulated in vegetation biomass were expressed per hectare for each treatment.

Ecological Site Classification (G. Pyatt, Forestry Commission *pers comm.*), defined by the vegetation present, was used to determine soil conditions within + R and - R treatment assessment plots. The method assigns indicator values to vegetation (determined by Ellenberg 1988) for three soil variables; nitrogen availability (N), moisture (F) and reactivity (acidity/alkalinity, R), where 1 is low and 9 is high. Each value is multiplied by an estimate of percentage cover for the respective species in each quadrat. The figure obtained is divided by the total percentage cover for all vegetation possessing indicator values before being averaged for each plot. Some species of vegetation have not yet been assigned an indicator value (F, R or N). Therefore, a reliability ratio is calculated which expresses the proportion of the total plant cover that may be explained by vegetation with associated Ellenberg values. In cases where all species have been allocated a value, a reliability ratio of 1.00 is obtained. However if large proportions of the vegetative cover are not described, a low value (close to 0) is calculated.

A survey of fungal species present in + R and - R treatment plots was performed in autumn 1995. Fruiting bodies occurring on the forest floor and on woody debris within the assessment areas and buffer zones of each treatment plot were identified (see *Appendix 3.2*).

3.2.5 *Data presentation and statistical analysis*

Treatment means and standard errors (n = 3) were calculated for moisture content, loss on ignition and pH on each sampling occasion. The ability of contained *in situ* soil samples to reflect conditions in the bulk soil at the end of the confinement period is discussed (*Chapter 3.4.1*) without statistical evaluation. The presence of consistent differences in moisture, organic matter and pH, between incubated and immediately sampled cores collected on the same date would suggest that;

- soil characteristics in the core suffer a lag period before responding to external conditions,
- exclusion of the sample reduces the influence of the surrounding soil,
- the presence of a steel can modifies conditions within the core, or
- a combination of any of these factors.

Further comparison of contained and immediate samples taken at the beginning of each incubation period may give insight into the presence of a lag period or reduced responses due to isolation from external influences.

Soil horizon volume and bulk density (expressed as oven dried soil weight) were calculated from sample depths (with known diameter) and weights. Total horizon mass and nutrient contents in oven dried soil were expressed per hectare. All variables recorded on individual measurement dates were compared between treatments using analysis of variance. Net NH_4^+ and NO_3^- mineralisation rates were calculated for each incubation period and the total inorganic nitrogen release determined for the 1994 growing season. In addition, annual net mineralisation was estimated as the sum of the actual mineralisation occurring during the growing season, plus that predicted for the beginning and end of the year. Using the relationship recorded between laboratory incubated soils and temperature, and the field soil temperatures recorded for the appropriate periods, nitrogen mineralisation could be estimated. This procedure was repeated for the L, FH and O horizons from each plot, expressed as a mean (n = 3) per hectare of oven dried soil and compared using analysis of variance.

Means and standard errors (n = 3) were calculated for vegetation biomass and nutrient contents, expressed as kg ha^{-1}, and treatment differences assessed using analysis of variance of log transformed data. Differences between species composition are discussed with reference to Ellenberg indicator values.

The occurrence of various species of fungal fruiting bodies in the + R and - R plots and differences occurring between treatments are detailed in *Appendix 3.2* without statistical evaluation.

3.3

RESULTS

3.3.1 *Physical characteristics of soils (from residue (+ R), residue with herbicide (+ RH), clear (- R) and herbicide (+ H) treated plots).*

Percentage moisture

Percentage moisture content of soils from *Site 1* varied depending on the time of sampling and the horizon. Mean values ranged from 64 % in mid June to 85 % in April. The L and FH horizons generally contained similar moisture. However, the FH demonstrated less seasonal variation. Large fluctuations were observed in the O layer which was strongly influenced by the mineral content of the sample. In the presence of sandy material, moisture retention was lower.

Seasonal variations were most apparent in the litter layer of the immediately sampled soils (*Figure 3.3.1a*). Moisture content dropped from approximately 80 % in April to a minimum of 68 % in + H plots, during July, before increasing to spring values in November. Small decreases were observed in the incubated litter layers and both incubated and immediately sampled FH soil horizons. Seasonal trends were not observed in the O layer.

Treatment differences recorded on individual sampling dates are summarised as significance levels in *Figure 3.3.1a.* On five of the seven immediate sampling dates, litter from the residue retained plots was significantly moister. Incubated litter demonstrated similar relationships, although significant differences were recorded during July and August only. In the deeper FH horizons, residue retained plots contained significantly greater moisture on three occasions from mid June to early September. At the beginning of the growing season, samples from herbicide applied plots were significantly lower. Significantly greater moisture contents were recorded under residue on four occasions in incubated FH horizons, from mid June to mid October. Large plot variation in the moisture contents of the O horizon resulted in large standard errors (*Figure 3.3.1a*). Treatment differences were apparent on one occasion in the incubated O horizon, at the beginning of July, when herbicide significantly increased moisture content.

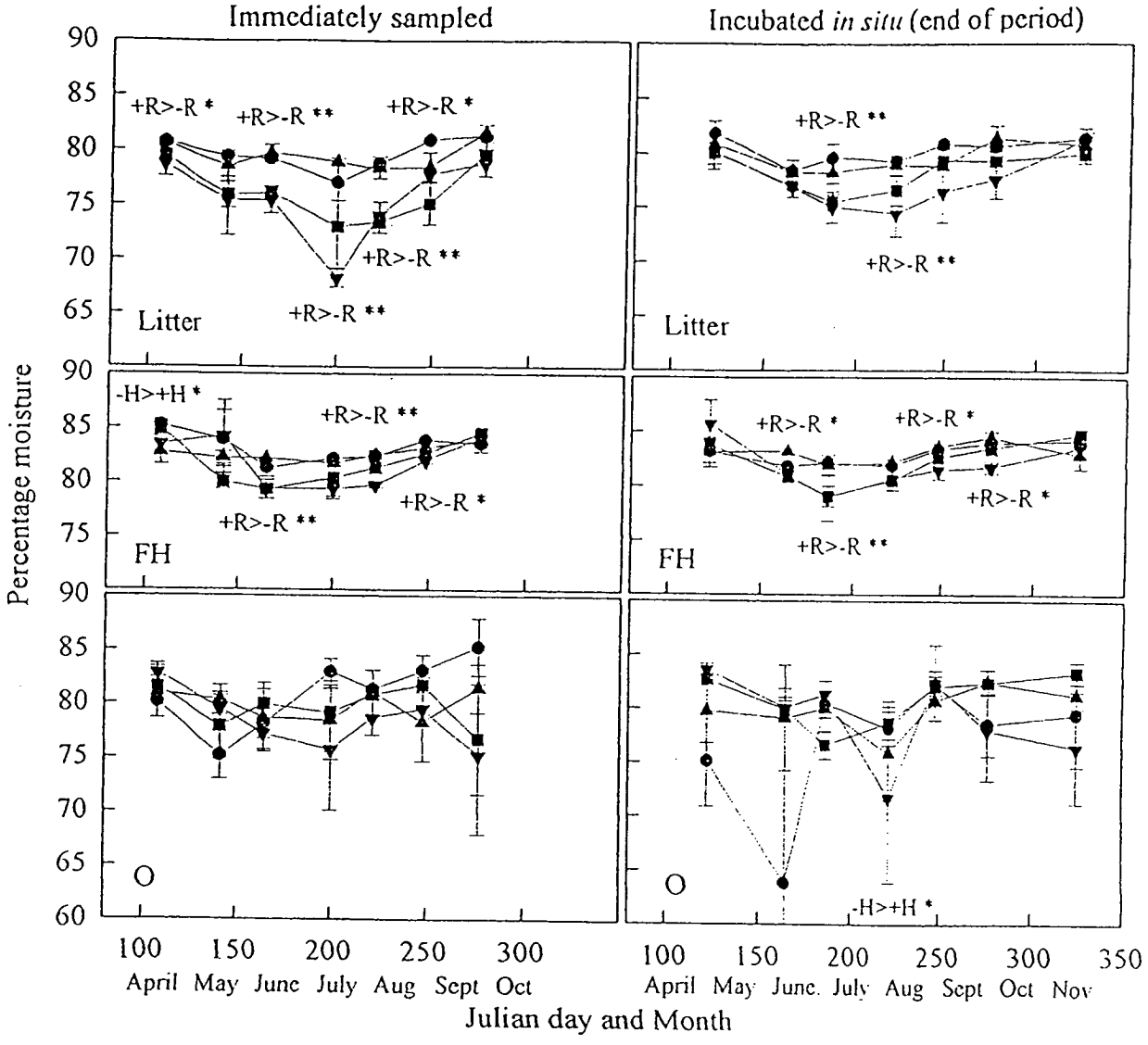


Figure 3.3.1a: Mean percentage moisture contents of fresh soil (± standard errors) (n = 3) for L, FH and O horizons from + R (●), + RH (▲), - R (■) and + H (▼) treatments. Immediate and *in situ* incubated samples (end of incubation period) are represented for the 1994 growing season, from April to November 1994. Treatment differences are shown; '*' , '**' and '***' indicate significance at the $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ levels, respectively.

Percentage organic matter

Percentage organic matter decreased from maxima of 97 % in the litter and FH horizons to 53 % in the O layer (*Figure 3.3.1b*). Values in the upper L and F H horizons were consistent throughout the growing season. However, increases were observed in the FH horizons of incubated samples in June and October. Greater variation was recorded in the O layer within plots and between treatments resulting in large standard errors and mean values ranging from 53 to 90 %. Significant treatment differences were observed occasionally in the L and FH horizons. However, the occurrence throughout the season and the influence of treatment were inconsistent.

pH

Soil pH decreased with increasing depth from between 3.7 and 4.7 in the litter layer to 3.5 and 3.9 in the O horizon (*Figure 3.3.1c*). Treatment differences were observed occasionally in the L and FH layers. For example, residue retention significantly decreased the acidity of immediately collected litter samples in September, while incubated samples were influenced in June. The presence of significantly greater pH values in residue retained samples from the FH horizon corresponded with those recorded in the litter layer. A herbicide/residue interaction was present in immediate litter samples in September, while herbicide significantly increased pH in the litter of immediate samples collected in May. Treatment did not affect the acidity of the O horizon.

Fluctuations during the growing season were largest in the litter layer, with variations decreasing with increasing depth. Although strong seasonal trends were not apparent, increased litter acidity was observed in mid July, when soil moisture contents were low. Lower pH values were also apparent at the start and end of the measurement period. Fluctuations demonstrated by incubated samples were not influenced by season (*Figure 3.3.1c*). Small decreases in pH occurred in the FH horizon at the beginning of the season, before stabilising just below 4.0. Whereas, values in the O layer were consistently low.

Incubation effects on soil characteristics (moisture, organic matter and pH)

Incubation influenced moisture, organic matter and pH of the L and FH horizons only. The litter layer of *in situ* samples remained wetter than immediately analysed soils during the summer, regardless of the initial content. However in the spring and autumn, when moisture contents were high, containment did not influence moisture retention. Fluctuations in the FH horizons were small, and could not be attributed to incubation. Organic matter content was not constant throughout the measurement period. Mean values tended to be lower in the incubated soil of the L and FH horizons. In June and September incubated FH layers

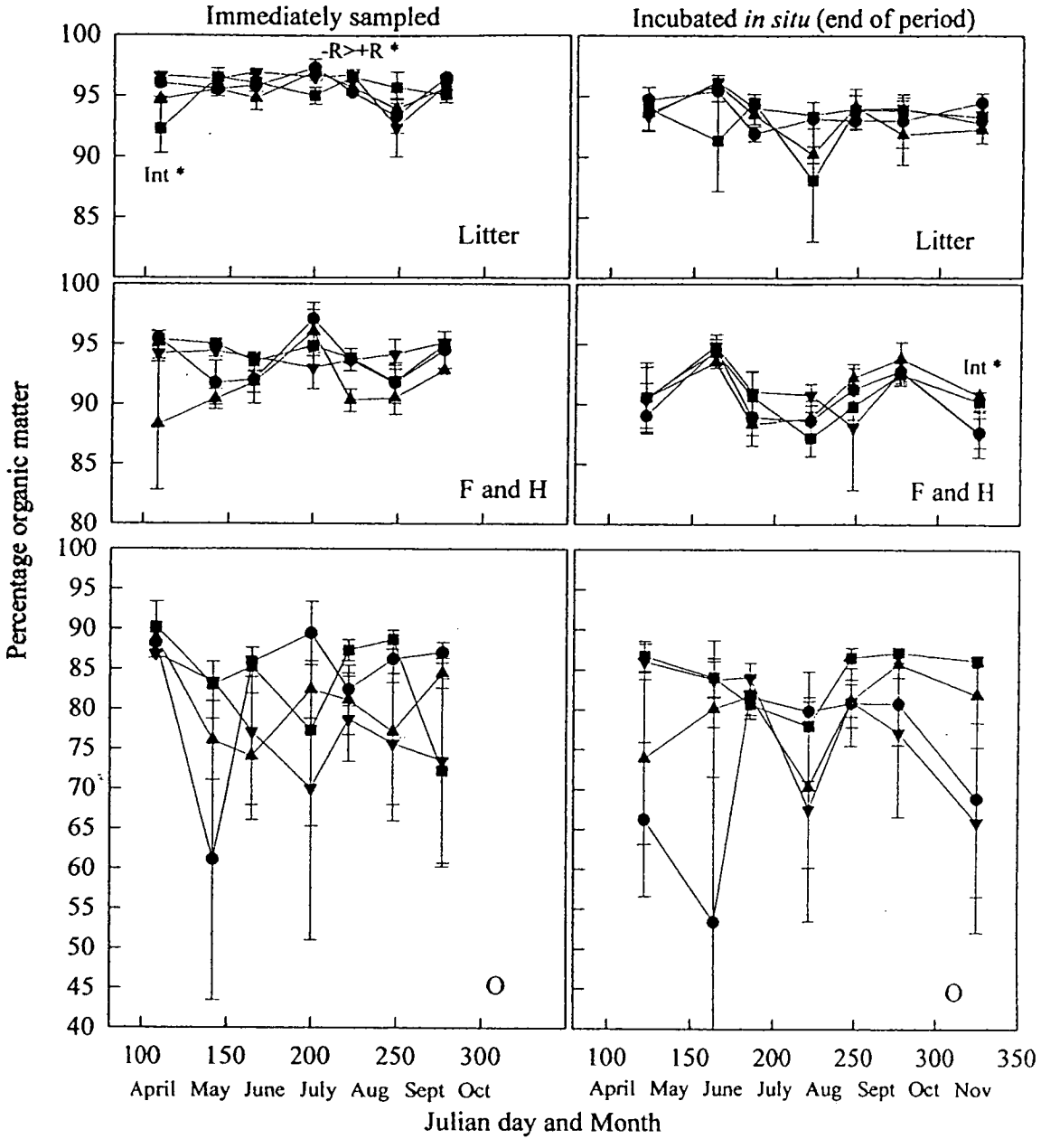


Figure 3.3.1b: Mean percentage organic matter (± standard errors) (n = 3) for L, FH and O horizons from + R (●), + RH (▲), - R (■) and + H (▼) treatments. Immediate and *in situ* incubated samples are represented for the 1994 growing season, from April to November 1994. Treatment differences are shown; '*' , '**' and '***' indicate significance at the $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ levels, respectively. 'Int.' = an interaction between the presence of residue and herbicide.

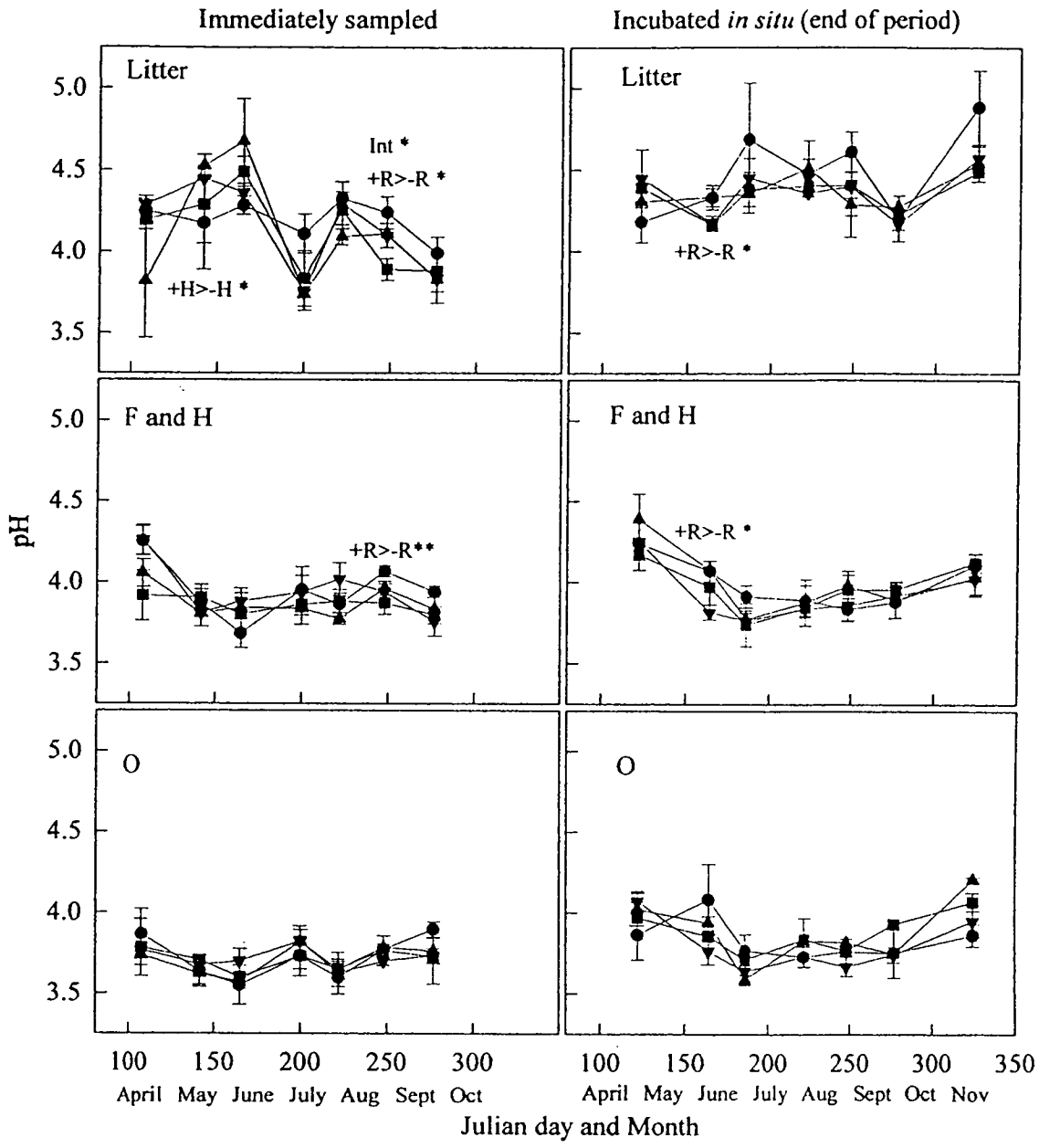


Figure 3.3.1c: Mean (± standard error) of soil pH (in water) of all horizons (L, F and H and O) and treatments (+ R (●), + RH (▲), - R (■) and + H (▼)) recorded during the 1994 growing season (n = 3). Immediate and *in situ* incubated samples are represented from April to November 1994. Treatment differences are shown; '*' , '**' and '***' indicate significance at the $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ levels, respectively. 'Int.' = an interaction between treatments.

from all treatments contained greater proportions of organic matter than that in immediately collected samples. Comparison of immediately sampled material with that of contained cores taken from the soil on the same date demonstrated that the pH of litter at the start of each incubation was lower. The largest difference was observed in July, when immediately sampled soils were dry. A corresponding decrease in pH was not recorded in the incubated litter. In addition *in situ* samples did not experience a drop in pH at the beginning or the end of the growing season.

Soil bulk density and horizon depth

Table 3.3.1a: A summary of soil physical characteristics including bulk density, soil horizon depth and total horizon biomass (oven dried) per hectare. Means (± standard errors) are listed for all treatments (+ R, + RH, - R and + H) and soil horizons (L, F and H and O) (n = 3).

		Year and Soil Variable					
		1994			*1995*		
Treatment and Horizon		***Bulk density (g cm^{-3})***	***Soil depth (cm)***	***Total horizon o.d. biomass (tonnes ha^{-1})***	***Bulk density (g cm^{-3})***	***Soil depth (cm)***	***Total horizon o.d. biomass (tonnes ha^{-1})***
+ R	***L***	0.08	4.47	35.14	0.08	2.79	26.41
		(± 0.002)	(± 0.78)	(± 7.59)	(± 0.001)	(± 0.94)	(± 3.39)
	FH	0.11	4.20	43.66	0.12	4.63	54.34
		(± 0.005)	(± 0.17)	(± 1.92)	(± 0.010)	(± 0.47)	(± 1.33)
+ RH	***L***	0.09	4.36	41.98	0.11	3.87	52.49
		(± 0.008)	(± 0.12)	(± 5.94)	(± 0.011)	(± 0.82)	(± 10.01)
	FH	0.14	3.16	41.63	0.11	4.58	42.51
		(± 0.015)	(± 0.68)	(± 4.55)	(± 0.008)	(± 0.41)	(± 8.18)
- R	***L***	0.11	4.77	37.87	0.12	2.91	35.17
		(± 0.010)	(± 0.48)	(± 13.08)	(± 0.003)	(± 0.22)	(± 3.40)
	FH	0.11	3.50	41.45	0.13	3.17	47.41
		(± 0.008)	(± 0.30)	(± 3.86)	(± 0.003)	(± 0.46)	(± 5.14)
+ H	***L***	0.13	3.61	45.36	0.11	3.46	35.43
		(± 0.011)	(± 0.41)	(± 1.03)	(± 0.010)	(± 0.43)	(± 3.59)
	FH	0.11	3.52	42.23	0.11	4.75	54.11
		(± 0.011)	(± 0.90)	(± 13.92)	(± 0.004)	(± 0.13)	(± 2.36)

The bulk density of soils ranged from 0.08 in the litter layer to 0.14 g cm^{-3} in the FH horizon (*Table 3.3.1a*). Values increased with soil depth (in all except the 1994 + H treatment). Changes from the time of felling were small and inconsistent, depending on treatment. In the + R and - R plots, values increased through time. Similar observations were recorded in the + RH litter layer. However, bulk density decreased in the + RH FH horizon and + H litter layer and remained unchanged in the FH horizon of + H plots. Residue retention significantly reduced the litter layer bulk density in 1994 ($P = 0.034$). Treatment differences decreased with time and herbicide application did not influence results.

Horizon depth demonstrated different trends depending on sampling year (*Table 3.3.1a*). In 1994 the L layer was between 0.27 cm and 1.27 cm deeper than the underlying FH horizon. However, in 1995 this trend reversed, with the FH horizon being up to 1.94 cm deeper. Observations between years indicated that there was a decrease in the mean depth of litter (except in + H plots) and a corresponding increase in the FH from 1994 to 1995. Treatment differences were not significant in either year.

The mean biomass of oven dried litter ranged from 10.4 and 13.4 t ha^{-1} (+ R and + H treatments, respectively) in 1994, and decreased slightly a year later to between 7.8 and 12.5 t ha^{-1} (+ R and + RH plots). Small variations were recorded between values in the FH horizon in 1994 (12.2 and 12.9 t ha^{-1}, in - R and + R treatments, respectively. In 1995 values increased to between 13.0 and 16.0 t ha^{-1}, (in - R and + R plots respectively). Residue retention did not influence results, although herbicide application significantly increased litter weight in 1994 ($P = 0.048$).

3.3.2 Chemical characteristics of soils

Total soil N and P contents were greater in 1994 than 1995, for all treatments and horizons except in the FH layer of residue retained plots (*Figure 3.3.2a*). In contrast, K contents increased from 1994 to 1995 in + RH, - R and +H treatments. Magnesium and Ca also accumulated in FH horizons in 1995, resulting in greater contents. However, in the litter layer Mg was greater in 1994 for +R, -R and +H treatments, whereas Ca contents tended to decrease in the second year in all plots except + H.

Despite large differences between 1995 means (especially for Ca), treatment effects were not usually significant. Disparity in nutrient concentrations and biomass across the site resulted in large variations in content per hectare. However, treatment effects were observed in 1994.

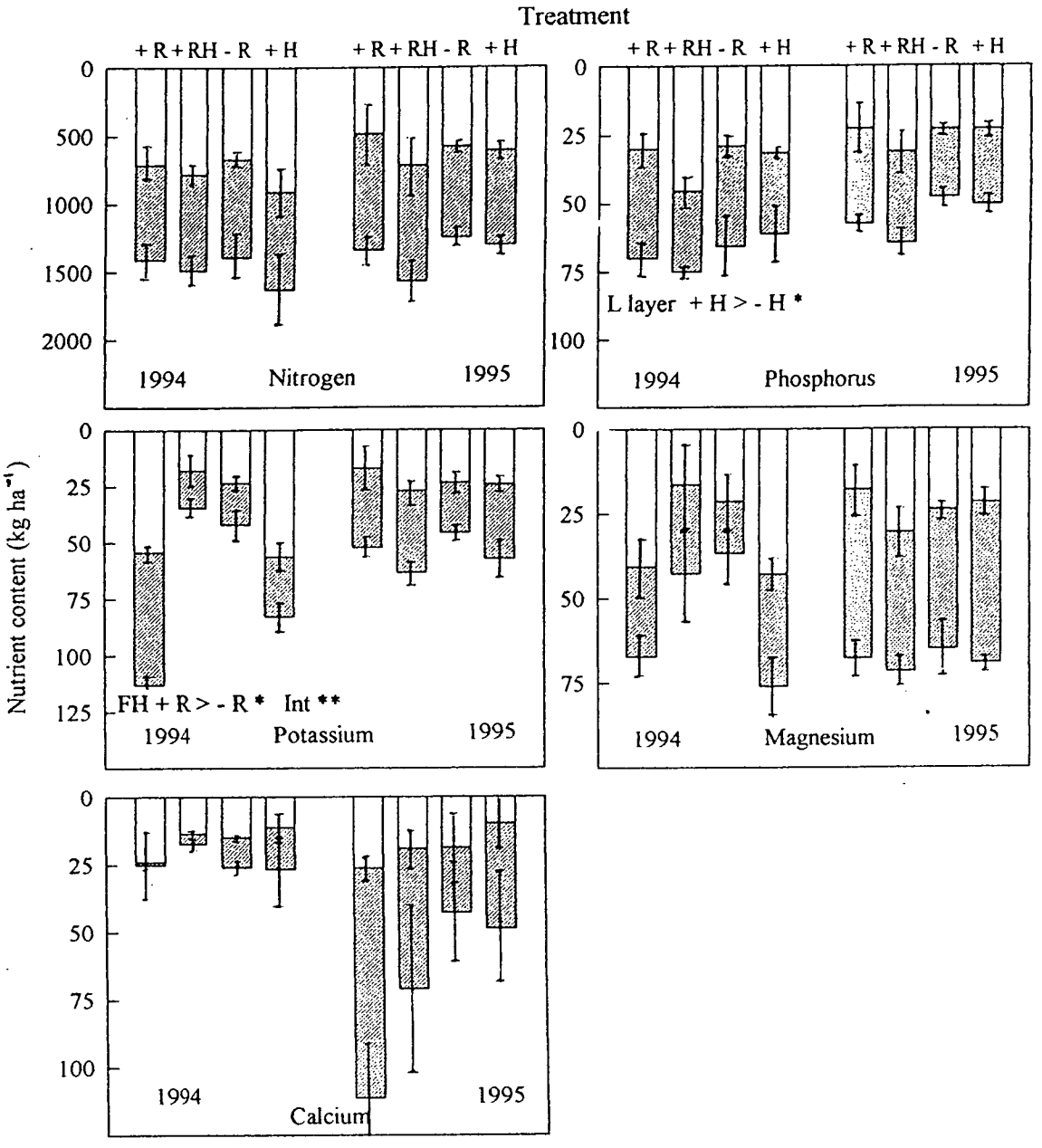


Figure 3.3.2a: Total soil nutrient contents (kg ha^{-1}), recorded in November 1994 and 1995. Each bar represents the nutrients present in the litter (□) and FH (■) soil horizons. Means (± standard errors) are represented for + R, + RH, - R and + H treatments (n = 3). Treatment differences are shown; '*' , '**' and '***' indicate significance at the $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ levels, respectively. 'Int.' = an interaction between the presence of residue and herbicide.

Litter layer P contents were greater in herbicide applied plots (P = 0.032), while residue retention significantly increased K content in the FH horizon (P = 0.044). Nitrogen, Mg and Ca (transformed data) contents were not affected by treatment.

The C/N ratios measured at the end of 1994 and 1995 ranged between 26 and 39 in the L and FH horizons (*Table 3.3.2a*). Treatment did not significantly affect the value in either year.

Table 3.3.2a: C/N ratios from + R, + RH, - R and +H treatments recorded in November 1994 and 1995. Means (± standard errors) are tabulated (n = 3).

	Year and Horizon			
	1994		*1995*	
Treatment	*L*	*FH*	*L*	*FH*
+ R	26.0 (± 2.3)	31.9 (± 3.9)	27.5 (± 1.1)	33.7 (± 4.8)
+ RH	27.5 (± 1.4)	30.1 (± 2.2)	34.1 (± 5.8)	31.5 (± 0.6)
- R	29.5 (± 1.0)	27.7 (± 2.2)	31.4 (± 2.5)	36.6 (± 3.8)
+ H	27.0 (± 3.6)	28.5 (± 0.3)	30.2 (± 0.6)	39.6 (± 2.3)

Mineralisation of nitrogen during the 1994 growing season

Ammonium-N

Depending on treatment, total net NH_4^+ mineralization within the upper 15 cm of soil ranged between 58 and 92 kg ha^{-1}, for the 1994 growing season (*Figure 3.3.2b*). Of this, over 70 % occurred in the litter layer (from 48 to 68 kg ha^{-1} GS^{-1} in + H and + R treatments, respectively) while least NH_4^+ was released in the O horizon (between 4 and 11 kg ha^{-1} GS^{-1} for + RH and + R treatments, respectively). In the presence of residue, mean total release of NH_4^+ from the L, FH and combined horizons (L, F, H and O) was 15, 7 and 25 kg ha^{-1} GS^{-1} greater than from the clear soils, respectively. However, treatment differences were not significant for combined or data from individual horizons.

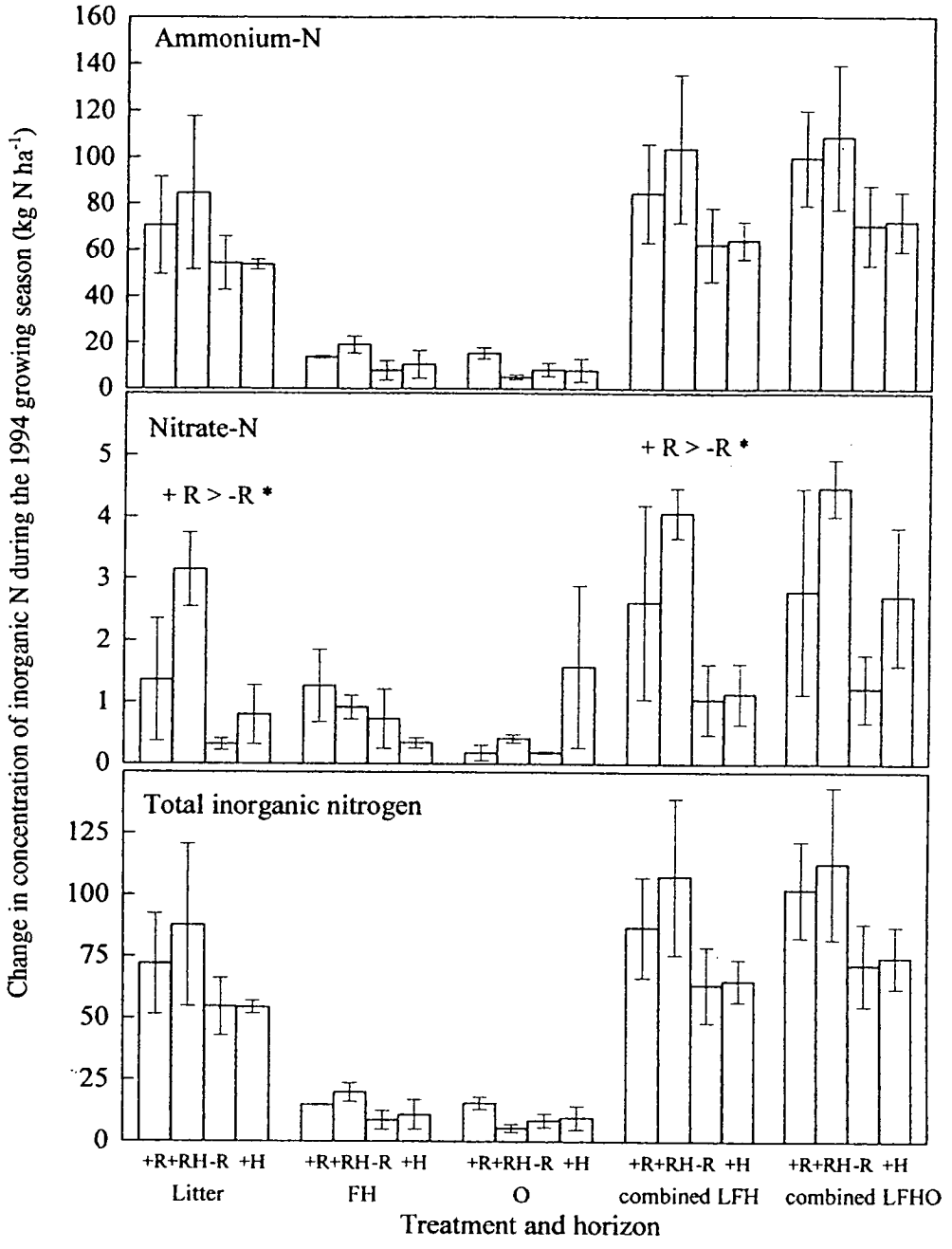


Figure 3.3.2b: Total mineralisation of NH_4^+, NO_3^- and total inorganic N throughout the 1994 growing season. Quantities from the L, FH and O horizons, and totals from combined horizons are presented for all treatments (+ R, + RH, - R and + H). Means (± standard errors) are represented (n = 3) and significance levels given in the case of treatment differences; '*' , '**' and '***' indicate significance at the $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ levels, respectively.

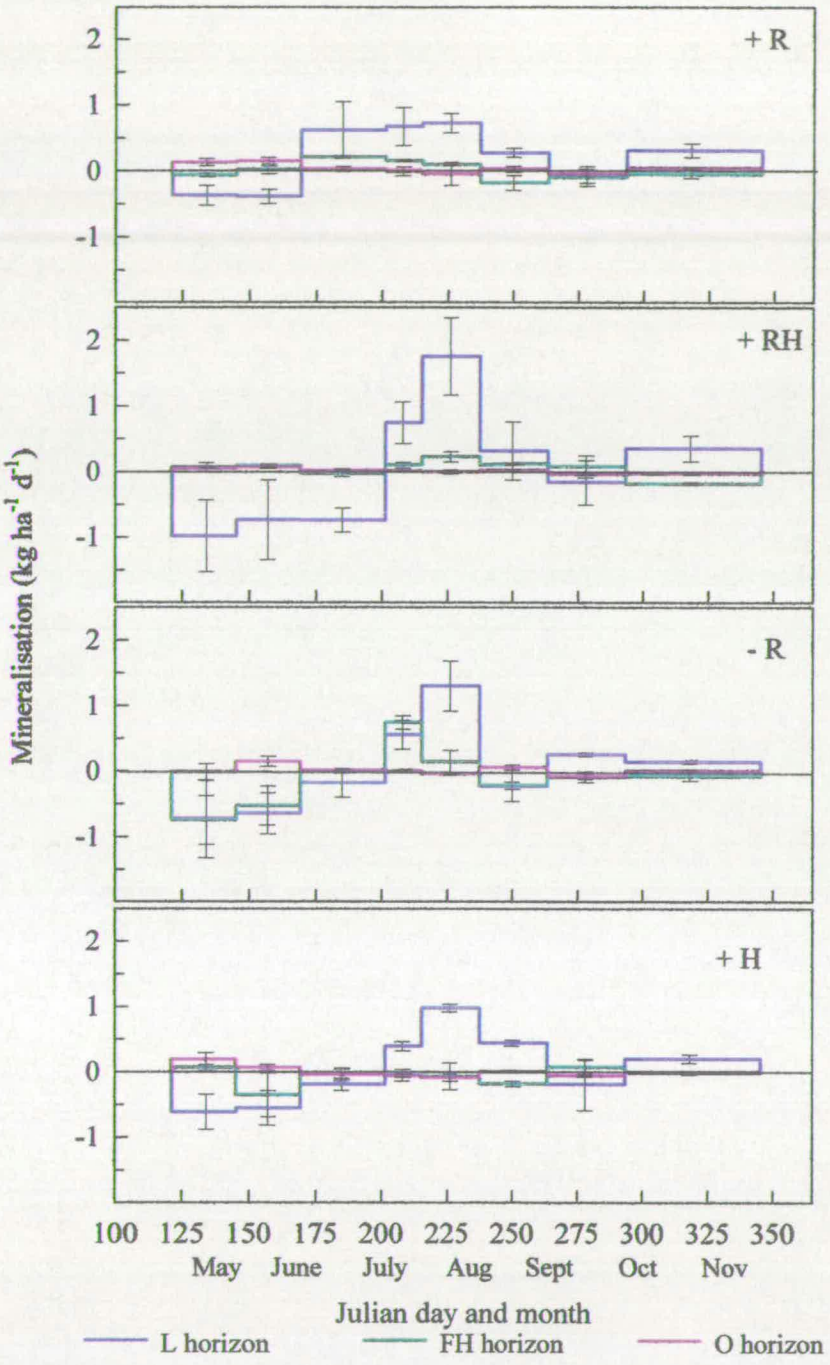


Figure 3.3.2c: Chart demonstrating mineralisation rate of NH_4^+ during the 1994 growing season. Bars represent rate means (± standard error) from all treatments (+ R, + RH, - R and + H), and horizons (L, F and H, and O) (n = 3).

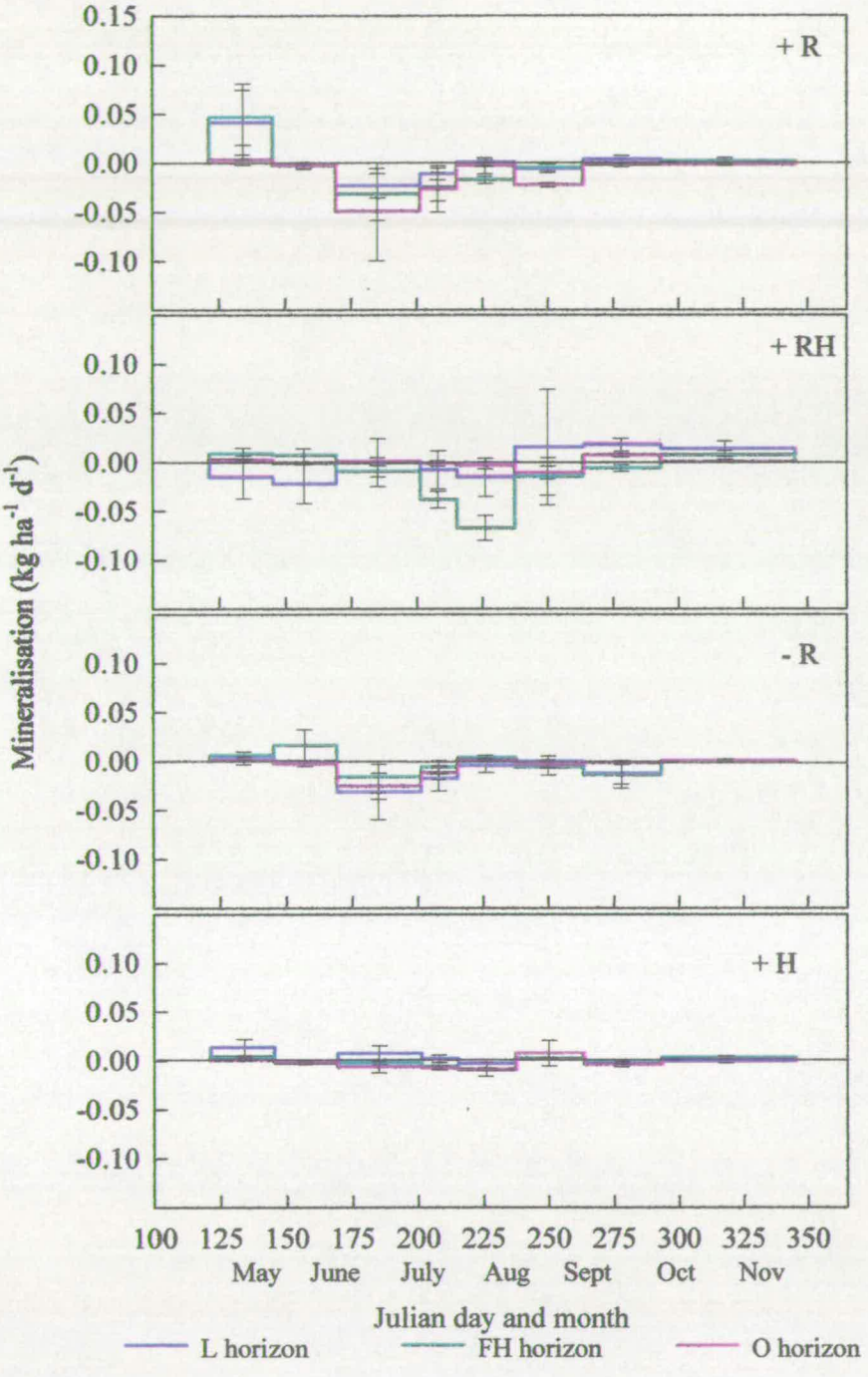


Figure 3.3.2d: Total mineralisation of NO_3^- throughout the growing period of 1994. Quantities from L, F and H, and O horizons and totals from combined horizons are presented for all treatments (+ R, + RH, - R and + H). Means (± standard errors) are represented (n = 3).

From April to the beginning of June NH_4^+ was immobilised in the litter layer of all treatment plots with net mineralisation first detected in mid June (*Figure 3.3.2c*). Rates of release continued to increase until maximum levels were reached from the end of July to the middle of August (between 0.7 to 1.7 kg ha^{-1} d^{-1}). Thereafter, net mineralisation and immobilisation were recorded until the end of November.

Differences in NH_4^+ release through time were not consistently affected by treatment, although the rate of net mineralisation was increased by the presence of residue during October and November. Litter from + R plots maintained higher net mineralisation rates for a greater duration of the growing season resulting in larger total release. Similar quantities became available in the + RH plots, which were attributed to the greater daily rates (during July) experienced for a shorter period of time. In - R and + H plot litter, rates of net ammonification were low and the total released through the growing season was reduced.

Nitrate-N

Small amounts of NO_3^- became available during the 1994 growing season. Total quantities mineralised in the upper 15 cm of soil ranged between 1.2 and 4.5 kg ha^{-1} GS^{-1} for - R and + RH plots, respectively (*Figure 3.3.2b*). Within the different soil horizons, NO_3^- release was greater in the L and FH horizons (from 0.3 to 3.1 kg ha^{-1} GS^{-1} for - R litter and + H FH, respectively) than the O layer.

The total availability of NO_3^- for the 1994 growing season was higher in the FH horizon than the litter layer, and was significantly increased in the litter and combined L, F and H horizons where residues were retained ($P \leq 0.039$). Although the rates of net immobilisation and mineralisation of NO_3^- varied throughout the year, there was no trend associated with season (*Figure 3.3.2d*).

Total inorganic nitrogen

Availability of inorganic N in each soil horizon was not significantly affected by the presence of residue. Although total quantities varied between horizons and treatment, greater amounts were recorded in the litter layer and samples from the forest floor originating from under logging debris.

3.3.3 Vegetation survey and harvest

A complete species list for *Site 1* is given *Chapter 2.6*. At the end of the 1994 growing season total oven dried weight of above ground vegetation and nutrient contents did not differ significantly between treatments (*Figure 3.3.3a*). However, biomass was greater in - R than + R plots (497.2 (± 353.4) and 283.7 (± 129.4) kg ha^{-1}, respectively). In addition N, P and K

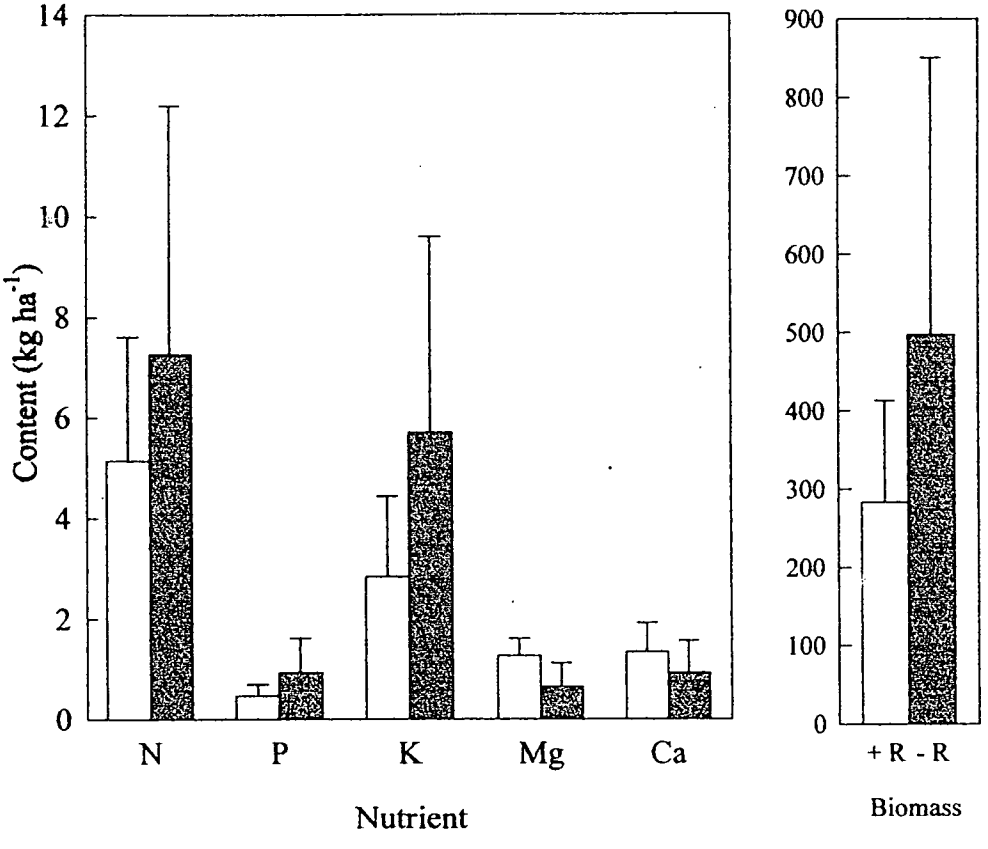


Figure 3.3.3a: Nutrient content and biomass of above ground vegetation removed from the site, in + R (□) and - R (■) treatment plots. The sample mean (+ standard errors) are shown (n = 3).

contents increased in the absence of residue, reflecting similar vegetation nutrient concentrations between treatments. The greatest removals by plant uptake were observed for N, followed by K, Ca, Mg and P (*Figure 3.3.3a*). Despite the larger biomass present in the - R plots, absolute removals of Mg and Ca were slightly greater in the residue grown vegetation.

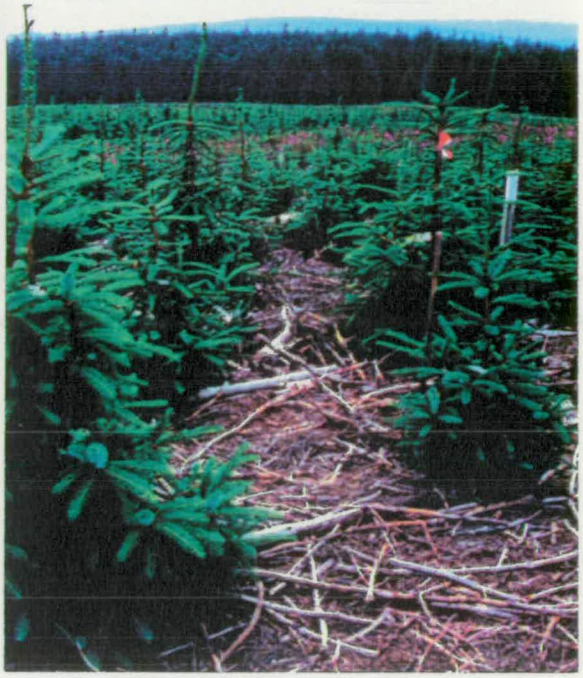
Table 3.3.3a lists the species recorded within + R and - R treatment plots at the beginning of August 1994. In addition, the associated ecological indicator values (determined by Ellenberg 1988) are given for soil N status, moisture and reactivity where available. Residue retained plots contained greater numbers of herbaceous species (including *Chamerion angustifolium*, see *Plate 3.3*), while graminoids, rushes and sedges were predominant in the - R plots. Woody species were uncommon and grew in both treatment plots.

Table 3.3.3a: The presence (✓) and absence (-) of species occurring in +R and -R treatment plots in August 1994. Vegetation types have been classes as herbs (H), grasses (G), woody (W) or moss (M). Ecological indicator values F (moisture), R (reactivity) and N (nitrogen status) are listed.

Species	*Vegetation type*	*Occurrence*		*Ecological indicator values*		
		+R	*-R*	*F*	*R*	*N*
Carex spp.	G	✓	-	-	-	-
Digitalis purpurea	H	✓	-	5	3	6
Dryopteris spp.	H	✓	-	6	0	7
Chamerion angustifoliun	H	✓	-	5	5	8
Galium saxatile	H	✓	-	5	2	3
Holcus lanatus	G	✓	-	6	0	5
Rumex acetosa	H	✓	-	0	0	6
R. acetosella	H	✓	-	3	2	2
Vaccinium myrtillus	W	✓	-	0	2	3
Polytrichum spp.	M	✓	✓	-	-	-
Naturally regenerating Sitka spruce	W	✓	✓	-	-	-
Agrostis stolonifera	G	-	✓	7	0	5
Calluna vulgaris	W	-	✓	0	1	1
Eriophorum vaginatum	G	-	✓	9	2	1
Juncus squarosus	G	-	✓	7	1	1
Molinia caerulea	G	-	✓	7	0	2

Residue + R

Residue and herbicide + RH



Clear - R

Clear and herbicide + H

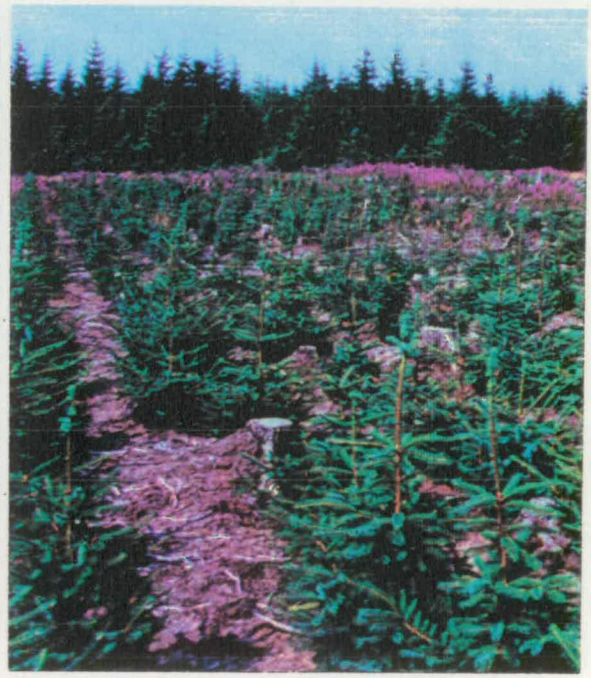


Plate 3.3: Photographs of vegetation cover at *Site 1*, in the fourth growing season. *Chamerion angustifolium* is present in the + R plots while gramminoids, rushes and sedges are more abundant in the clear areas.

Due to the poor re-establishment of vegetation following clearfelling, in both treatment plots, the reliability ratios calculated during indicator species analysis were poor (maximum value 0.22). Therefore the results and analysis of variance should be treated with caution (*Table 3.3.3b*). Variables (F, R and N) were significantly different between treatments. Residue retention increased R and N values ($P \leq 0.019$) indicating growth of species characteristic of less acid soils and greater N availability. While F values, of vegetation growing in the absence of logging debris were greater ($P = 0.004$), suggesting that soils were moister.

Table 3.3.3b: A summary of indicator values and reliability ratios calculated from vegetation present in + R and - R treatments. Means (± standard errors) are presented (n = 3).

Indicator	***Treatment***	
	+ R	***- R***
F	4.74 (± 0.27)	7.75 (± 0.4)
R	4.52 (± 0.37)	1.20 (± 0.10)
N	6.96 (± 0.72)	1.18 (± 0.12)
Reliability ratio	0.13 (± 0.05)	0.04 (± 0.03)

3.4

DISCUSSION

3.4.1 *Soil characteristics and nutrient availability*

During the following sections, soil variables (LFH horizon depth, bulk density, nutrient content and weight) will be compared with results obtained during a five year chronosequence incorporating recently felled sites within Kielder Forest (Titus 1985). However, the residue treatments reported in the current study differed from those observed by Titus (1985). At *Site 1*, logging debris consisted of branches and needles grown by trees occurring within the plot. Whereas, the residue mats studied by Titus (1985) resulted after trees were felled and delimbed in a 'herring bone' fashion (*Chapter 1.1.1*). Consequently the number of spruce crowns supplying residue to the brash swathes was proportionately greater than that remaining in the residue plots at *Site 1*. Comparison between the two studies is complicated further because the sites utilised during the chronosequence represented soil dynamics 0, 1, 2 and 5 years after felling. Whereas variables in the current study were recorded during the third and fourth years only.

Low bulk densities measured in the L, F and H horizons (between 0.08 and 0.14 g cm^{-3}) reflected the high content of undecomposed organic matter. The values were similar to results from combined LFH horizons recorded shortly after harvesting (Titus 1985). Titus (1985) recorded fluctuations in bulk density depending on treatment. Under clear strips values increased after two years (from approximately 0.10 at felling to 0.12 g cm^{-3}), before dropping to felling levels in the fifth year. Whereas, densities in the residue strips remained constant until the second year, when decreases from approximately 0.10 to 0.08 g cm^{-3} occurred, due to the incorporation of felling residue. Differences between treatments and years at *Site 1* were very small. Settling of the residue and incorporation of litter to the lower horizons in the three years following felling are suggested to have reduced the effects of treatment.

Titus (1985) recorded that the depth of the organic horizon (LFH) decreased during the first 5 years after felling in both CON and WT areas, from approximately 6.5 to 5.5 cm. However under residue, an increase of about 1 cm was observed in the first year after felling, due to the drop of needles and small woody components from logging debris. This was followed by a 2.5 cm decrease by year five. Weight of the organic horizon also decreased during the measurement period, after an initial increase during the first year. Five years after felling, weight in both treatment plots measured approximately 50 t ha^{-1} (Titus 1985). At *Site 1*, decreases in the combined LFH horizon depth (*Table 3.4a*) and weight per hectare (*Table*

3.4b) were recorded in the + R and - R plots only, following reductions in the litter layer. The large spatial variation between blocks and the small number of sampling occasions are likely to account for the inconsistent trends between treatments and years.

Table 3.4a: Depth (cm) of combined LFH horizons from + R, + RH, - R and + H treatment plots recorded in November 1994 and 1995. Means (± standard errors) are given (n = 3).

	Year	
Treatment	***1994***	***1995***
+ R	8.11 (± 0.82)	7.42 (± 1.26)
+ RH	7.30 (± 0.73)	8.46 (± 1.12)
- R	6.92 (± 1.19)	6.37 (± 0.59)
+ H	6.92 (± 1.18)	8.00 (± 0.45)

Invasion of + R and - R plots by shallow rooting vegetation may accelerate combination of litter into the upper horizons and enhance decomposition rates above those occurring in herbicide applied plots. Active roots exude carbon compounds which increase the abundance of soil fauna and aid breakdown of substrates. The resistant organic substances produced accumulate in the humus layer, where conditions of temperature and moisture are more constant (Waring and Schlesinger 1985).

Table 3.4b: Weight of combined LFH horizons (oven dried t ha^{-1}) from + R, + RH, - R and + H treatment plots recorded in November 1994 and 1995. Means (± standard errors) are given (n = 3).

	Year	
Treatment	***1994***	***1995***
+ R	78.8 (± 5.7)	80.8 (± 11.6)
+ RH	83.6 (± 9.8)	95.0 (± 17.0)
- R	79.3 (± 15.3)	82.6 (± 8.1)
+ H	87.6 (± 17.4)	89.5 (± 5.1)

Seasonal trends and treatment differences in moisture content, organic matter and pH from May to November 1994 are discussed below using results from cores collected immediately. These samples reflected actual conditions within the bulk soil more accurately than the incubated horizons (*Chapter 3.4.1*).

Moisture content in the litter layer decreased during the summer, from approximately 80 % to between 79 and 68 %, depending on treatment (*Figure 3.3.1a*). Reductions occurred in response to low precipitation inputs and warmer soil temperatures during July to September (*Chapter 2.*) which caused increased evaporation from the soil surface and evapotranspiration by vegetation. On five of the seven measurement dates, moisture content was significantly greater in the residue retained plots (by approximately 5 %). The logging debris reduced evaporation from the soil surface by reflecting solar radiation, lessening transfer of heat from the air to the soil surface by convection and slowing wind speed above the ground. However the elimination of vegetation by herbicide did not significantly affect soil moisture. The greatest treatment difference occurred in mid July when percentage moisture contents were lowest in + H plots (by at least 5 %). It is suggested that the low water tables characteristic of the herbicide plots (*Chapter 2.8.4*) did not replenish moisture in the litter during warm weather with little precipitation. The excessive drying of the litter was not observed in the + RH plots probably due to the presence of the residue mulch.

In agreement with observations by Smethurst and Nambiar (1990b), removal of logging residue decreased water content of the litter, but had little effect on the soil beneath. Small fluctuations in the FH moisture content resulted due to the mulch effect of the litter layer and the poor hydraulic conductivity of the organic horizon (Boggie and Knight 1980). Despite these characteristics, residue retention significantly increased FH layer moisture on three sampling occasions and the application of herbicide reduced contents at the beginning of the growing season. Moisture content in the O horizon was low, compared to the L and FH layers. Large variations between sample date and treatment were attributed to the presence of sand in the sample. It is suggested that the lower percentage moisture contents of organic horizons containing mineral soil resulted from an interaction between the improved drainage of water and the greater dry bulk density. The sand present was distributed in a manner characteristic of mixing within the O and mineral horizons, rather than due to sampling of deeper soil layers. Therefore, it is suggested that the mineral component was incorporated during disturbance at felling.

Litter inputs originating from the trees currently growing at *Site 1* will be low. Crown size and root plate diameter continue to increase and, as yet, competition for resources such as light, nutrients and water is minimal. Therefore, any difference in percentage organic matter occurring two to three years after clearfelling is likely to be a response to residue input at felling.

Throughout the 1994 growing season, the litter layer contained high percentages of organic matter (between 92 and 98 %). However, like results from a North American mixed hardwood stand, values did not decrease with increasing harvest intensity (Hendrickson *et al.* 1989). In the deeper horizons, material became partially decomposed and organic matter decreased to between 88 and 97 % (in the FH horizons). Although treatment differences were not significant in the FH horizon, high values were recorded in residue retained plots in mid July. Increased temperature in the summer may enhance macro and mesofaunal activity and accelerate the incorporation of new material from the litter layer. This trend was not observed in the clear plots and it is suggested that the low moisture restricts the activity of soil fauna. Organic matter in the O horizon was extremely variable (between 61 and 91 %) due to the inconsistent presence of sandy material.

Within the organic horizons pH decreased with increasing depth from between 3.7 - 4.7 in the litter to 3.5 - 3.9 in the O layer. Seasonal changes were inconsistent between horizon. The greatest variation was recorded in the litter layer, where the impact of environmental influences including moisture, temperature, and soil chemistry are less buffered due to the intimate relationship with aboveground conditions. In the litter, pH was low at the start and finish of the growing season. Acidity also increased during July when percentage moisture contents were low, especially in the + RH, - R and + H plots. Similar trends occurred in the FH and O horizons during the summer. Acidification of soils can take place when H^+ ions are released during nitrification. However, the low levels of NO_3^- measured in the soils at *site 1* suggest that rates of nitrification and the associated potential to acidify the soil is small.

Total inorganic N released from the LFH horizon during the third growing season (start of May to the end of November) ranged between 63 and 108 kg N ha^{-1} in - R and + RH plots, respectively. Additional release during the winter was expected to be small as microbial activity declines at low temperatures (see *Chapter 4*). Assuming that similar relationships between microbial activity and temperature occur in the field as in laboratory incubations (see *Chapter 4.4.1*), inorganic N released from the end of November (1994) to the beginning of April (1995) could be estimated. The number of days with a mean daily soil temperature ≥ 4 °C was multiplied by the daily mineralisation rate of the litter and FH horizons at 4 °C collected from + R and - R plots (see *Chapter 4.3.1*). During the winter months, approximately 8.4 and 4.6 kg N ha^{-1} were estimated to be mineralised in + R and - R treatments, respectively. Lower quantities were estimated in clear soils due to the cooler temperatures and the slower rates of mineralisation in substrate from - R plots (see *Chapter 4.3.1*). The additional inorganic N represented 8.0 and 6.7 % of the annual inorganic N released in + R and - R plots, respectively.

Total mineralisation for the year starting April 1994, compared favourably with estimates from peat soils (90 kg N ha^{-1} y^{-1}, Wiklander and Nommik 1987). Although results were greater than those recorded for undisturbed stands of Sitka spruce growing on a peat (28 kg N ha^{-1} y^{-1}, Carlyle 1984). Intensive management (including felling, ploughing and raking) and disturbance of forest soils are known to enhance mineralisation (Matson and Vitousek 1981; Burger and Pritchett 1984; Van Cleve and Yarie 1986; Stevens and Hornung 1988; Smethurst and Nambiar 1990b), by modifying factors such as soil temperature, moisture content, substrate quality, aeration or a combination of these factors. For example, Stevens and Hornung (1988) recorded increased fluxes of inorganic N through the C horizon from 10 to 70 kg N ha^{-1} y^{-1} following clearfelling. The larger values yielded at *Site 1*, compared to those of Carlyle (1985) probably arose due to enhanced mineralisation rates following disturbance at harvesting.

Most (96 to 98 %) of the inorganic N mineralised in the LFH horizon during the growing season was in the form of NH_4^+. This proportion has frequently been recorded for dissolved inorganic N within British conifer plantations (Williams 1983; Adams 1986; Carlyle and Malcolm 1986). Low concentrations of NO_3^- may result from a number of factors including inhibition of nitrification at low soil pH (Roseburg 1986) and competition for NH_4^+ between heterotrophs, plants and nitrifiers (Riha *et al.* 1986). Estimates of NO_3^- may also be underestimated due to uptake by vegetation (Carlyle 1986) and denitrification. However, a series of papers detailing results from a Sitka spruce plantation in North Wales (Stevens and Hornung 1988; Emmett *et al.* 1991a; Stevens *et al.* 1995), reported increased NO_3^- especially in the lower horizons. At *Site 1* NO_3^- mineralisation was present and increased significantly under residue strips. Emmett *et al.* (1991a) recorded similar results from lysimeters placed under woody residue and inert artificial mulch. It is suggested that the more favourable conditions underneath residue (Emmett *et al.* 1991a) and the slow adaptation of nitrifiers to increasing acidity (Williams 1995) may enable low rates of NO_3^- production in these soils.

Like results from peaty soils recorded by Wiklander and Nommik (1987), mineralisation decreased with depth. The greatest treatment effects were recorded in the litter layer where differences in substrate quality and environmental modifications were most pronounced. Residue retention provided more favourable conditions of moisture and temperature for microbial activity, which promoted net mineralisation of NO_3^- and NH_4^+ in the litter. Net ammonification was greatest during August, when litter temperatures were highest. Towards the end of the growing season, temperatures were unaffected by treatment and moisture contents were similar. Yet NH_4^+ release was more rapid in the residue retained plots, suggesting a difference in the quality of the litter between treatments or the accumulation of

microbial organisms during the course of the summer. Rewetting of dry soil may result in temporary increases in decomposer activity. However, no response was observed in the litter from clear plots after moisture contents increased from below 75 %. It is possible that rewetting did influence mineralisation in the bulk soil, but that the changes were not detected by analysis of contained soils. Nitrate release did not appear to exhibit seasonal trends. However, difficulties associated with the detection of very low values may have obscured relationships.

The annual N requirement of natural temperate coniferous forest ecosystems averages 46 kg ha^{-1} (Cole and Rapp 1981). Demands of 50 kg ha^{-1} y^{-1} were quoted for Sitka spruce in North Wales (Stevens and Hornung 1988), while greater uptake (69 kg ha^{-1} y^{-1}) was reported by Miller *et al.* (1979) for Corsican pine growing on sand. Assuming similar demands by Sitka spruce at *Site 1*, growth will not be limited by N supply rate during the third season. (The nutrient uptake of Sitka spruce during the third growing season is discussed further in *Chapter 7.2.*) However, it is unlikely that the nutrient dynamics observed are indicative of conditions immediately after harvesting or of long term availability. In addition, uptake by ground vegetation in the + R and - R treatment plots was not considered. Changes in the decompositional state of the residue, including the C/N ratio, leachable nutrients, and physical influences of the mulch interact to modify net mineralisation in the organic soil horizons (see *Chapter 1.5*). At *site 1*, it is expected that soil mineralisation will continue to be influenced by logging debris until canopy closure. Substrate quality will play an increasingly large part in determining nutrient release, as the physical influence of the residue diminishes, due to debris break down and the increasing tree crown size.

The C/N ratio is important in controlling the rate of mineralisation (Adams and Attiwill 1982 and Vitousek 1982). However, it is a crude figure and more recent studies have suggested that particular fractions of carbon and N are more important in determining soil nutrient release (Flanagan and Van Cleve 1983; Attiwill 1986). Therefore little importance should be given to the estimates of total C/N ratios obtained during the current experiments in determining soil nutrient dynamics. Values calculated for the L and FH horizons were variable and treatment influences were difficult to determine. Compared to the C/N ratio recorded under residue at *Site 2* (61 (see *Chapter 4.3.4*)), values obtained at *Site 1* were low (between 25 and 40). Berg and Ekbohm (1983) demonstrated that the values at which net mineralisation occurs alters with site conditions. They recorded inorganic N release at C/N ratios of 63 in Scots pine litter from a clear cut forest and 109 in the same litter from a mature forest. This suggests that nutrient mineralisation at *Site 1* is unlikely to be limited by the C/N ratio of the litter.

Total contents of macronutrients (except Ca) in the LFH horizons were greater at the current site than those recorded during a chronosequence covering 5 years post felling (Titus 1985). Unlike results obtained by Titus (1985) the presence of residue did not increase nutrient contents. However, between the 1994 and 1995 measurements, large increases in the calcium content of the FH horizon occurred under residue. Accumulation of this base cation may arise in response to increased losses from debris, following slow initial release rates documented by Maheswaran and Attiwill (1987) and Fahey *et al.* (1991). In addition, the humus layer possesses a high capacity to store basic cations which bind to acidic groups in the organic matter as an exchangeable or complex form

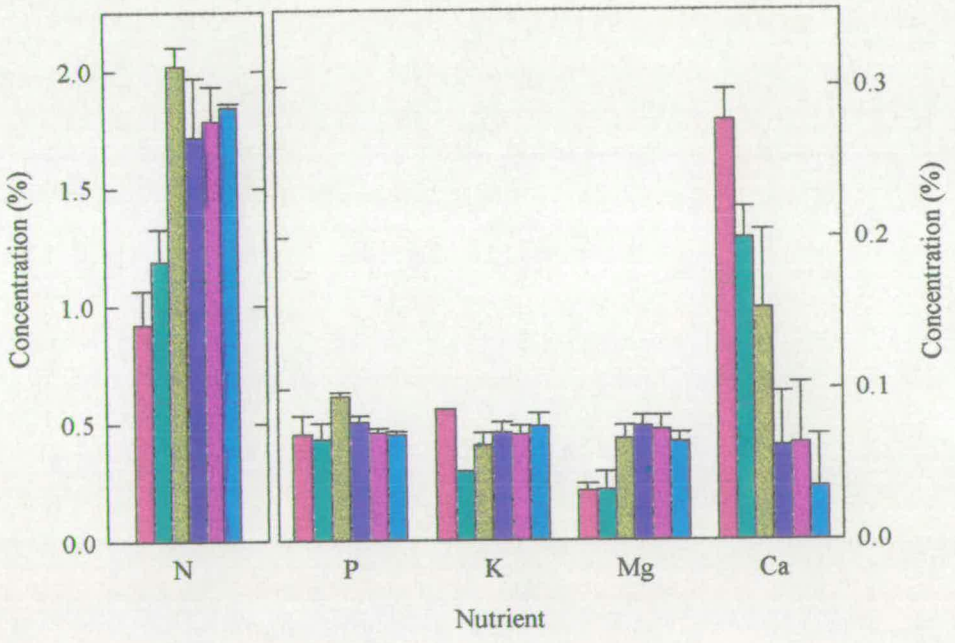


Figure 3.4: Concentrations of N, P, K, Mg and Ca in litter from recently fallen logging debris (■), from the old forest floor six months after clearfelling (■) (*Site 2*) (n = 4), and four years after felling in + R (■), + RH (■), - R (■) and + H (■) treatment plots at *Site 1* (n = 3).
Treatment means (+standard errors) are plotted.

Nutrient concentrations in needle litter collected 6 months after clearfelling (under harvesting residue and from the old forest floor at *Site 2* (see *Chapter 4.3.4*)) were compared with values measured in the litter layer of + R, + RH, - R and + H treatment plots four years after clearfelling (*Figure 3.4*). Like results from Berg and Staaf (1981), Maheswaran and Attiwill (1987), DeCatanzaro and Kimmins (1984), Fahey *et al.* (1991a) and Cortino and Vallejo (1994) N concentrations in needle litter increased shortly after felling. However, P levels were variable, in agreement with observations by DeCatanzaro and Kimmins (1984). At *Site 2*, K concentrations in the old forest floor were lower than those from recently fallen litter and *Site 1* treatments. The mobility of K renders it susceptible to rapid leaching loss. For example, Maheswaran and Attiwill (1987) observed that nutrients were released in the order K > Na > Mg > P > N > Ca over a 15 month period in litter. Accumulation of Mg, four years after felling (*Figure 3.4*) may result from deposition of cations in precipitation. Trends for increasing Ca in the FH horizon of *Site 1* soils under residue (see above) were associated with decreases in the total calcium concentration of the litter, compared to initial values after felling. This substantiates evidence that calcium release is delayed.

Mean accumulation of vegetation biomass in the third year after felling was greater in clear than residue retained treatment plots. This reflected the more rapid invasion of gramminoids, sedges and rushes in clear areas, where the physical effects of logging residue on soil surface radiation and temperature, and alterations to the seed bed did not suppress growth (Fahey *et al.* 1991). Similar observations were made during the first five years following WT and CON felling by Outcault and White (1981), Cox and Van Lear (1985), Hendrickson (1988), Stevens and Hornung (1990), Fahey *et al.* (1991b) and Olsson and Staaf (1995). Above ground biomass was approximately 25 to 50 % (Cox and Van Lear 1985) and 50 % (Fahey *et al.* 1991b) greater after WT harvest than CON. At *Site 1*, mean biomass was 75 % greater in - R plots during the third growing season. However, the difference was not significant. Low percentage cover by vegetation in all plots was thought to be responsible for large variation across the blocks.

Uptake of nutrients by vegetation during the 1994 growing season could not be accurately determined, as both annual and perennial species were present and below ground material was not harvested. Greater quantities of N, P and K occurred in above ground vegetation of - R plots, whereas Mg and Ca contents were larger in plants harvested in + R treatments. Availability of these cations in the soil of residue retained plots may be larger due to release from logging debris.

Changes in vegetation type following slash removal are generally thought to parallel the nutrient conditions (Olsson and Staaf 1995) and moisture (Fahey *et al.* 1991b) within the soil. Initially the species present will be dependent largely on the pre treatment understory cover (as influenced by canopy density), the seed bank and its response to soil disturbance during logging (Fahey *et al.* 1991b). Influx of seed to *site 1* from surrounding areas will be low, as neighbouring stands of Sitka spruce support little ground vegetation. In addition, the response of vegetation post felling may be delayed by the slow growth of stress tolerant species common in boreal forests or the physical inhibition of growth by woody residue. In clear areas, the vegetation present after three years included *Molinia caerulea*, *Juncus squarosus*, *Eriophorum vaginatum*, *Calluna vulgaris* and *Agrostis stolonifera*. The presence of *Juncus* spp. and *M. caerulea* usually indicate strong flushing (the influx of soil water from adjacent higher ground) and nutrient availability, characteristic of a peaty moorland (Toleman and Pyatt 1974; Ellenberg 1988). *A. stolonifera* and *E. vaginatum* are also typical of wet areas, and poor soils (Ellenberg 1988). While the presence of *C. vulgaris* is an indicator of infertile conditions (Toleman and Pyatt 1974; Ellenberg 1988).

In comparison to the clear treatment plots, the majority of species present in the residue retained areas were typical of more favourable acid soils. This was substantiated by results obtained from analysis of the ecological indicator values assigned by Ellenberg (1988) and *in situ* mineralisation trials, which indicated greater mean availability of inorganic N in + R plots. However, the low percentage cover attained by the plants reduces the certainty with which conclusions may be drawn. The presence of acid conditions was suggested by the growth of *Carex* sp., *R. acetosella*, *V. myrtillus* and *D. purpurea* (Ellenberg 1988). Previous reports from Swedish clearfelled forests indicate that *V. myrtillus* growth responds negatively to full residue retention or needle addition (Olsson and Staaf 1995). Such observations were not recorded in the current experiment. Of the other species identified in the residue retained plots, *H. lanatus* is characteristic of good N supply (Miller *et al.* 1977), *R. acetosa* responds positively to phosphate supply (Ellenberg 1988) and *C. angustifolium* is an indicator of available N (Miller *et al.* 1977; Ellenberg 1988), in particular of an increasing potential for nitrification in the humus (Kovacs 1969; Miller *et al.* 1977).

In the + R treatment plots of *Site 1*, woody debris reduced the growth of graminoids, but promoted tall herbs, especially *C. angustifolium*. Similar results were recorded by Ingelog (1974), Kardell (1992) and Olsson and Staaf (1995). Messier (1993) also recorded invasion by *C. angustifolium* after disturbance at a site during felling or residue burning. It was proposed that this vegetation type grew in response to the greater nutrient supply following conventional harvesting (Olsson and Staaf 1995). Invasion of felled sites by *C. angustifolium*

may also be accelerated by the method of seed dispersal. The white silky plumed fruits are thought to become entangled in the woody residue, whereupon the seed is deposited to the soil below. Therefore the high abundance of *C. angustifolium* in + R plots probably results in response to an interaction between the ability of the residue to capture seed and the growth of the annuals on soils with higher NO_3^- availability.

3.4.2 Advantages and disadvantages associated with coring procedure

Use of disposable steel cans proved to be an efficient method of collecting soil cores provided the upper horizons were soft, stone free, absent of woody root (> 3 to 5 mm) and logging residue (> 3 mm). At *Site 1* the stone free, peaty gley substrate allowed easy insertion of the cans. These could be removed from the bulk soil as required, allowing collection of undisturbed cores containing the L, F, H and some O horizon or O/mineral soil mixture. In residue retained plots large intertwined branches prevented access to some randomly selected sampling areas. Where possible the debris was lifted allowing the soil to be sampled. If the branches could not be moved or the procedure caused damage to neighbouring trees or disturbance to the forest floor, the nearest suitable position was chosen. Therefore, sampling was biased to areas with less residue. The presence of smaller woody twigs and bark sometimes caused the cans to crumple during insertion. This was prevented by brushing the surface debris from the area to be sampled. Consequently, measurements of litter layer depth, annual mineralisation and bulk density within residue retained plots may not reflect exactly quantities and characteristics in the field.

Additional problems possibly associated with contained soil samples during *in situ* incubation included;

- modification of soil physical characteristics such as, moisture, organic matter and temperature,
- conduction of heat via the can walls to and from the soil surface and underlying horizons,
- elimination of precipitation inputs,
- the severing of vegetation and tree roots,
- the prevention of vegetation and needle litter additions to the forest floor,
- additions of oxidised iron (Fe^{3+}) to the soil during can rusting,
- compaction of the upper soil horizons by trampling during access and can insertion, and
- the potential for underestimated values of available NO_3^-, if denitrification occurs in anaerobic soils with high available C.

Build up of heat energy within the cans was prevented by the reflection of solar radiation from the polished exterior and the poor conductivity of the soil in transferring heat away from the

can surfaces. Despite this, soil temperature in the upper horizons of incubated cores is expected to demonstrate less diurnal and seasonal fluctuation than the bulk soil, especially in clear areas. For example, reflection of direct solar radiation and modification of air flow in the head space of the can would lower daily maximum and increase minimum temperatures, respectively. During *in situ* incubation, wetting and drying cycles within the forest floor caused the cans to rust. However, when soils were anaerobic or waterlogged, oxidation was absent. By discarding the soil surface in contact with the can walls, the influences of modified temperature and Fe^{3+} inputs were minimised. Insertion of cans severed tree and vegetation roots possibly causing the organic matter within the core to increase and modify mineralisation. However, measures of organic matter would be influenced only if the root died before assessment, as all live material was removed. Exclusion of fresh litter inputs would not affect contained soils as accumulation during incubation periods (maximum 7 weeks), by needle senescence and vegetation dieback, was low. Forest floor compaction during passage between sampling positions, was expected in all treatment plots and could not be prevented.

During the 1994 growing season the effect of coring procedure on variables including soil moisture content, organic matter and pH were ascertained by comparing immediate and incubated samples.

Drying of incubated upper horizons during the summer months was reduced by the presence of capped cores. This was especially evident in the litter layer of clear plots, where moisture contents maintained percentages similar to those under residue. Consequently, significant treatment differences arising due to the presence of logging debris were observed on only two occasions, compared to five in immediately sampled cores. Within the cans, evaporative losses were prevented by reducing the heating influence of direct solar radiation and minimising air flow above the litter layer. In addition, evapotranspiration was eliminated by severing plant roots during can insertion and checking penetration of soil by new roots. Moisture content of the litter layer throughout the growing season was more strongly influenced by evaporation and evapotranspiration losses than reductions in precipitation inputs. During periods of high rainfall and low soil moisture loss, some rewetting of the upper horizons within isolated cores may occur if water moves laterally below the core and percolates up the wall edges. However, the volume of water undergoing capillary action is likely to be very small.

Organic matter content of L and FH layers was reduced slightly by incubation. Modification of moisture levels and temperatures within the cores may accelerate decomposition of organic matter. However on two occasions, in June and October, large increases were observed in the

FH layer. Corresponding peaks were not recorded in the litter layer of incubated cores or the associated immediate values. It is possible that sampling errors are responsible for this observation.

Soil pH varied between and within sampling dates, making the influence of incubation within cans difficult to evaluate. The litter layer of immediate samples became more acid during very dry periods in the summer. Corresponding decreases were not observed in incubated samples where moisture was retained.

Isolation of soil in cores dampened the effects of the surrounding above and below ground environmental conditions and reduced the differences between residue and clear treatments. Despite the modifications of conditions within the core and the problems associated with inserting the can to residue covered soils, this method was favoured as it is inexpensive, and preparation of cans and removal of the soil sample is simple.

3.5 SUMMARY

The retention of residue during conventional harvesting modifies the conditions experienced in the underlying soil. Moisture losses are reduced, the amplitude of diurnal and seasonal temperature fluctuations is decreased and substrate quality in the upper organic horizons is altered. These conditions enhanced net mineralisation during the third growing season after felling, and increased the availability of NH_4^+ and NO_3^- within the L, F and H horizons. Consequently, species composition of the + R treatment plots was dominated by plants characteristic of greater inorganic N availability (especially NO_3^-).

After whole tree harvesting, the mineralisable substrate remaining at the site consists of the forest floor and severed roots from the previous spruce rotation. The lack of a residue mulch renders the upper soil horizons prone to more extreme temperatures and greater moisture losses during the summer. Therefore, in dry climates where soil moisture may limit microbial processes, the effects of whole tree harvesting are likely to be more detrimental to forest productivity (Lundmark 1983) than reported in the current study. The conditions present in the clear areas of *site 1*, during the third growing season, were less favourable for the mineralisation of N. However, vegetation biomass was greater. Rapid invasion, soon after felling, by species tolerant of low N conditions and high moisture levels are responsible for increased vegetation.

The uptake of inorganic N and base cations by trees and ground vegetation is an important mechanism mitigating leaching losses from the system (Fahey *et al.* 1991b). However, where vegetation growth is killed or suppressed by herbicide application or residue retention, uptake of nutrients may be reduced and leaching losses increased. For example, very high leaching losses of base cations and NO_3^- resulted when regrowing vegetation was eliminated by herbicide treatments for 3 years after clearcutting a northern hardwood forest (Likens *et al.* 1970). At a study site in Wales, reductions in NO_3^- losses to 10 % of that in conventionally harvested areas occurred after approximately 50 % of the ground area was covered by *Agrostis capillaris* (Emmett *et al.* 1991a). However, the inputs of organic N, P and K were found to be greater in the throughfall of residue retained plots, relative to the incoming rain (Emmett *et al.* 1991a). Similar reductions in leaching losses from whole tree harvested sites were recorded by Fahey *et al.* (1991b), in the presence of regrowing vegetation. Annual inputs of vegetation during dieback and shading after canopy closure, may act as important sources of nutrient and long term fertilisers. DeCatanzaro and Kimmins (1985) recognised

that *C. angustifolium* litter is easily decomposed, and may act as a source of carbohydrates and nutrients for soil microfauna and flora (Messier 1993)

The advantages associated with reduced leaching losses and long term nutrient inputs after colonisation by vegetation, may be offset by the presence of competition for nutrients and subsequent reductions in crop growth (Cox and Van Lear 1985). Twenty months after planting, Smethurst and Nambiar (1989) observed 46 % less biomass in trees grown with weeds than those grown in a weed free environment. Strong competition for N was the major limiting resource. However, mineralisation at *Site 1* released sufficient quantities of N during the third growing season to support growth of all vegetation without restricting tree height increment or biomass. Whether this supply would satisfy the crop and vegetation until canopy closure cannot be determined at present.

The absence of treatment differences in bulk density, horizon weight, nutrient content and depth, probably arise due to the time from felling, during which processes in the soil reduced the effect of litter inputs. The high degree of spatial heterogeneity in forest soils means that a large number of samples is required to detect subtle changes in soil properties (Johnson *et al.* 1990). Smethurst and Nambiar (1990b) and Gholz *et al.* (1985) observed similar high variations and error for soil mineralization studies after clear felling. The lack of significant differences recorded at the current site may be a reflection of the actual conditions or indicate that the methods used were not suitable to measure small fluctuations in mineralisation.

Chapter 4

NITROGEN AVAILABILITY IN THE FOREST FLOOR AFTER HARVESTING MEASURED UNDER CONTROLLED CONDITIONS

4.1 INTRODUCTION

The decay rate of litter and consequent nutrient release from the upper soil layers can be a controlling factor in tree growth (Miller 1981). Therefore, it is important to ascertain potential supply from these horizons when estimating site productivity. In addition to the field techniques discussed in *Chapter 3.1*, various laboratory procedures have been developed including aerobic and anaerobic incubations and controlled condition bioassays (discussed extensively in Keeney (1982), Stanford (1982), Rowell (1994) and Binkley and Vitousek (1994)). From these methods, biological indices may be calculated which characterise microbial conversions of organic to inorganic constituents and the subsequent availability of nutrients to plants (Van Miegroet *et al.* 1994).

Quantities of available N may be determined simply in the laboratory by the anaerobic incubation of water saturated soils (Keeney 1982). Only potential ammonification is measured during this process, as the waterlogged conditions prevent nitrification (Binkley and Vitousek 1994; Van Miegroet *et al.* 1994) and cause denitrification of any NO_3^- initially present (Binkley and Vitousek 1994). Therefore this method is unsuitable for estimating proportions of NH_4^+ and NO_3^- in the available inorganic N. Quantities of available NH_4^+ and NO_3^-, and net mineralisation may be determined after aerobic incubation. This method is easy to conduct and has the additional advantage that moisture content and temperature of the samples may be manipulated to reflect field conditions.

Bioassays performed under controlled conditions may be used to determine the quantity of plant available N in a given substrate (Binkley 1983). Care should be taken to use appropriately sized pots and fast growing indicator species tolerant of conditions present within the soils to be investigated. Manipulation of the substrate to accommodate different plants, for example by the application of lime, modifies microbial action within the soil and may distort the amount of inorganic N released.

Chemical extraction of soil samples by boiling with water or KCl solution provides an empirical index of the pool of labile N most susceptible to mineralisation (Binkley and

Vitousek 1994) and is similar to the anaerobic incubation technique. The procedure described by Keeney and Bremner (1966) and Hart and Binkley (1985) has been modified for agricultural soils (Smith and Li 1993). As the substrate is boiled in salt solution for a short period of time before analysis, the method yields results quickly compared to incubations or bioassays.

Implementation of the methods above avoids the problems associated with field incubations, including complicated sampling design and spatial and temporal variability (Van Miegroet *et al.* 1994). However, the nutrient release potential when measured by laboratory assays may be overestimated. Sample pretreatment (sieving, homogenising (Van Miegroet *et al.* 1994), air drying and grinding (MacDuff and White 1985)), the absence of plant influences and the lack of fluctuations in soil environmental conditions experienced in the field (Van Miegroet *et al.* 1994; see *Chapter 3.1*) may stimulate mineralisation of inorganic N in the soil. Despite the presence of artefacts, the available N determined by anaerobic methods has been found to correspond with *in situ* N mineralisation (Powers1980), plant uptake in agricultural (Keeney and Bremner 1966) and forest (Adams and Attiwill 1986) systems, and the site productivity of Ponderosa pine (*Pinus ponderosa*) (Powers 1980) and eucalypt forests (*Eucalyptus pauciflora* and *E. delegatensis*) (Adams and Attiwill 1986). Also, plant biomass production in field and greenhouse bioassays was related to estimates of N mineralisation measured during aerobic incubations (Pare and Van Cleve 1993). In contrast, results from chemical extraction with boiling KCl solution have been variable. For example, high correlations were recorded between plant uptake (ryegrass and oats) and potentially available N (Smith and Li 1993), and a strong relationship between stem volume growth of fertilised loblolly pine (*Pinus taeda*) and NH_4^+ was observed by Hart *et al.* (1986). However, in unfertilised loblolly pine stands the relationship was poor (Hart *et al.* 1986).

In general, the rate of N mineralisation is assumed to be proportional to the temperature within the mesophilic range (Stanford *et al.* 1973) or within other more specific temperature ranges (Campbell *et al.* 1988). For example, the ratio of the reaction rate constant for two temperatures differing by 10 °C (the Q_{10} value or Arrhenius coefficient (Williams and Williams 1967)), is commonly determined between 5 and 35 °C. In many forest soils the Q_{10} for ammonification is approximately 2 (Powers 1980; Carlyle 1985), while the value for total net mineralisation (NH_4^+ and NO_3^-) is slightly lower at 1.4 (Emmer and Tietema 1990). However, the kinetics for nitrification in relation to temperature are generally less well defined, as microbial inhibition occurs at temperatures below 5 and higher than or equal to 30 °C (Carlyle 1985; Emmer and Tietema 1990).

4.1.1 Objectives

This chapter details results from laboratory, greenhouse and growth room experiments used to determine various indices of N mineralisation in the forest floor following harvesting. Studies of inorganic N release in the field (*Chapter 3*) and growth of Sitka spruce roots (*Chapter 5*) indicated that nutrient availability and the potential for plant uptake were highest in the L and FH horizons. Consequently the procedures detailed in this chapter (including aerobic and anaerobic incubations, boiling KCl extractions and plant bioassays) were performed on material from the organic horizons of the forest floor.

Inorganic N availability in the field was not significantly influenced by treatment. However, changes in mineralisation rate resulting from modifications in substrate quality after harvesting, may have been negated by complicating factors including microclimate. Therefore a series of experiments were performed under controlled conditions which eliminated the influence of physical variables. The objectives of the studies were to;

- quantify the effect of temperature on mineralisation rates within the L and FH horizons following CON and WT harvesting, and to compare Q_{10} values with those calculated in previous studies,
- assess the potential mineralisation of L and FH material from CON and WT harvested areas using anaerobic incubations and chemical extractions modified by Smith and Li (1993), and
- quantify the potential of litter after CON and WT harvesting practices to act as a source of nutrients, 6 months after clearfelling.

4.2

METHODS

4.2 Laboratory incubations (Soil sampling and preparation)

Soil samples were collected from *Site 1* using stainless steel cans detailed in *Chapter 3.2.1.* For each incubation four cores were collected from each treatment plot (+ R, + RH, - R and + H). The samples were separated into the L and FH horizons, before homogenising, removing all roots, large woody material and stones. At the start of each incubation, the moisture content and pH of the soil were measured, and a 10 g sample was extracted with 1 N KCl solution for inorganic N (NH_4^+ and NO_3^-). All methods and analyses were performed as outlined in *Chapter 3.2.3* and duplicated for each treatment and horizon.

4.2.1 Incubation at 4, 10, 20 and 30 °C

In October 1995 soil samples were collected from the field and prepared as above. Approximately 30 g of each soil was subsampled, placed in a plastic jar and sealed with cling film before incubating in a dark, controlled temperature cabinet at 4, 10, 20 or 30 °C. Jars were aerated weekly to prevent the build up of carbon dioxide in the head space above the soil and distilled water was added as necessary to replace moisture lost during incubation. After 29 days, 10 g subsamples were taken from each jar to assess moisture content and net mineralisation of N by extraction with 1 N KCl solution. Net mineralisation was calculated as the difference between the final and initial N contents.

4.2.2 Nitrogen release through time at 10 and 20 °C

The same procedure was adopted as in *4.2.1.* From soil collected in October 1995, 30 g samples were incubated in dark, controlled temperature cabinets at 10 and 20 °C. After periods of 10, 17 and 29 days, moisture content was determined, and inorganic N was extracted using 1 N KCl solution. Net mineralisation of NH_4^+ and NO_3^- was calculated for samples from each temperature and duration of incubation. From this the rate of inorganic N release could be estimated for each soil horizon through time.

4.2.3 Potential nitrogen availability

Potentially available N in the L and FH horizons was assessed by two methods; anaerobic incubation and chemical extraction by boiling with 1 N KCl (see *Chapter 4.1*). Soil samples were collected in March 1995, and prepared as above (*Chapter 4.2*). However, the initial inorganic N was not determined.

Anaerobic incubation

Fresh soil (10 g) was added to a 25 ml plastic screw top tube with 20 ml of distilled water. The samples were incubated in a dark, controlled temperature cabinet at 30 °C for 30 days. On completion, each soil sample was shaken thoroughly transferred to a 200 ml jar and 1.13 N KCl solution added. When mixed with the liquid already present in the sample a 1 N KCl solution was produced. After extraction, available NH_4^+ and NO_3^- were assessed.

Boiling with 1 N KCl solution

Ten grams of fresh soil were transferred to 250 ml pyrex glass conical flasks. Each sample was boiled with 50 ml of 1 N KCl solution for one hour on a heating mantle. Evaporative losses were reduced by covering the flasks with watch glasses, and distilled water was added as necessary to maintain a 50 ml volume of liquid. After cooling the solution was transferred to a measuring cylinder. The soil samples were rinsed two to three times with distilled water and the wash used to bring the KCl solution to exactly 100 ml volume.

4.2.4 Nutrient availability and mineralisation of inorganic nitrogen in litter

Results from a preliminary bioassay indicated that leaf area and nutrient contents of birch (*Betula pendula* Roth.) seedlings grown in undisturbed soil cores were more closely related to the oven dried weight of litter (L) than that of the FH or O horizons (see *Appendix 4*). Therefore an additional birch bioassay and laboratory incubation was performed to determine the N availability in various quantities of Sitka spruce litter of different qualities. There were several reasons for selecting birch seedlings when performing the bioassay. This species regenerates naturally at *Site 1*, is tolerant of the acid soil conditions present, and is more sensitive to nutrient availability than conifer seedlings, as growth is more rapid and not predetermined. Consequently, the seedlings demonstrate greater plasticity in response to environmental conditions.

Two qualities of substrate were collected from *Site 2* which originated from;

- the original forest floor (pale in colour), (- R_o) and
- underneath banks of residue, piled during felling 6 to 8 months previously (dark red/brown colour) (+ R_n). Litter from the original forest floor and that fallen from the branches of felled trees were included.

Litter was mixed thoroughly, air dried for 48 hours, and woody material, bark and moss removed before comminuting half the substrate using a centrifuge mill (with no mesh). Four quantities (10, 20, 30 and 40 g) of each litter type (- R_o and + R_n, unground and ground) were mixed with moist vermiculite in 0.12 m square pots to give a standard volume.

After incubating for 7 days at 20 °C, 75 % humidity, 250 mol m^{-2} s^{-1} photon flux density and watering as required, two birch seedlings, approximately 15 mm high and of Newtyle Hill (Dunkeld, Perthshire) origin, were added to each pot. All combinations were replicated four times resulting in a total of 72 pots. Eight control pots containing vermiculite were planted with two seedlings. These were fertilised with phostrogen (containing nutrients in the following proportions 10, 10, 27, 1.3, 0.4 and 0.02 % of N, P, K, Mg, Fe and Mn, respectively) twice a week. After six weeks, one seedling was removed from all pots and weekly height measurements initiated (to the nearest millimetre). The bioassay continued for 151 days, during which the control trees received a total of 141, 141, 381, 18, 5.6 and 0.3 mg of N, P, K, Mg, Fe and Mn, respectively.

At the end of the bioassay all seedlings were harvested. Birch plants were carefully removed from the root media, and the roots washed. Total fresh weight and the weight of the shoots and roots were recorded. Leaf area was assessed using a LI-COR model 3000, and seedling nutrient concentrations (N, P, K, Mg and Ca) were analysed (as in *Chapter 6.2.4*). Concentrations of nutrients (N, P, K, Mg and Ca) and loss on ignition of the litter was determined at the start and conclusion of the bioassay (as in *Chapter 3.2.3*). Percentage carbon was estimated using the Van Bemmelen *equation 3.2.3*).

Slow growth rates were recorded during the early stages of the bioassay which may have resulted from the lack of available nutrients, poor root establishment or a lack of mycorrhizal associations. In order to investigate the role of net mineralisation rates and mycorrhizae in the early growth of birch, additional experiments were conducted. The first involved aerobic incubation of + R_n and - R_o, ground and unground litter at 20 °C (the same temperature as the bioassay) for 15, 30 and 50 days. Samples were moistened with distilled water and aerated regularly (as in *Chapter 4.2.1*). Two 10 g samples were removed at the beginning and on each measurement date in order to determine moisture content, and inorganic N. In the second study, pots were prepared with mixtures of vermiculite and 40 g of each litter type and planted with seedlings, as above. After an initial lag period of 4 weeks, the seedlings initiated more rapid growth rates. The percentage of root tips infected by mycorrhiza was determined on day 48.

4.2.5 Data presentation and statistical analysis

From the 4, 10, 20 and 30 °C laboratory incubation, the temperature coefficient (Q_{10} ratio) for N mineralisation in the litter was calculated using the equation;

$$Q_{10} = (\text{net N mineralisation at temp.}_1\ ^\circ C) / (\text{net N mineralisation at temp.}_1 - 10\ ^\circ C)$$

Values were obtained between the temperature ranges 10 to 20 °C and 20 to 30 °C, only, (where $temp._f$ was either 20 or 30 °C).

Daily rates of net mineralisation at 10 and 20 °C, were calculated from the release of inorganic N for each incubation period (0 to 10, 10 to 17 and 17 to 29 days).

As the quantity of litter present in the forest floor at *Site 2* was not determined, values of nutrients available to the birch seedlings have been expressed as mg kg^{-1} of oven dried litter. Means and standard errors (n = 3) were calculated for all variables and have been used for graphical representation of results. Analysis of variance was performed to assess differences between treatments in all experiments. The relationship between potential N mineralisation measured using boiling KCl extractions and anaerobic incubations was investigated using regression analysis and differences between absolute values determined using a paired t-test. Examples of all statistical procedures are presented in *Appendix 1*.

4.3

RESULTS

4.3.1 4, 10, 20 and 30 °C temperature incubations

Mineralisation of NH_4^+ generally increased with temperature to 30 °C, whereas maximum NO_3^- release occurred at 20 °C (*Figure 4.3.1*). Rates were affected by both horizon and treatment.

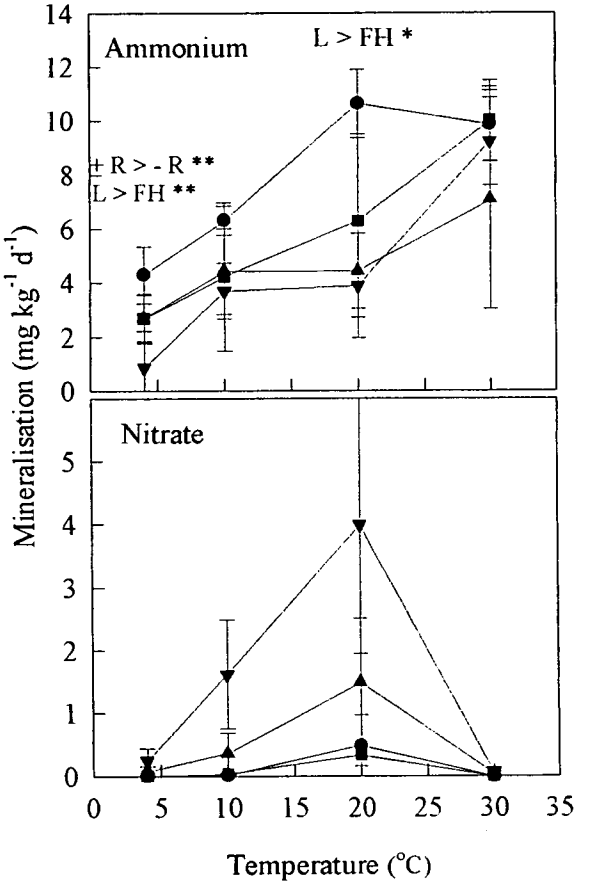


Figure 4.3.1: Net mineralisation (mg kg^{-1} d^{-1}) of NH_4^+ and NO_3^-, at four temperatures (4, 10, 20 and 30 °C). Means (± standard errors) are presented for +R (● litter; ▲ F and H) and - R (■ litter; ▼ F and H) treatments (n = 3). Significance levels are presented from analysis of variance between horizons and treatments; '*', '**' and '***' indicate $0.05 \geq P > 0.01$, $0.01 \geq P > 0.001$ and $P \leq 0.001$, respectively.

Net NH_4^+ mineralisation was generally greater in the litter than the FH horizon, although significant differences were observed at 4 and 20 °C only ($P \leq 0.025$). In addition, a trend was observed for greater ammonification in the litter layer of + R_n treatments, at all temperatures except 30 °C. At 4 °C the influence of residue retention significantly increased release of NH_4^+ in L and FH material ($P = 0.006$). Net nitrification increased with temperature to 20 °C before dropping to negligible levels at 30 °C in all samples measured. Release was greater in the FH horizons, and material from the -R plots demonstrated greater NO_3^- availability than that under residue. Although small increases in the presence of NO_3^- were observed in the litter layer at 20 °C, availability remained very low at all temperatures (*Figure 4.3.1*).

Q_{10} values calculated for the release of NH_4^+ between 10 and 20 °C, and 20 and 30 °C ranged between 0.9 (± 0.1) and 2.7 (± 1.0) (*Table 4.3.1*). Significant treatment differences were not observed. However as the temperature became warmer, mean Q_{10} ratios decreased in the litter and rose in the FH horizons.

Table 4.3.1: A summary of Q_{10} values calculated for NH_4^+ availability (treatment means (± standard errors)) between two temperature ranges (10 to 20 °C and 20 to 30 °C) (n = 3).

		Temperature range	
Treatment	*Soil horizon*	*10 to 20 °C*	*20 to 30 °C*
+ R	*L*	1.7 (± 0.3)	0.9 (± 0.1)
	FH	1.0 (± 0.1)	2.6 (± 1.8)
- R	*L*	1.6 (± 0.4)	1.3 (± 0.2)
	FH	1.4 (± 0.5)	2.7 (± 1.0)

4.3.2 10 and 20 °C temperature incubations

As the release of NO_3^- was negligible in all treatments and horizons the results have not been presented below.

Net mineralisation of NH_4^+ generally continued to the end of the incubation, resulting in increased availability with time. Increased temperature also modified results, by enhancing release in all treatments and horizons except that of the - R, FH layer (*Figure 4.3.2*). The effects of temperature, soil horizon and residue retention did not significantly influence NH_4^+ release after 10 days. However, the influence of substrate increased through time resulting in

significantly greater net mineralisation of NH_4^+ in the litter layer after 17 and 29 days (P = 0.023 and P = 0.007, respectively) (*Figure 4.3.2*).

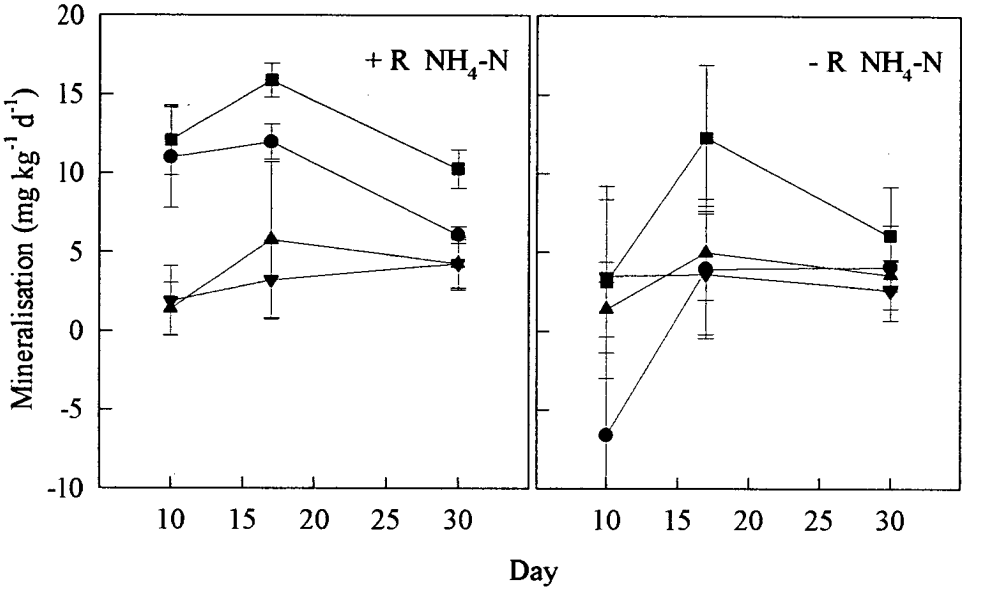


Figure 4.3.2: Net mineralisation of NH_4^+ (mg kg^{-1} d^{-1}) in soils originating from + R and - R treatment plots, incubated at 10 and 20 °C for 29 days. The means (± standard errors) represent the release of inorganic N for each incubation period (0 to 10, 10 to 17 and 17 to 29 days). Results are presented for 10°C (● litter; ▲ F and H) and 20 °C (■ litter; ▼ F and H) treatments (n = 3).

4.3.3 Potentially available nitrogen

Values for potentially mineralised NH_4^+ obtained from anaerobic incubations and boiling KCl extractions were strongly correlated ($R^2 = 0.82$, $P < 0.001$) (*Figure 4.3.3a*). As absolute differences between the two methods were not significant, the values and responses to treatments have been described using results from the anaerobic incubation only. Values obtained for NO_3^- were negligible and have not been discussed below.

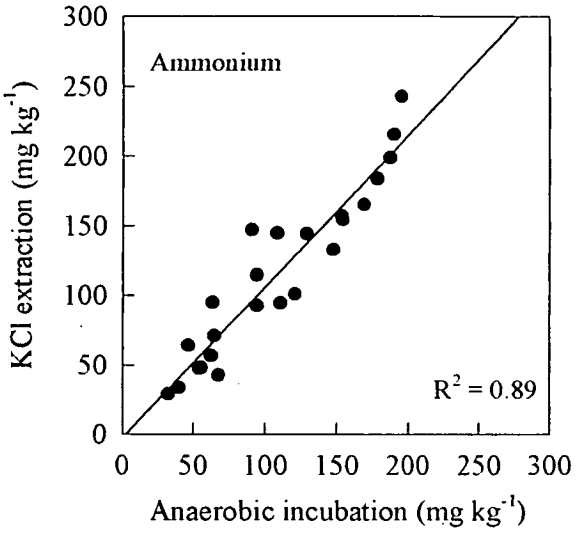


Figure 4.3.3a: The relationship between values of potentially mineralised N obtained from two methods; anaerobic incubations and boiling KCl extractions. Each point represents an individual soil sample.

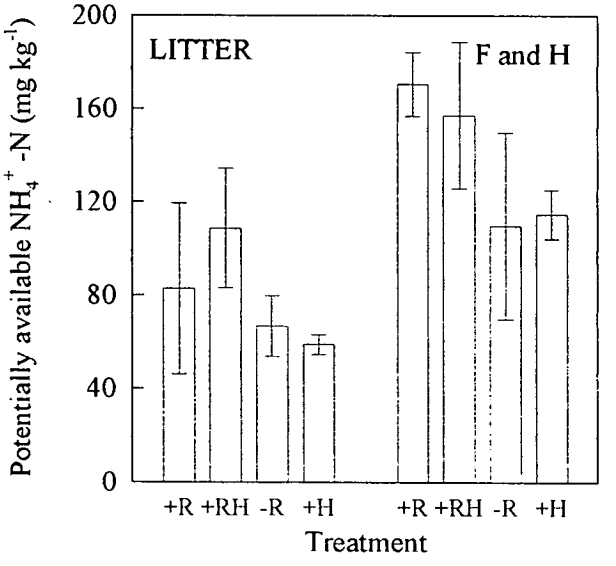


Figure 4.3.3b: A summary of potentially available NH_4^+ (mg kg^{-1}). Treatment means (± standard errors) from + R, + RH, - R and + H are represented (n = 3).

Mean potentially available NH_4^+ was almost twice as great in the FH horizon (138.1 mg kg^{-1}) compared to that in the litter layer (79.4 mg kg^{-1}) (*Figure 4.3.3b*). The application of herbicide did not modify nutrient levels, but the retention of residue resulted in greater NH_4^+ in both the litter and FH horizons. Treatment differences approached significance for values obtained from the FH layer only (P = 0.099).

4.3.4 Birch bioassay to determine nutrient availability of litter

The initial growth of birch was slow, although exponential increases in height were observed in - R_o and unground + R_n treatments after 8 weeks (*Figure 4.3.4a*). However, temporal differences in the initiation of the growth were observed. Plants from + R_n treatments demonstrated more rapid growth rates approximately 1 month later than those from the - R_o pots. Seedlings grown in ground + R_n remeained small and exhibited slow rates of growth to the end of the experiment (*Figure 4.3.4a*). In all treatments except ground + R_n, final heights were greatest (between 180 and 200 mm) in the presence of 40 g of litter. As litter quantity decreased, plant height decreased accordingly to between 60 and 80 mm in the lowest litter treatment (10 g). Seedlings grown in the presence of ground + R_n litter exhibited comparatively small increases in height after 16 weeks, attaining final sizes of between 40 and 70 mm in all litter weight categories. The final height of the fertilised seedlings was 396 (± 34) mm (*Figure 4.3.4a*).

Final leaf area and oven dried weights exhibited similar trends in all treatments. With increasing litter weight, values generally increased (*Figure 4.3.4b*). However, seedlings grown in - R_o unground and + R_n ground litter attained smaller mean leaf areas and oven dried weights in 40 g of substrate compared to 30 g. Excluding the + R_n ground treatment, leaf areas ranged from 50 cm^2 in the lowest litter additions to between 170 and 210 cm^2 in the presence of 40 g, and oven dried weights increased from 1.0 to between 3.8 and 5.5 g in the highest litter applications. The low areas (between 10 and 60 cm^2) and weight (between 0.3 and 0.95 g) recorded in the + R_n ground treatment were consistent with measures of final height. Root:shoot ratios ranged between 1.2 and 1.9 and were not influenced by the quantity of litter present (*Figure 4.3.4b*).

Seedlings from the fertilised treatments attained large leaf areas (598 ± 56 cm^2) and oven dried weights (10.4 ± 0.70 g) compared to those recorded for litter grown plants. However the mean root:shoot ratio (1.31 ± 0.10) was similar to the values obtained for unfertilised seedlings.

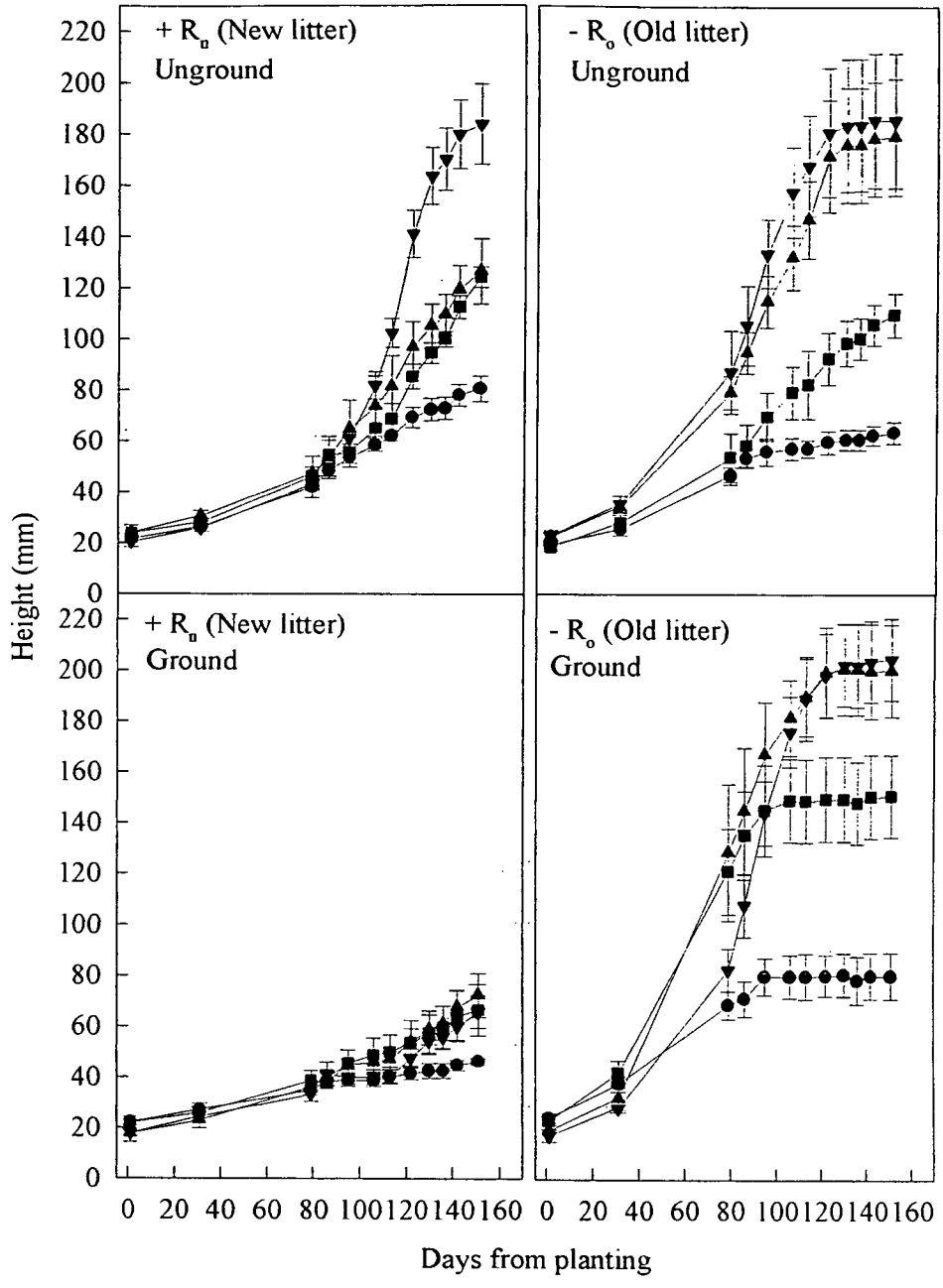


Figure 4.3.4a: Height increases of birch seedlings grown in a Sitka spruce litter and vermiculite mixture. Means (± standard errors) are represented for plants grown in different quantities (10 g , 20 g ■, 30 g ▲ and 40 g ▼) of unground and ground litter from two sources (+ R_n and - R_o) and new) (n = 4).

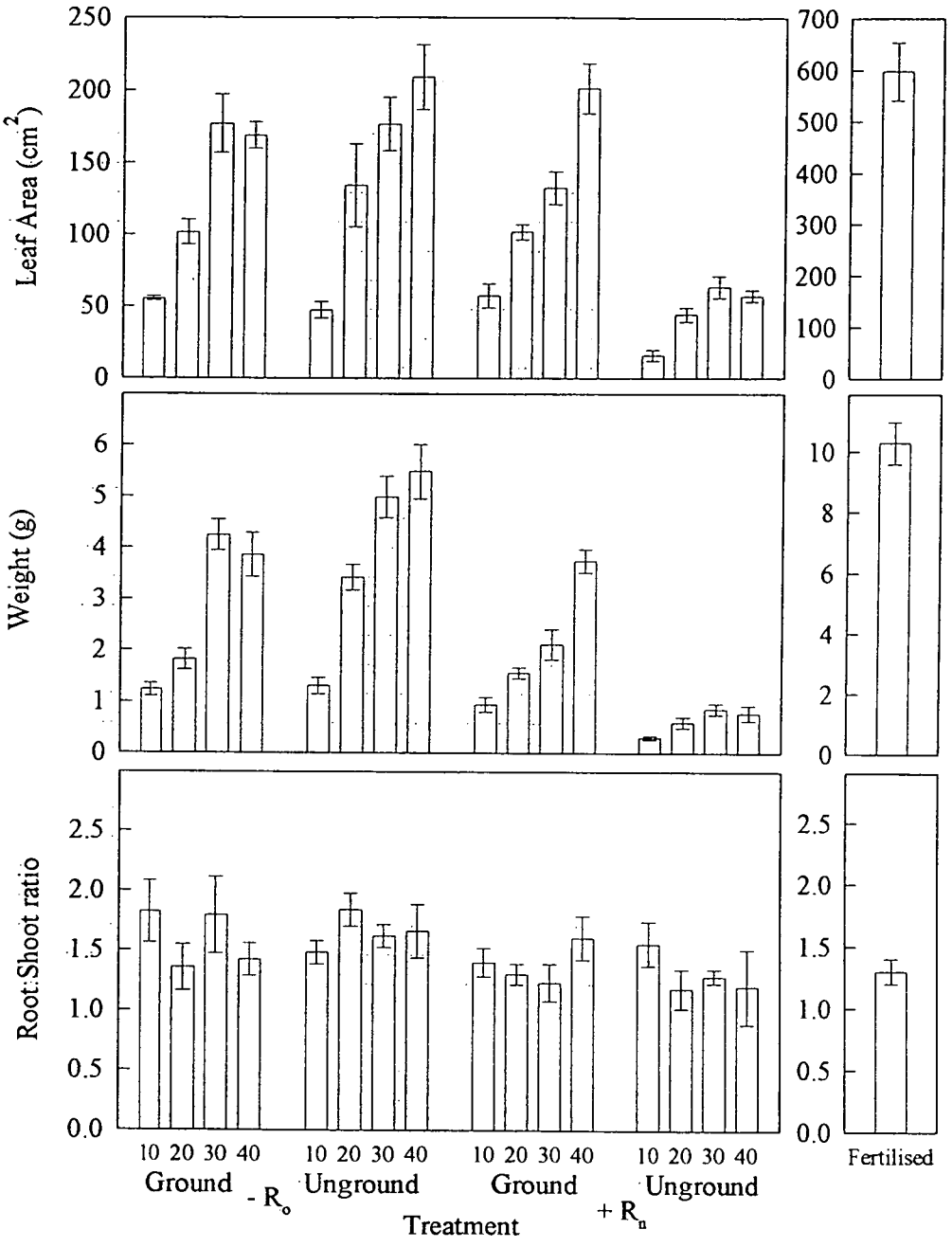


Figure 4.3.4b: Birch seedling leaf area, weight and root:shoot ratio recorded after 151 days growth in various quantities (10, 20, 30 and 40 g) of - R_o (ground and unground) and + R_n (ground and unground) litter mixed with vermiculite (n = 4) and fertiliser treatments (n = 8). Means (± standard errors) are presented.

Significantly greater shoot heights, leaf area, seedling oven dried weights and root:shoot ratios were attained by plants (*Table 4.3.4*) from - R_o treatments with all litter additions (except shoot height with 10 g litter). Occasionally significantly smaller values were recorded for plants grown in ground litter, whereas the measurements resulting from the interaction between litter source and pretreatment were significantly lower for all variables except root:shoot ratio (*Table 4.3.4a*).

Table 4.3.4a: A summary of the significance levels (P values) from analysis of variance performed on final birch heights, leaf areas, oven dried weight and root:shoot ratio. The effect of litter source, grinding and their interaction are considered (n = 4). 'n.s.' indicates non-significant treatment differences.

Variable		*Significance levels (P) from ANOVA* *Litter weight (g)*			
		10	*20*	*30*	*40*
Shoot height	*source*	n.s.	0.05>P>0.01	P < 0.01	P < 0.01
	grinding	n.s.	n.s.	n.s.	0.05>P>0.01
	interaction	P < 0.01	P < 0.01	0.05>P>0.01	P < 0.01
Leaf area	*source*	0.05>P>0.01	0.05>P>0.01	P < 0.01	P < 0.01
	grinding	P < 0.01	n.s.	0.05>P>0.01	P < 0.01
	interaction	0.05>P>0.01	0.05>P>0.01	0.05>P>0.01	P < 0.01
Seedling weight	*source*	P < 0.01	P < 0.01	P < 0.01	P < 0.01
	grinding	0.05>P>0.01	n.s.	n.s.	n.s.
	interaction	0.05>P>0.01	P < 0.01	P < 0.01	P < 0.01
Root:shoot	*source*	n.s.	0.05>P>0.01	0.05>P>0.01	0.05>P>0.01
	grinding	n.s.	n.s.	n.s.	n.s.
	interaction	n.s.	n.s.	n.s.	n.s.

In agreement with trends for biomass, seedling nutrient content generally increased with greater additions of litter, and low values were recorded in all seedlings grown in ground + R_n litter (*Figure 4.3.4c*). Significantly greater nutrient contents were recorded in plants grown in - R_o litter compared to R_n, regardless of the quantity of litter added. Nitrogen content was significantly greater in birch seedlings from unground litter, and an interaction between substrate quality and preparation was frequently recorded (*Figure 4.3.4c*). Where interactions were observed, a combination of - R_o litter and no grinding resulted in higher nutrient contents. Different nutrients did not exhibit identical trends with increasing litter quantity. For example,

seedlings from the ground - R_o treatments demonstrated declines in K and Mg between litter additions of 30 and 40 g, whereas other nutrient contents increased.

Nutrient concentrations did not vary greatly with different litter additions and the effect of treatment was inconsistent (*Figure 4.3.4d*). Comparisons between fertilised seedlings (*Table 4.3.4b* and *Table 4.3.4c*) and plants grown with 40 g of litter revealed differences in the proportions of each nutrient present. In the fertilised plants the proportions of P and K were greater, whereas Ca levels were greater in the unfertilised seedlings (*Table 4.3.4c*).

Table 4.3.4b: Mean nutrient contents and concentrations of fertilised seedlings (n = 8).

	Nutrient				
	N	***P***	***K***	***Mg***	***Ca***
Concentration (%)	1.0 (± 0.1)	0.2 (± 0.01)	1.5 (± 0.1)	2.5 (± 0.4)	0.4 (± 0.01)
Content (mg)	96.3 (± 2.7)	18.6 (± 1.2)	153.4 (± 14.2)	268.2 (± 51.3)	43.2 (± 2.7)

Table 4.3.4c: The mean proportions of nutrients occurring in seedlings grown with fertiliser (n = 8) and 40 g of litter (n = 4).

		Nutrient				
Treatment		***N***	***P***	***K***	***Mg***	***Ca***
	Fertilised	10	2.0	15	25	4.0
R_n	***unground***	10	0.6	12	24	5.6
	ground	10	1.0	11	17	6.8
R_o	***unground***	10	0.8	9	12	6.0
	ground	10	0.9	14	23	6.9

The nutrient concentrations and C/N ratios at the start of the experiment varied considerably between the different sources of litter (*Table 4.3.4d*). For all variables except N concentrations, macronutrients and C/N ratios were higher in the + R_n substrate. However, at the end of the birch bioassay, C/N ratios were higher in the - R_o litter, with greater values occurring for the ground substrate. Concentrations of all nutrients had increased in the + R_n litter, whereas greater values were recorded for the cations within the - R_o substrate (*Table 4.3.4d*).

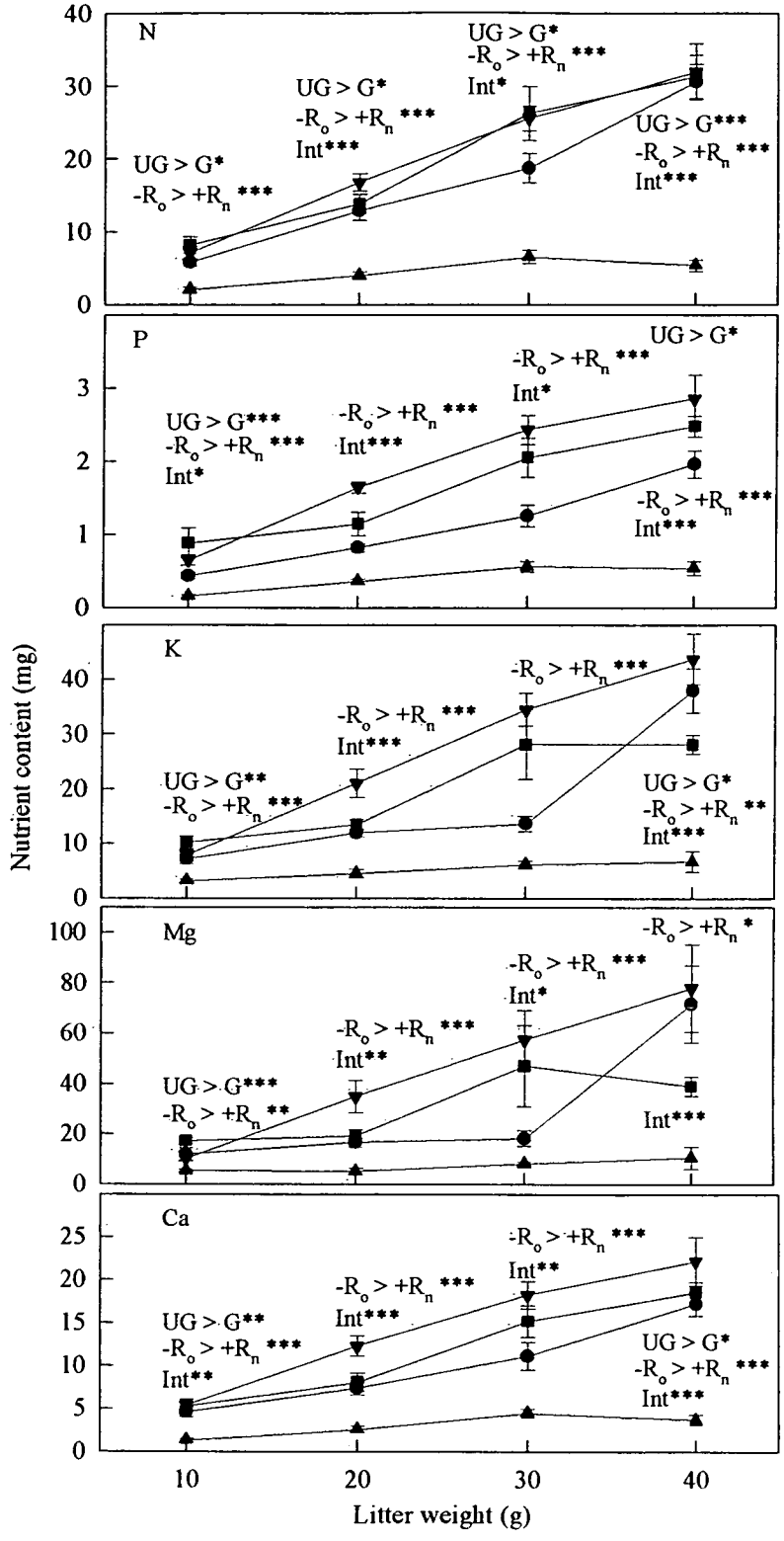


Figure 4.3.4c: Nutrient contents (N, P, K, Mg and Ca) of birch seedlings grown in + R_n (ground (G) ▲ and unground (UG) ●) and - R_o (ground (G) ▼ and unground (UG) ■). Means (± standard errors) and significance levels are presented from analysis of variance between horizons and treatments; '*', '**' and '***' indicate $0.05 \geq P > 0.01$, $0.01 \geq P > 0.001$ and $P \leq 0.001$, respectively (n = 4). Int. = signifies the presence of an interaction between litter source and grinding.

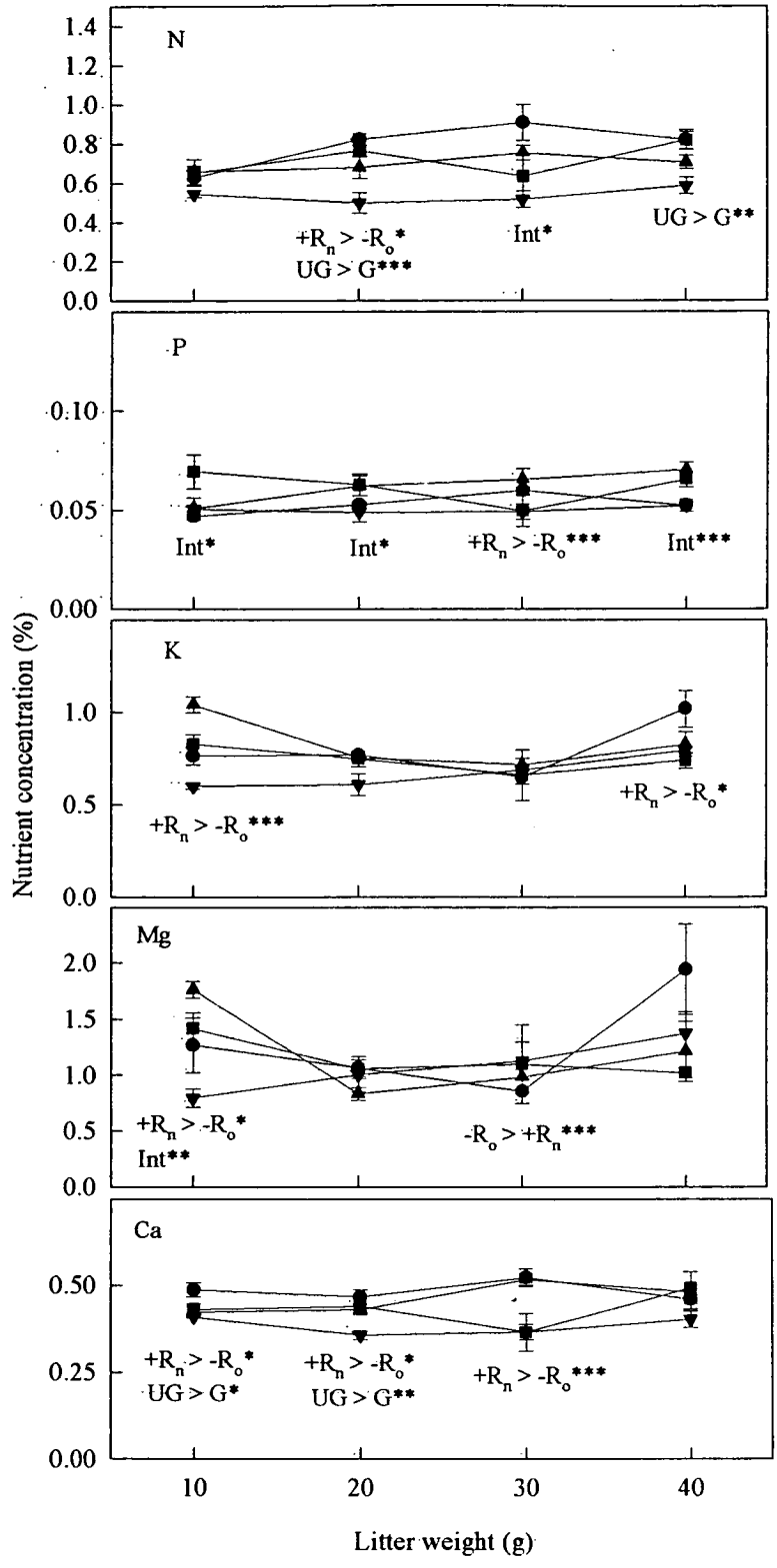


Figure 4.3.4d: Nutrient concentrations (N, P, K, Mg and Ca) of birch seedlings grown + R_n (ground (G) ▲ and unground (UG) ●) and - R_o (ground (G) ▼ and unground (UG) ■). Means (± standard errors) and significance levels are presented from analysis of variance between horizons and treatments; '*', '**' and '***' indicate $0.05 \geq P > 0.01$, $0.01 \geq P > 0.001$ and $P \leq 0.001$, respectively (n = 4). Int. = signifies the presence of an interaction between litter source and grinding.

Table 4.3.4d: Nutrient concentrations and C/N ratios of litter immediately after collection from the field and after harvesting the birch bioassay (40 g of litter additions).

Treatment			C/N ratio	Nutrient concentrations (%) N	P	K	Mg	Ca
Immediate	R_n		61	0.9	0.07	0.08	0.03	0.28
	R_o		47	1.2	0.06	0.05	0.03	0.20
After bioassay	R_n	*Unground*	32	1.7	0.12	0.24	0.51	0.43
		Ground	31	1.7	0.11	0.25	0.51	0.39
	R_o	*Unground*	47	1.1	0.10	0.21	0.47	0.26
		Ground	66	0.8	0.05	0.25	0.49	0.22

Mineralisation of N during aerobic incubation was low (*Figure 4.3.4e*). In both - Ro treatments NH_4^+ levels increased, whereas negligible amounts were released from the + R_n unground treatment and immobilisation occurred in the + R_n ground litter. Nitrate increased rapidly after 60 days incubation in + R_n litter and - R_o unground. However, absolute values were low compared to those of NH_4^+. The initiation of net mineralisation of NO_3^- and NH_4^+ in some treatments coincided with increases in birch tree height in - R_o treatments.

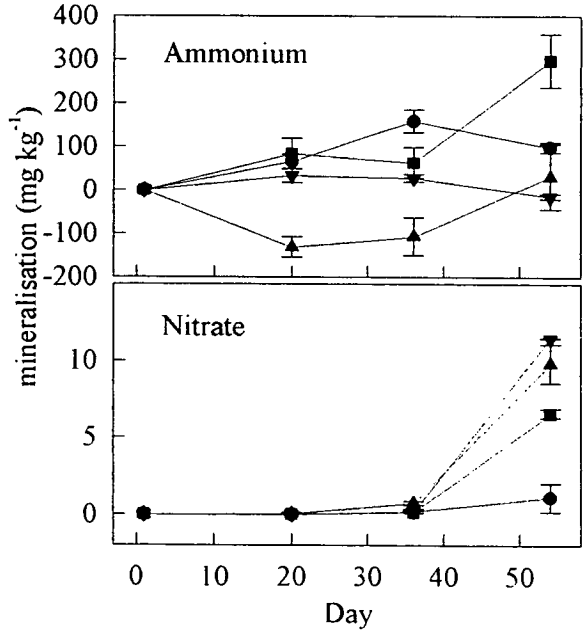


Figure 4.3.4e: Mineralisation of N in litter from - R_o (ground ■ and unground ●) and + R_n (ground ▲ and unground ▼) treatments expressed as mg kg^{-1} of oven dried soil. Means (± standard errors), where available, are presented (n = 4).

Percentage mycorrhizal infection of birch roots ranged between 20 (± 4) and 34 (± 6) % for ground and unground + R_n, respectively (*Figure 4.3.4f*). Treatment did not significantly affect the occurrence of mycorrhizal associations. However there was a trend for increasing infection of root tips in seedlings grown in the unground litter substrate.

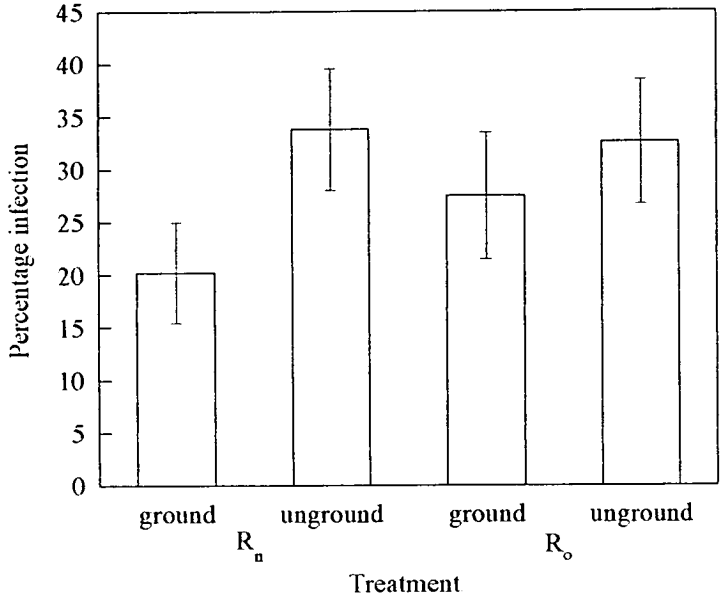


Figure 4.3.4f. Percentage infection of birch roots by mycorrhiza grown in $+R_n$ and - R_o (ground and unground) treatments (n = 6).

4.4 DISCUSSION

The incubations and chemical extractions reported in this chapter were performed on homogenised samples consisting of 4 soil cores collected from each plot. Despite the replication and thorough mixing, variations in soil characteristics resulting from the heterogeneous nature of the substrate sometimes masked treatment differences. Unfortunately, logistical limitations prevented more intensive sampling.

4.4.1 Temperature incubations (4, 10, 20 and 30 °C, and 10 and 20 °C)

Net mineralisation of N was dominated by NH_4^+ at all temperatures and in all horizons sampled. Like previously recorded results (Stanford *et al.* 1973; Tietema *et al.* 1989; Emmer and Tietema 1990), the rates of NH_4^+ release increased with temperature, throughout the mesophilic range. In addition, the type of substrate influenced net ammonification. Significantly greater net mineralisation occurred in the litter layer (at 4 and 20 °C), compared to the FH horizon, and the retention of residue consistently increased NH_4^+ availability in the litter layer. Generally the Q_{10} ratios calculated between 10 and 20 °C lay within ranges previously recorded from 1.4 to 2, by Emmer and Tietema (1990) for total net mineralisation (NH_4^+ and NO_3^-), and Powers (1980) and Carlyle (1985), respectively. However between 20 and 30 °C, the Q_{10} values decreased in the litter layer and increased in the FH horizon. As ammonification is performed by a wide range of aerobic and anaerobic heterotrophs with considerable biochemical diversity, it is possible that the L and FH horizons supported different species of microbes with various responses to temperature. The acidity of the substrate was unlikely to have caused differences in mineralisation between substrates or horizons as the range of pH occurring at the beginning of the incubation was narrow (between 3.6 and 3.8).

Nitrification occurred within a relatively small temperature range (greater than 4 and less than 30 °C). Similar trends were observed by Emmer and Tietema (1990) who attributed the limited nitrifier activity to the complex kinetics involved. In the litter layer less than 10 % of the inorganic N present was represented as NO_3^-. However, the proportion in the FH horizon was higher and equalled the N released through ammonification at some temperatures. Differences between the two horizons may arise in response to substrate quality.

Although different rates of net mineralisation were recorded throughout the 29 day incubation, a trend for increasing release of NH_4^+ was observed until day 17, followed by decreases to initial rates or lower towards the end of the experiment. The lag in net ammonification at the

beginning of the study may have arisen during the acclimatisation of microbes to the modified temperatures. Declines in NH_4^+ release recorded in the latter half of the incubation were generally greater at 20 °C. At this temperature available nutrients are used more rapidly as microbial activity is higher. Consequently, competition for resources may limit net mineralisation through time. In addition the higher concentrations of NH_4^+ present in samples incubated at 20 °C may have disturbed the available C/N balance within the sample leading to enhanced immobilisation or decreases in the net mineralisation of inorganic N.

From incubation results (4 to 30 °C) and daily mean ((minimum + maximum)/2) soil temperatures recorded in *Block 2* (see *Chapter 2.8.1*), net mineralisation occurring throughout the 1994 growing season (beginning of May to the end of November) was estimated. As rates of ammonification and nitrification were determined at four discrete temperatures only, release of inorganic N in the field was calculated by allocating laboratory indices to broad ranges of soil temperatures. The thresholds for each range were determined by the midpoint between the stepwise increases in temperature used for the incubation study. For example, between 4 and 10 °C , the mineralisation calculated using the rate of release at 4 °C was allocated to all daily mean soil temperatures < 7 °C, whereas the release of inorganic N between temperatures ≥ 7 and < 15 °C was determined using the rate measured at 10 °C. The following equation (*4.4.1*) enabled values to be obtained for the L and FH horizons of + R and - R plots (*Table 4.4.1*).

$$Mineralisation\ (mg\ kg^{-1}gs^{-1}) = \sum_{1}^{4}(d * m)/(1000\ 000 * w) \qquad 4.4.1$$

where *gs* is the growing season,
d is the number of days with a mean temperature of
1) < 7 °C
2) ≥ 7 but < 15 °C
3) ≥ 15 but < 25 °C, and
4) ≥ 25 °C
m is the mineralisation rate (mg kg^{-1} d^{-1}) at
1) 4 °C,
2) 10 °C,
3) 20 °C, and
4) 30 °C,
w is the weight of each soil horizon per hectare.

Table 4.4.1: Estimated values for NH_4^+, NO_3^- and total net mineralisation from laboratory incubation indices (normal text) and *in situ* mineralisation rates (*italics*) recorded during the 1994 growing season.

	Mineralisation (kg ha^{-1} gs^{-1}) throughout the 1994 growing season											
Soil	*+R*						*-R*					
layer	NH_4^+	*NH_4^+*	NO_3^-	*NO_3^-*	Total	*Total*	NH_4^+	*NH_4^+*	NO_3^-	*NO_3^-*	Total	*Total*
L	51.4	*70.6*	0.8	*1.3*	52.2	*71.9*	32.8	*54.2*	0.4	*0.3*	33.2	*54.3*
FH	39.3	*13.6*	1.7	*1.2*	41.0	*14.8*	30.3	*7.9*	14.0	*0.7*	44.3	*8.6*
Total	90.7	*84.2*	2.5	*2.5*	93.2	*86.8*	63.1	*62.1*	14.4	*1.0*	77.5	*63.5*

Total net mineralisation, ammonification and nitrification in the combined LFH horizons were slightly overestimated by laboratory incubations. However, the values provide a reasonable estimate of mineralisation rates and demonstrate similar treatment differences as values obtained from *in situ* techniques (especially for NH_4^+). Predictions of total NO_3^- release in the - R treatment were less accurate, probably due to the greater errors associated with multiplying up small figures with large sample variation. Within the individual horizons net mineralisation was underestimated in the litter, whereas values were overestimated in the FH layer. Under field conditions, large diurnal fluctuations in temperature occur in the litter horizon (see *Chapter 2.8.1*) which may promote release of inorganic N. However, Ross (1985) observed little difference between net mineralisation of N in soils maintained at fixed temperatures, compared to those experiencing field conditions. In addition, differences between field and predicted values of net N mineralisation were not increased in the - R litter, despite the greater diurnal temperature range experienced. Although the discrepancies recorded between calculated and *in situ* mineralisation occurring in the FH horizon cannot be explained, similar values of total inorganic N in the combined LFH horizons suggest that an interaction or transfer process may occur between the soil layers in the field.

4.4.2 Potential N availability

Estimates of potentially mineralised N at *Site 1* were lower (between 59 and 170 mg kg^{-1}) than those recorded in soil under Sitka spruce in Wales (321, 334 and 237 mg kg^{-1} in oven dried deep peat, peaty gley and peaty ironpan soil, respectively (Williams 1995)), but higher than in soils from unfertilised and fertilised loblolly pine in North Carolina, USA (26.9 and 29.8 mg kg^{-1} oven dried soil, respectively (Hart and Binkley 1985)). Mean quantities were greater in the FH layer than the litter and were enhanced in both horizons by the presence of residue. The input of needles in treatment plots with logging residue shortly after felling and changes in the structure and constituents of the substrate during decomposition are thought to account for these differences.

The two methods used to measure potentially available N produced similar results. However, it was suggested from the regression equation that the degree of extraction from identical soils was slightly greater after the chemical method than the anaerobic incubation. This trend may have resulted due to experimental error, the greater efficiency of KCl solution as an extractant or loss of N through denitrification during anaerobic incubation. In contrast, Hart and Binkley (1985) observed greater values after incubation (26.9 mg kg^{-1}) compared to boiling with KCl solution (7.2 mg kg^{-1}). The large differences between methods recorded by Hart and Binkley (1985) may have arisen from modifications in the techniques used. For example, the anaerobic incubation was performed at 40 °C and extracted after 7 days with 2 N KCl solution, whereas samples were boiled with 1 N KCl solution for only 10 minutes in a microwave during the chemical extraction. As the boiling salt solution method (detailed in *Chapter 4.2.3*) is easy to perform, can be replicated in large numbers and yields results within a few days, this procedure could be adopted instead of anaerobic incubation.

4.4.3 Nutrient availability and mineralisation of inorganic nitrogen in litter

Birch seedlings grown in mixtures of litter (collected 6 months after clearfelling) and vermiculite demonstrated various patterns of growth. Rapid extension of the shoot was first observed after approximately 40 days in the - R_o treatments followed by the + R_n unground (after 85 days). Exponential increases continued for approximately 80 days in all treatments, except the + R_n ground which demonstrated very small height increases throughout the bioassay. Declines in the rate of height growth during the latter stages of the experiment (- R_o treatments) were attributed to the exhaustion of available nutrients.

Ingestad (1962) suggested that the rate of nutrient uptake and growth of birch seedlings were determined by the amounts of nutrients supplied per unit time in relation to the growth rate, rather than the concentration of nutrients in solution. Therefore, the initiation of exponential growth during the current study was an indicator of the onset of nutrient release from the litter. Evidence from laboratory incubations supported this as the height growth of birch seedlings was more rapid in the litter of - R_o treatments, in which greater rates of net NH_4^+ mineralisation were recorded during incubation. In comparison the growth of seedlings was very slow in the ground + R_n treatment, as NH_4^+ was immobilised during the first 50 days. Nitrification rates remained low throughout the incubation, but large relative increases in release were observed after day 36 (to between 1.1 and 9.8 mg kg^{-1} d^{-1}). Infection of root tips by mycorrhiza was not considered to be responsible for differences in the initiation of height growth between treatments.

Net mineralisation and immobilisation are determined by concentrations of N, cellulose and lignin in the litter (Aber and Melillo 1982; McClaugherty and Berg 1987; also see *Chapter 1.5.3*). Therefore, temporal differences in the initiation of inorganic N release may have occurred in response to changes in the proportions of these substances over time. At the beginning of the incubation, litter collected from the old forest floor had a lower total C/N ratio (47) than that originating from under residue mats (61), which probably promoted earlier turnover of microbes and release of inorganic N. In contrast, the incorporation of recently fallen needles in the + R_n litter enhanced immobilisation and delayed net mineralisation. Similar results were observed by Theodorou and Bowen (1983) during laboratory incubations. However the differences in net mineralisation and birch growth in the ground and unground + R_n treatments, cannot be explained by changes in the total C/N ratio of the litter as the value was identical regardless of pretreatment. Previous research cited in *Chapter 1.5.3* reported that the release of inorganic N in various substrates could be predicted by the different C and N components present. Therefore, it is suggested that comminution of + R_n litter influenced the availability of various forms of C and N by breaking down the cell walls, which led to net immobilisation. The absence of such process in the - R_o litter probably resulted after losses of available C during partial decomposition in the field.

At the beginning of the bioassay, concentrations of all nutrients except N, were equal to, or greater in the litter collected from under residue mats. This trend probably resulted from the leaching of soluble cations (especially K) from the - R_o litter, and the input of green needles to the forest floor from the residue mats following harvesting. Premature losses of foliage after disturbance limits the retranslocation of nutrients (N, P and K) from the needles to the tree (Miller *et al.* 1996) resulting in increased concentrations of some nutrients in the litter.

The total C/N ratio of each litter type at the end of the bioassay was largely determined by the N concentrations of each substrate. For example, reductions in N concentration within the - R_o litter increased values, whereas decreases were recorded in the + R_n substrate in the presence of higher proportions of N. During the initial stages of litter decomposition, easily extractable C present in recently fallen needles may be leached or utilised by microbes resulting in weight loss and relative increases of some nutrients and reduction of the total C/N ratio. In contrast, the partial decomposition of - R_o litter in the field may have resulted in the loss of such C derivatives before collection. Unfortunately, weight loss was not ascertained after harvesting the bioassay.

Stepwise additions of litter resulted in increasing values of shoot height, leaf area and biomass in all treatments except -R_o (ground) and +R_n (unground). Similar results were recorded for nutrient levels in each treatment (except -R_o (ground) K and Mg which declined slightly between 30 and 40 g). The relationship between the weight of litter application and nutrient content demonstrated that the litter/vermiculite mix acted as a source of macronutrients necessary for the growth of birch seedlings and that the availability was proportional to the weight of litter added. However, the N concentration of whole seedlings (< 1 %) was considerably lower than the level considered to be deficient for foliage (2.5 %) (Taylor 1991). In addition, an imbalance between the nutrients was thought to be present as the ratio of N:P:K was approximately 10:1:12 (*Table 4.3.4.c*) rather than 10:1:5 expected in birch (Taylor 1991). The analysis of complete seedlings, including less nutrient rich stems and roots, was responsible for the dilution of N concentrations present in the foliage, and may have influenced the optimal N:P:K ratio.

Of the four litter treatments, seedling nutrient contents followed the trend - R_o ground > - R_o unground > + R_n unground > + R_n ground indicating that the availability of all elements was greater in the old substrate. However, Ingestad and Lund (1979) observed that within sub-optimum ranges of nutrients, growth of leaves and leaf area efficiency is controlled directly and closely by N. Therefore, if N availability drives the demand for other macronutrients, the higher contents present in - R_o litter may have resulted, in part, from greater net N mineralisation within the substrate from the original forest floor.

Table 4.4.3: Percentage uptake of nutrients from litter.

		Percentage nutrient uptake				
		N	*P*	*K*	*Mg*	*Ca*
+ R_n	***Unground***	8.5	6.8	118.1	599.2	15.4
	Ground	1.5	2.0	21.3	88.3	3.3
- R_o	***Unground***	6.5	10.4	140.5	326.7	23.3
	Ground	6.7	12.1	219.2	650.8	27.8

The efficiency of element acquisition from the needle litter (nutrient content of seedlings planted in 40 g of litter expressed as a percentage of the total nutrients in the litter) varied greatly for each nutrient and treatment (*Table 4.4.3*). Very low uptake occurred from the ground + R_n, probably in response to the low rates of net N mineralisation and an associated small demand for the remaining nutrients. Excluding the ground + R_n treatment, between 6.5 and 12.1 % of the N and P and 15.4 to 27.8 % of Ca was acquisitioned. Very large percentages were calculated for Mg and K which indicated that additional nutrients were

available to the seedlings. The source of the cations was the vermiculite rooting medium which is an Al-Fe-Mg silicate, containing 5 to 8 % available K, and 9 to 12 % available Mg (Bunt 1988).

4.4.4 Implications for plant growth in the field

Growth of tree seedlings and ground vegetation is influenced by many physical and chemical factors. Like the observations of Smethurst and Nambiar (1990b) and Cortina and Vallejo (1994), results from the birch bioassay suggest that 6 to 10 months after harvesting, the availability of N was greater in litter from the old forest floor than that collected under residue. This was probably due to increased rates of net mineralisation which resulted from higher N concentrations and lower C/N ratios within the litter. The greater nutrient availability and bare soils present in WT harvested areas immediately after felling are suggested to be responsible for the enhanced establishment of vegetation and the rapid increases in its biomass compared to CON felled plots at *Site 1*.

Through time the C/N ratio alters and the litter originating from underneath the residue mats becomes a source of nutrients. For example, Smethurst and Nambiar (1990b) observed changes in the release of N in the field. Initially net N mineralisation was greatest in the ploughed litter and removal of residue and litter treatments. However during the first 3 years after clearfelling, rates of inorganic N release increased in the litter from residue retained treatments, whereas rates in the forest floor of clear areas decreased. Staaf (1984) recorded similar increases in net mineralisation of N in needles originating from residue mats. Maximum rates were measured 3 to 6 years after harvesting whereupon release of inorganic N decreased. Evidence from aerobic incubations reported in this chapter supported these findings, as net mineralisation of N was greater in the litter layer of CON treatments compared to WT harvested areas at all temperatures.

In the field the microclimate and substrate quality influence mineralisation rates. Depending on the interaction between the two factors, release of inorganic N may be enhanced or decreased. However from the estimates calculated for the 1994 growing season, the mulch effect of the residue and the modified quality of the organic horizons resulted in increased net mineralisation in the + R plots compared to the - R treatment. In addition the potentially available N was greater in residue retained plots, indicating that the organic horizons under residue may act as a longer term source of N.

The indices used throughout this chapter give estimates of available N in the soil. However, plants may access additional types of N. For example, Vitousek and Andariese (1986)

recorded that the total release of N into inorganic forms was much greater than net N mineralisation. They suggested that if roots and mycorrhiza can take up more N than that not immobilised by decomposers, then incubation based methods may yield misleading results. Where possible, plant uptake should be determined in conjunction with laboratory procedures in order that processes occurring in the field may be accounted for when making predictions of site productivity.

Rates of net ammonification were higher in the litter than the FH horizon. Therefore plant uptake of inorganic N is favoured by proliferating root tips in the litter layer. However, measurements of root abundance in the L and FH horizon (*Chapter 5*) indicated that the biomass per unit weight of soil was similar in both horizons. The benefits of the greater nutrient availability in the litter may be negated by large fluctuations in environmental conditions. For example, extreme drying and high temperatures in the upper soil horizons are detrimental to root survival.

4.5

SUMMARY

Various laboratory and growth room techniques were used to determine the availability of inorganic N in the forest floor (L and FH horizons) 6 months and 3 years after clearfelling. Treatment differences and the effect of temperature were investigated using procedures including aerobic and anaerobic incubations, chemical extractions and a birch bioassay.

Net mineralisation of NH_4^+ increased at higher temperatures in both soil horizons, and there was a trend for greater rates of release from the litter layer and substrates sampled within CON treatments. Differences in substrate quality and soil pH are thought to be responsible for the changes in ammonification. In contrast, treatment did not produce detectable differences in net nitrification. However, availability was greater in the FH horizon than the litter layer and increased with temperature to 20 °C. Dramatic decreases in available NO_3^- were recorded at 30 °C due to the limited activity of nitrifiers at high soil temperatures. *In situ* soil temperature measurements and results obtained during laboratory incubations were used to provide a good estimate of net mineralisation of inorganic N in the field.

Potentially available N was greater in the FH horizon than the litter layer and demonstrated a trend for increasing values with residue retention. The differences between soil horizons and treatments were attributed to changes in substrate quality. As similar results were obtained from both the methods used to determine potentially available N, chemical extractions are favoured above anaerobic incubations due to the short preparation time.

Results from the birch bioassay indicated that the litter layer acts as an important source of nutrients. However, the timing of release and nutrients available are determined by the age, source and pre treatment of the substrate. Six months after clearfelling, nutrient release was greater and more rapid in litter from the original forest floor. In contrast, the recently fallen litter contained less N per weight and exhibited delayed net mineralisation which was attributed to the higher available C allowing microbes to immobilise available nutrients. In addition grinding the new litter dramatically reduced release. It is suggested that the breakdown and comminution of the litter, destroys the cell walls and makes available and extractable C accessible. Consequently N is immobilised rather than released. Seedlings planted on clearfelled sites may experience competition for N from microbial activity during the first year, especially within the litter layer under CON treated areas.

Chapter 5

ROOT DISTRIBUTION OF SECOND ROTATION SITKA SPRUCE GROWING ON A PEATY GLEY SOIL

5.1 INTRODUCTION

The growth form of tree root systems is largely regulated by genetics, but is also influenced by the local site conditions (Pritchett 1979). Like most boreal forest species (Coutts 1989), Sitka spruce roots demonstrate a 'sinker' habit dominated by strong laterals (Pritchett 1979) which explore the soil and form the main structural roots (Coutts 1983). The direction of lateral growth is controlled by two opposing influences. Initially, the vigorous root tips originating from the base of the taproot are 'programmed' to grow upwards (Coutts and Nicoll 1990a). However, on reaching the upper soil horizons the roots respond to certain signals near the surface, including reduced water status (Coutts and Nicoll 1993), causing them to deflect downwards. Together, these processes produce horizontal roots growing to depths of approximately 0.2 m (Fayle 1975).

Two types of second order root originate from the main laterals; side roots and sinkers. Side roots in association with ectomycorrhiza are responsible for the exploitation of soil nutrients and moisture from the upper horizons (Alexander and Fairley 1983; Persson 1993). Vertically growing sinkers are considered important for anchorage (Coutts 1989) and for supplying water (Persson 1993), especially during dry periods (Coutts 1989). The type of root produced from the first order lateral is thought to be determined by the angle of initiation (Coutts 1989). For example, an examination of 10 year old Sitka spruce trees demonstrated that sinkers and side roots were predominantly initiated in a downward and horizontal direction respectively (Coutts 1989). Thereafter, second order laterals demonstrate diageotropic growth that is modified in response to the environment (Coutts 1989). The mechanisms controlling vertical growth in sinkers is uncertain. It is possible that the roots are weakly plagiotropic and that the direction results due to the angle of initiation. Alternatively, the root tips may become positively geotropic (Coutts 1989). The rooting depth of Sitka spruce sinkers varies greatly with soil conditions (Coutts and Philipson 1987) and estimates of depth depend on the methodology used. For example, tree pulling and soil coring produced maximum values of 1.20 m (Fraser and Gardiner 1967) and 0.85 m (Pyatt and Smith 1983), respectively, for pole stage crops growing on a brown earth in the UK. However in gley soils, both techniques measured roots to depths of 0.40 m beneath similar aged trees. Despite the difference in depth

attained, the majority of all roots occurred within 0.25 m of the surface, regardless of soil type.

Sitka spruce root depth and distribution are influenced by the environment and the presence of impenetrable barriers, including waterlogged soil and anaerobic peds. High water tables are common at *Site 1* (*Chapter 2..8*) and in many areas of upland Britain (Pyatt and Smith 1983) and Northern Ireland, and restrict deep vertical growth of roots (Adams *et al.* 1972). Characteristics of waterlogged soil include a lack of oxygen, increased levels of carbon dioxide and ethylene, and other chemical changes (Armstrong 1982). Tree species vary in their sensitivity to these factors. Sitka spruce roots are intolerant of anaerobic conditions compared to other species such as Lodgepole pine (*Pinus contorta* var. *latifolia* Wats) which possess cavities in the stele of roots adapted to waterlogged soils (Coutts and Philipson 1978b). These spaces allow diffusion of gas from above the anaerobic zone to the submerged root enabling aerobic respiration. Three other mechanisms are thought to aid survival within Lodgepole pine (Coutts and Philipson 1978b);

- the tolerance to toxic concentrations of substances produced in the soil,
- the metabolic adaptation of respiratory pathways to produce non-toxic products of anaerobic respiration, and
- oxidation of toxic compounds in the rhizosphere.

However, within each species, the extent of damage caused by anaerobic soils depends on the condition and structure of the root (primary or secondary) at the time of waterlogging (Coutts 1982).

Primary root injury is dependent on the metabolic activity of the cells (Coutts and Philipson 1987; Coutts and Nicoll 1990b). Measurements of respiration rate in the growing roots of Scots pine, Norway spruce (Lahde 1966) and Sitka spruce (Coutts and Philipson 1978a) indicate greater cell activity in the apex than the basal regions. Therefore apical cells have a greater oxygen demand and are more sensitive to anaerobic conditions. Dieback of primary roots is also affected by the duration of waterlogging, the soil temperature (Coutts and Philipson 1978a) and the depth of waterlogged root (Coutts and Philipson 1978b). For example, in the active roots of Lodgepole pine and Sitka spruce, submergence for 1 month at 15 °C soil temperature resulted in dieback. The region affected was related to the depth of root below the water table (Coutts and Philipson 1978a). However, for dormant roots at 6 °C, waterlogging for 1 month did not cause root death, and growth resumed once the water table had dropped. Secondary, woody roots of both species exhibit greater tolerance to waterlogging (Coutts 1982).

In cases where waterlogging causes death of Sitka spruce roots, regeneration occurs when the water table lowers during drier weather. Periodic regrowth and dieback produce characteristic 'shaving brush' roots (Armstrong *et al.* 1976; Coutts 1989), capable of limited exploitation of the lower soil horizons (Armstrong *et al.* 1976), and a shallow root plate which renders trees unstable and susceptible to wind throw (Savill 1976; Pyatt and Smith 1983; Coutts and Philipson 1987). Attempts to alleviate the effect by draining are generally limited by low soil permeability (Savill 1976).

Sitka spruce root growth also responds directly to changes in soil temperature and nutrients. Seedlings grown under controlled conditions demonstrated increasing dry weight (including roots) as temperature rose from 5 to 20 °C (Coutts and Philipson 1987). However, substantial decreases resulted at 30 °C. Other studies performed under controlled growth conditions investigated the influence of different nutrient applications to seedlings with split root systems (Coutts and Philipson 1976). Roots receiving solutions containing N, P and K exhibited enhanced primary and woody root growth on that part only. Further experiments demonstrated that N stimulated greatest localised growth, that P was also important while K was not (Philipson and Coutts 1977). Root growth in the field occurs in the surface horizons where relatively high nutrient conditions result from the decomposition of fresh plant materials (Ford and Deans 1977). Litter input also retains moisture at the soil surface which is essential for uptake of nutrients by mass flow.

5.1.1 Objectives

At *Site 1*, various factors may influence patterns of root growth including fluctuating water table depth, anaerobic soil, extreme temperature and different rates of nutrient mineralisation. This chapter investigates whether root growth is constrained by the conditions experienced and to assess the effects of treatment. A series of experiments was performed with the principal objectives;

- to determine the depth of root growth and its distribution between the different soil horizons,
- to investigate the role of different soil physical characteristics in restricting growth and distribution, and
- to assess the influence of treatment (residue retention and herbicide application) in modifying the physical characteristics of the soil regarding fine root growth (less than approximately 3 mm diameter).

Two methods of root assessment were adopted. First order laterals from the root collar to the apex were described initially. From this, the lateral root length and the depth attained by

sinkers was estimated. Secondly, soil cores were used to measure the distribution of fine root (< 3 mm diameter) within the L, FH and upper O horizons in relation to soil moisture content and depth. Additional soil measurements referred to during this chapter include continuous temperature recordings, and discrete assessments of water table depth and depth to the aerobic/anaerobic soil boundary. Of these, only the depth of aerobic soil will be detailed in the methods and results sections. Soil temperature and water table measurements are discussed in *Chapter 2.8.1* and *2.8.4,* respectively.

5.2 METHODS

5.2.1 *Sampling procedure*

On wet soils, the use of heavy machinery during forest harvesting disrupts the structure of the surface horizons. Consequently, soil aeration and drainage are altered, resulting in changes in root growth and distribution (Malcolm 1979). To minimise these influences during root observations, *in situ* studies and soil core sampling was performed within the treatment assessment plots, where harvesting machinery had not passed. Measurements of water table and aerobic soil depth were performed within the central zones also.

Three assumptions were made before deciding when to take root samples. Firstly, maximum root depth is attained at the end of the summer after long periods of favourable growing conditions. Secondly, that the water table depth increases during the summer, when rainfall is low and air temperatures and evapotranspiration high. Finally, that active roots are killed soon after the water table submerges them. Therefore, sampling was performed in November after completion of annual root growth and subsequent die back due to waterlogging. This represented the root stock available to the tree at the beginning of the following growing season.

5.2.2 In situ *root observation (+ R and - R treatments)*

At the beginning of November 1995, roots from one Sitka spruce tree growing in each + R and - R assessment plot were excavated. The trees studied had been selected randomly by M.F. Proe and J. Griffiths (MLURI) and all aboveground biomass harvested. Litter was gently removed from around the tree stump until one root, at least 6 mm in diameter and growing obliquely to the line of planting was located. Selection of roots growing in this direction eased excavation and observation by reducing above and below ground interference from neighbouring trees. The following measurements were recorded from each tree; root collar diameter, depth of the root at initiation, estimated average depth of the root, total length of the root, the position and diameter of all second order laterals and the depth to the deepest sinker root tip originating from the selected root. Sinkers were defined as roots that adopted an angle of less than 45 ° to the vertical within 12 to 15 cm from the point of origin (Coutts 1989).

All measurements were recorded to the nearest millimetre, except overall depth of the lateral which was estimated to the nearest centimetre.

5.2.3 Soil coring technique (+ R, + RH, - R and + H treatments)

During November 1995, core samples were extracted from + R, + RH, - R and + H treatments. The position of coring was standardised to minimise variation in above and below ground conditions including, soil aeration, nutrients, and shelter and shade from planted spruce. Root development can be severely restricted by plough furrows and shallow turf ditches on wet soils (Savill 1976). Therefore, growth tends to occur along the ridges where aeration is better (Lees 1972). Where small plough ridges remained from the original rotation, coring was performed along the line of planting in soils favouring root growth. All samples were taken equidistant between planted Sitka spruce. From each plot, four corers (steel cans described in *Chapter 3.2.1*), were inserted vertically into the soil to a depth of approximately 0.15 m. Sampling to this depth was considered adequate as previous experiments (Fraser and Gardiner 1967; Pyatt and Smith 1983) and *in situ* root observations (*Chapter 5.2.2)* suggest that the majority of roots occur in the organic L and F layers. The undisturbed soil sample was stored within the can and in plastic bags at 2 to 3 °C for a maximum of 5 days before observation. Compaction of the sample during extraction from the can was avoided by cutting the can open, allowing the complete soil cylinder to be carefully removed. The sample was sliced into three layers; the L, F and H, and O horizons, and the depth of each layer was measured (to the nearest 5 mm). From each horizon living Sitka spruce roots were removed, before measuring the fresh weights of root and soil. All samples were dried at 80 °C for 48 hours (until constant weight) and re-weighed.

5.2.4 Depth of aerobic soil (+ R, + RH, - R and + H treatments)

Aerobic soil depth was measured using mild steel welding rods (Armstrong *et al.* 1976; Bridgham *et al.* 1991). This technique exploits the redox attributes of iron, which forms reddish-brown rust in the oxidised Fe^{3+} state but is reduced under anaerobic conditions to grey Fe^{2+}. The boundary between these two conditions is approximated by the water table (Bridgham *et al* 1991). Strong correlations have been found between the water table depth and the steel rod rusting depth for different soil types under different vegetation types (McKee 1978; Carnell and Anderson 1986; Hook *et al.* 1987 and Bridgham *et al.* 1991). However, under fluctuating hydrology, a rapid drop in the water table results in the rod oxidation demonstrating a lag period and once heavy rust forms on the rods it does not redissolve upon reflooding (Bridgham *et al* 1991).

On three occasions between September and late November 1995, four rods were randomly inserted into the soil of each + R, + RH, - R and + H plot assessment area. The rods measured approximately 0.8 m and were pushed vertically into the soil at positions equidistant between trees and along the line of planting. Insertion occurred to a maximum depth of 0.65

m. The rods remained in the soil for various periods of time ranging from 12 to 25 days. At the end of each sampling period, the position of the soil surface was marked on each rod, before being removed, cleaned and dried. The rods were stored in a dry container and assessed within 6 hours of removal from the soil. The depth to the anoxic layer was recorded as the difference between the soil surface position and the first unbroken area of uncorroded steel (grey colour). Brown rust and patchy grey areas were removed from the rods using coarse grade sand paper before being replaced randomly within the treatment buffer zones.

5.2.5 Data presentation and statistical analysis

Due to the limited number of *in situ* root observations performed, the results are presented descriptively and without statistical evaluation.

Roots sampled using cores were statistically analysed using the oven dried weights. This eliminated any variability that might arise as a result of different root moisture contents. Comparisons of oven dried root between different soil horizons and treatments were analysed per unit volume (or depth).

Site means and standard errors were calculated for each treatment and for all variables measured from the three plot means. Differences in root distribution and anaerobic soil boundary depth with relation to treatment and horizon were investigated using analysis of variance. The relationship between soil variables, including moisture and horizon depth, and oven dried root weights was assessed using regression analysis.

5.3 RESULTS

5.3.1 In situ *root observation (+ R and - R treatments)*

First order lateral roots originated at depths between 25 and 50 mm from the soil surface, and grew horizontally within the L, F and H horizons (*Plate 5.3.1*). Diameters ranged between 6 and 13 mm at initiation with the tap root, and progressively decreased to the root tip. Total surface root length varied between 0.68 and 1.64 m and supported from 9 to 34 second order roots, of diameters 3 mm or less (*Table 5.3.1*). The position of laterals along each root is demonstrated in *Figure 5.3.1*. There was no evidence of a treatment effect, or of a relationship between the number of secondary laterals and the total length of root.

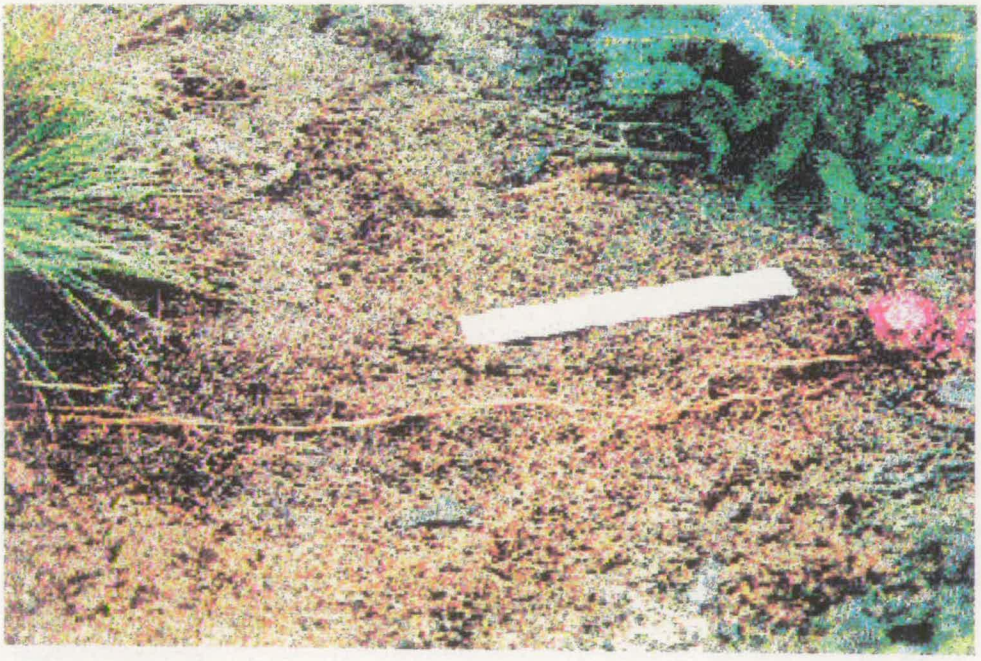


Plate 5.3.1: An excavated lateral root taken from a - R treatment plot. The horizontal growth habit and second order laterals are visible from the stem base (pink) to the root tip. (Scale: white bar = 30 cm.)

The estimated overall depth of roots was generally 20 mm greater (50 mm below the soil surface) in residue retained treatments than those growing in clear plots (20 to 30 mm average depth) (*Table 5.3.1*). Similar trends were observed for sinker root growth, which attained greater depths (by approximately 5 mm) in residue retained plots than clear (*Table 5.3.1*). The roots generally reached the lower H horizon, although occasional penetration of the O layer was observed (in treatment plot +R, block 2). Lateral root tips were pale brown and stubby, possibly indicative of mycorrhizal associations.

Table 5.3.1: Root lengths, diameter and depth of root at initiation, number of laterals per root, and the depth of deepest sinker are presented for + R and - R treatments. Means and standard errors are listed (n=3).

	Treatment							
	+ R				*- R*			
Block	*1*	*2*	*3*	*Mean (± St. Err.)*	*1*	*2*	*3*	*Mean (± St. Err.)*
Surface root length (m)	1.63	0.68	1.03	1.01 (± 0.36)	0.94	0.86	1.61	1.13 (± 0.24)
Diameter at initiation (mm)	13	13	10	12.0 (± 1.0)	10	10	6	8.67 (± 1.3)
Root depth at initiation (mm)	40	25	50	38.3 (± 7.3)	50	20	30	33.3 (± 8.8)
No. of secondary laterals	25	9	13	15.7 (± 4.8)	26	10	34	23.3 (± 7.1)
Sinker depth (m)	0.15	0.18	0.12	0.15 (± 0.02)	0.07	0.12	0.10	0.10 (± 0.02)

5.3.2 Soil coring (+ R, + RH, - R and + H treatments)

Due to the nature of sampling, first and second order lateral roots could not be distinguished.

The effect of treatment and soil horizon on oven dried weight of fine root

Treatment did not significantly affect the mean weight of oven dried root per sample core or volume of soil. Mean values per treatment core varied from 0.41 (± 0.11) g to 0.66 (± 0.07) g in + R and + RH plots, respectively. Quantities recorded per cubic centimetre of soil ranged between 1.05 (± 0.29) mg and 1.52 (± 0.20) mg in + R and + RH cores, respectively (*Table 5.3.2a*).

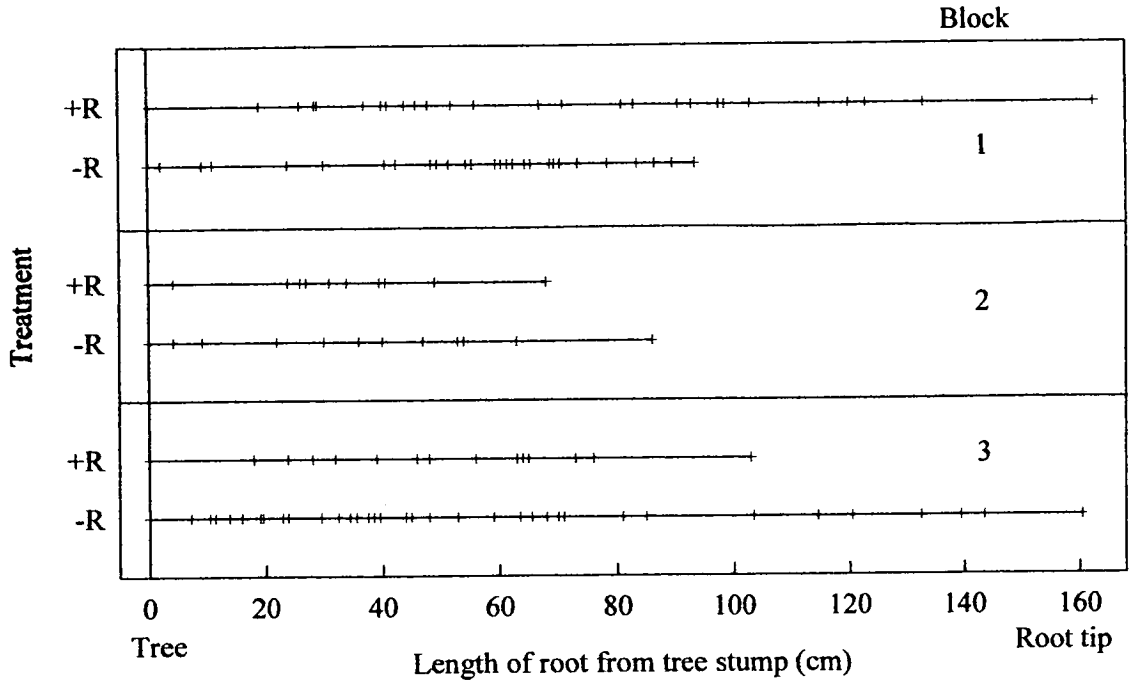


Figure 5.3.1: A diagrammatic representation of each excavated root. Total root length and the position of the second order laterals (as ticks) are shown.

Table 5.3.2a: Oven dried root weight present in complete cores and cubic centimetres of soil for treatments + R, + RH, - R and + H. Sample means (± standard errors) are given (n = 3).

	Treatment			
Root weight	***+ R***	***+ RH***	***- R***	***+ H***
g per core	0.41 (± 0.11)	0.66 (± 0.07)	0.49 (± 0.11)	0.53 (± 0.12)
mg per cm³	1.05 (± 0.29)	1.52 (± 0.20)	1.37 (± 0.23)	1.35 (± 0.20)

Root weight per unit volume of soil was significantly greater in the L and FH horizons, than the O layer in all treatments (L horizon > O horizon; P = 0.002 and FH horizon > O horizon; P = 0.001) (*Figure 5.3.2a*). The differences were most pronounced in the - R plots, where root quantities were five times greater in the L and FH horizons than the O (1.85 (± 0.35), 1.92 (± 0.36) and 0.34 (± 0.08) mg cm^{-3} soil, respectively). Although the weight of root in the L and FH layers was unaffected by treatment (*Figure 5.3.2a*), significantly greater weights were present in the O horizon of herbicide treated plots compared to non-herbicide (P = 0.016).

Relationships between the quantity of root present per horizon and the soil characteristics of each core (oven dried weight, percentage moisture and depth) were poorly correlated. Regression equations using combined data demonstrated that the best single predictor of oven dried root weight was horizon depth ($R^2 = 0.19$).

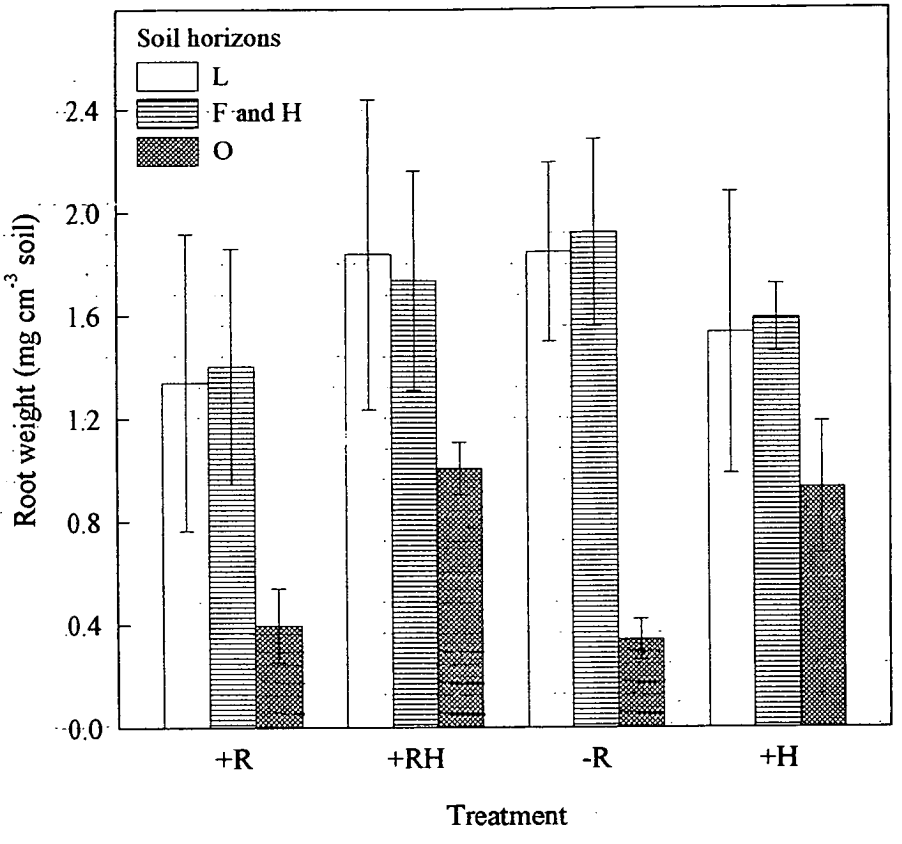


Figure 5.3.2a: Root weight per volume of soil (g cm^{-3}), showing distribution between L, FH and O horizons for each treatment (+ R, + RH, - R and + H). Sample means (± standard error bars) are represented (n = 3).

Separation of the data by horizon and treatment improved the relationship within the L layer only. In the absence of herbicide, R-squared values of 0.81 ($P < 0.001$) and 0.80 ($P < 0.001$) were calculated for + R and - R treatments, respectively (*Figure 5.3.2b*). However, the weight of root and depth of the litter layer were not significantly related in the herbicide applied treatments.

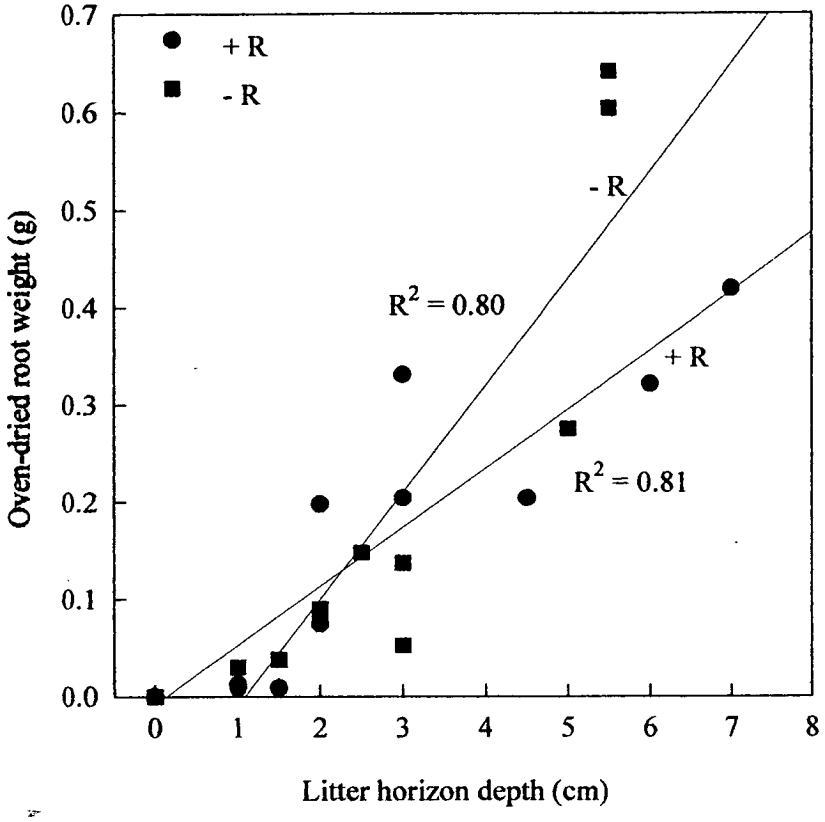


Figure 5.3.2b: The relationship between the weight of oven dried root and the depth of the litter layer in the + R and - R treatments (see legend). Regression lines are fitted through the individual points recorded from each replicated core.

Weight of dried fine root per hectare at Site 1

The weight of root per hectare was estimated from values of soil horizon depth (determined for each treatment) and the weight of oven dried root for each horizon (*Table 5.3.2b*). Unfortunately the figures obtained did not reflect the root present at the site as cores were extracted along the line of planting rather than randomly across the whole area.

Similar trends were observed for root weight per hectare as in unit volumes of soil. The majority of live root biomass occurred within the L and FH horizons in all treatments. Plots receiving herbicide contained greater total quantities of root which were more uniformly distributed between horizons.

Table 5.3.2b: Total dried root per hectare (kg ha^{-1}) expressed for individual and combined horizons. Means (± standard errors) are shown.

		Treatment			
		+ R	*+ RH*	*- R*	*+ H*
Horizon	***L***	443 (± 222)	680 (± 279)	530 (± 157)	481 (± 202)
	FH	670 (± 272)	790 (± 183)	791 (± 184)	788 (± 70)
	O	120 (± 51)	495 (± 111)	142 (± 42)	322 (± 100)
All horizons		1235 (± 336)	1966 (± 224)	1462 (± 332)	1591 (± 371)

5.3.3 Depth of aerobic soil (+ R, + RH, - R and + H treatments)

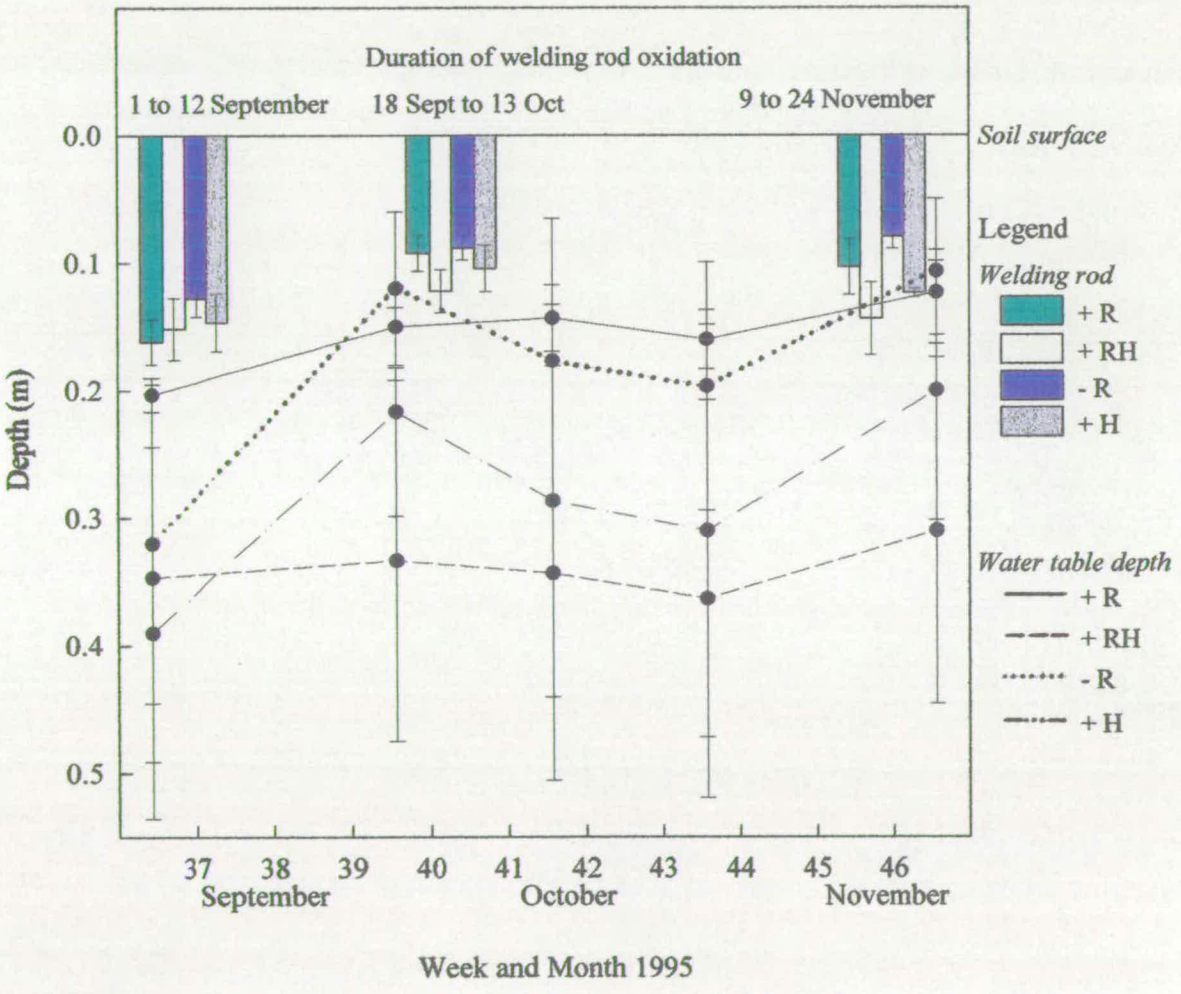


Figure 5.3.3: Water table depth (measured using bore holes) and depth to the anaerobic/aerobic soil boundary (assessed using mild steel rods) from the beginning of September to late November in all treatments (see legend). Means (± standard errors) are plotted (n = 3).

The watertable rose rapidly during August (see *Figure 2.8.4, Chapter 2*), resulting in waterlogging to within 0.4 m of the soil surface in all treatment plots. Aerobic soil depth was shallower than the watertable throughout the experimental period and decreased in mean depth from the beginning of September (0.15 m) to the end of November (0.11 m) (*Figure 5.3.3*).

Treatment did not significantly affect the depth of the anaerobic layer. However, similar trends were observed as those recorded for water table depth, as the depth of aerobic soil was generally deeper in the herbicide applied plots than the non-herbicide treated areas. This was evident during the second and third measurements especially (*Figure 5.3.3*).

5.4 DISCUSSION

The discussion is separated into several categories; the pattern of growth demonstrated by the main laterals and second order roots supported by them, and the quantitative distribution of root biomass within the upper soil horizons (expressed as the oven dried weight per volume of soil). Temporal changes in root growth and distribution are described with respect to 1995 records of soil temperature, precipitation and water table depth. Finally, expected below ground dynamics in the maturing plantation are considered.

5.4.1 Descriptive analysis of root growth

First order lateral roots

The uppermost first order lateral roots, initiated at depths within 50 mm of the soil surface and adopted a diageotropic growth habit. In common with other root observations from peaty gley soil (Adams et al. 1972; Fayle 1975; Armstrong et al. 1976; Pyatt and Smith 1983; Coutts and Philipson 1987), laterals sustained growth within the upper L , F and H horizons. Localised drops in the soil surface level generally resulted in corresponding fluctuations in root depth, so that constant positions within the organic horizons were maintained. Coutts and Nicoll (1991) observed similar trends in pot grown Sitka spruce after modification of the soil surface level. They suggested that the direction of growth resulted from two opposing influences, including the genetic tendency to grow upwards and the responses of roots to different soil environments. Although the abilities to sense stimuli and regulate growth are not fully explained (Coutts and Nicoll 1991), factors such as temperature, aeration, moisture and physical impedance affect the angle of curvature (Coutts 1989). At *Site 1*, decreases in the moisture content at the soil surface probably induce a hydrotropic response, causing the roots to deflect towards moister soil. The resulting direction of growth, allowed exploration of the well aerated, nutrient rich soil layers, and avoided exposing the root tips to desiccation above ground.

After four growing seasons, lateral root length ranged considerably from 0.68 to 1.64 m (for + R plots 1 and 2 respectively). As trees within assessment plots were planted at 1 m spacing, roots greater than 0.5 m length were potentially competing for localised resources. All roots measured exceeded this value, therefore belowground competition between trees had commenced. In addition, other vegetation types were present within the + R and - R plots, creating further demands for nutrients and moisture. From soil core analysis, it was evident that the majority of vegetation roots occurred in the L and F horizons. The limited number of deeper rooting plants was probably a result of the ephemeral nature of the weeds

present and the restricted growth imposed by the soil conditions. A previous study comparing roots of Sitka spruce growing on a cultivated peaty ferric stagnopodzol in Scotland recorded lengths of 2.5 m after the same period (Ross and Malcolm 1982). The enhanced growth probably resulted in response to improved soil conditions and a delayed invasion of competing vegetation following tilling.

Estimates of annual growth at *Site 1* were calculated by assuming that studied roots originated during the first year after planting, and that a consistent growth rate was maintained thereafter. Mean annual increases of 0.26 and 0.28 m y^{-1} were obtained for + R and - R treatments, respectively, during the first four years after planting. However, the increments obtained by Coutts (1983) for 8 year old Sitka spruce growing on a deep peat in Scotland were greater (between 0.42 and 0.78 m y^{-1}). These values did not include growth during the first year, which was regarded to be slowed by planting check. Root establishment after restocking is often delayed by damage during plant handling and insertion to the soil. However, adaptations in the angle of extension of laterals from the root collar can compensate by replacing the original roots. Burial of the stem base also stimulates growth (Coutts *et al.* 1990). Adventitious roots initiate at the hypocotyl, root collar or from the lower lateral branches (Coutts 1983). Recalculation of current growth at *Site 1* (to exclude extension in the first year) produced annual rates between 0.34 and 0.38 m y^{-1}, demonstrating that extension of the studied roots was low compared to results from similar sites in Scotland.

Second order roots

Two types of second order roots were observed; sinkers and horizontally growing laterals with diameters less than 3 mm.

Sinker roots

Sinker roots grew into the lower H and upper O horizons, and attained a maximum depth of 0.18 m. Within the + R and - R treatment plots, the water table and anaerobic soil levels rose rapidly during August and September, before settling by mid October at depths of 0.14 and 0.09 m, respectively. Both these variables restrict root growth by limiting transferral of oxygen to the root (Coutts and Philipson 1978a and b; Armstrong *et al.* 1976).

Observations at a nearby forest (Borders Region, Northumberland) demonstrated poor aeration in the O horizon even when the water table drops in the summer (Pyatt and Smith 1983). This is due to the fine texture of the particles within the lower soil horizons and their low conductivity. At *Site 1*, rooting depth is thought to be regulated by the shallower of the two variables rather than a single characteristic. For example, during the summer the water

table is low and rooting is determined by the presence of anaerobic zones, whereas, during the winter available depth is restricted by waterlogging close to the soil surface.

Lateral roots

Between 9 and 34 second order laterals with diameters less than 3 mm were present on each surface root. These tracked the soil surface within the upper L and F horizons where rates of N mineralisation were greatest (*Chapter 3.3.2*). The capacity for uptake of nutrients is increased by the formation of associations between root tips and mycorrhiza (Coutts and Nicoll 1990b). Although, the level of mycorrhizal infection was not recorded during this study, Alexander and Fairley (1983) recorded that 80 % of Sitka spruce fine roots formed associations.

5.4.2 Quantitative assessment of root distribution

The influence of soil horizon

Fine root distribution across the site was spatially heterogeneous. In all treatments, L and FH layers contained significantly greater root than the O horizon ($F = 8.27$; $P = 0.002$) (41.4 and 42.1 %, respectively), accounting for 83.5 % of the total (*Figure 5.4a*). Correspondingly high densities were recorded in the decomposition horizons of a Sitka spruce forest by Ford and Deans (1977) and during *in situ* observations discussed above. However, actual values are lower than those estimated for trees growing on a peaty gley in Northern Ireland, in which 80 % of fine root grew in the litter layer alone (Adams *et al.* 1976). The high concentration of root within the uppermost horizon was attributed to the growth restrictions imposed by the water table that lay 0.05 m from the soil surface for 7 months of the year. At *Site 1*, soil was waterlogged to within 0.3 m of the surface for 6 months during 1995, and at the time of soil coring. Therefore, the greater availability of aerobic soil at the current site permitted deeper rooting into the F and H horizons. Small quantities of root occurred in the O horizon due to the plagiotropic growth habit adopted by second order laterals (Coutts 1989). However the biomass was low due to the restricted penetration of anaerobic soil by sinkers roots.

The influence of treatment

Treatment did not influence mean root weight in the soil, although the distribution between horizons was affected. Herbicide applied plots contained the lowest proportions within the upper L, F and H layers (77.5%, compared to 89.5% in non herbicide treated plots) and corresponding, significantly greater root weights in the O horizon ($P = 0.016$) (*Figure 5.4.2*). Increases in aerobic depth available for rooting, during periods of high water tables are responsible. For example, at the time of root sampling, mean water table depths were greatest

for + RH (at approximately 0.3 m) followed by + H (0.25 m), - R (0.15 m) and + R (0.15 m) treatments.

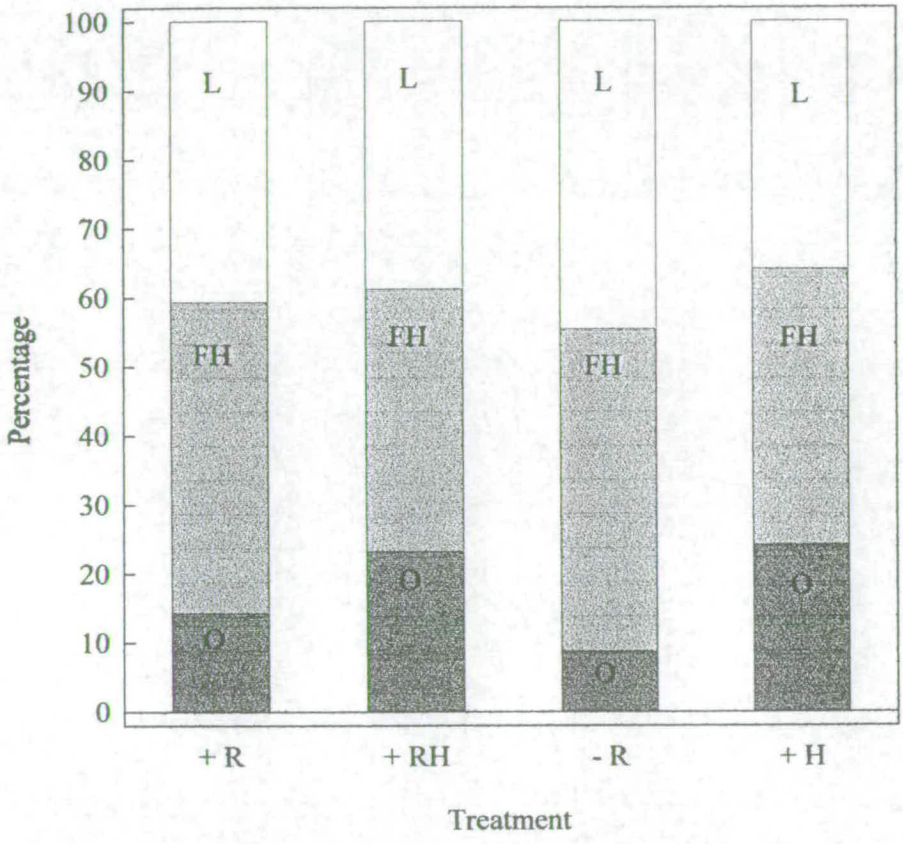


Figure 5.4.2: Oven dried root weight per volume of soil found in the L, F and H, and O horizons expressed as a percentage of the total. The sample mean is represented for + R, + RH, - R and + H treatments.

Consequently, tree roots growing in herbicide treated plots could penetrate the deeper O horizons and suffer less extensive die back during the winter. Although this effect was apparent across all blocks, differences in water table level arose due to variability at the site rather than the direct influence of treatment (see *Chapter 2.8.4*).

Increases in the aerobic soil depth of herbicide applied plots resulted in poor relationships between litter layer depth and root weight. However, regression analysis performed within + R and - R plots demonstrated strong correlation (R^2 values of 0.81 and 0.80, respectively). The presence of rooting restrictions, including shallow anaerobic soil in the + R and - R treatments, forced greater utilisation and exploitation of the substrate available and resulted in a closer relationship between root weight and litter depth. Where the available soil is deeper, trees of the same age experience fewer constraints allowing access to greater volumes. However, as trees grow and the fine root network becomes more extensive, the relationship between soil depth and root weight is expected to increase in all treatments.

Root weights per hectare

Studies of root biomass and distribution in young trees (< 10 years) are scarce. However, the standing crops of live and dead roots have been established for many coniferous ecosystems across Europe and North America. These have been summarised in McKay and Malcolm 1988) and Vogt *et al.* (1996).

Estimates of fine root weight per hectare at *Site 1*, ranged between 1 234 and 1 965 kg ha^{-1}. These values were greater than those recorded by McKay and Malcolm (1988) (1 120 kg ha^{-1}) for 15 year old Sitka spruce growing on an indurated gley with a shallow peaty layer (to 10 cm depth). However, the two studies cannot be compared directly as McKay and Malcolm (1988) recorded all fine root (< 2mm diameter) to a depth of 5 cm, whereas roots (< approximately 3 mm) to a maximum depth of 0.15 m were included in the current study.

Although estimates from *site 1* were not significantly affected by treatment, the biomass was generally greater in the herbicide treated plots where the mean watertable and anaerobic soil levels were deeper.

The estimates obtained during this study may not truly reflect the biomass of root occurring across the site, as cores were taken at standard distances from the stem. McKay and Malcolm (1988) used a similar procedure when collecting samples and suggested that systematic errors may be introduced. However, evidence from young stands is contradictory. Ford and Deans (1977) found 33 % fewer roots midway between Sitka spruce stems than adjacent to stems. In comparison, Persson (1980) found no significant difference in fine root biomass within the first 1.5 m from the stem base in 15 and 20 year old Scots pine forests.

5.4.3 Expected root growth dynamics during 1995, in response to soil temperature and aeration

The following section identifies periods of growth and sensitivity to environmental conditions, using records of soil temperature, precipitation and water table depth recorded during 1995 (detailed in *Chapter 2.8.4*). Only + R and - R plots will be considered as soil temperature data was not collected from herbicide applied treatments.

On the basis of previous research, six assumptions were made concerning Sitka spruce rooting behaviour. These were used to discuss root growth in response to different physical conditions and included the following factors;

- Roots are tolerant to waterlogging for one month at a temperature of 6 °C and when dormant (Coutts and Philipson 1978a),
- Root growth increases with increasing temperature between 5 and 20 °C but is severely limited by temperatures over 30 °C (Coutts and Philipson 1987),
- Actively growing roots may be susceptible to frost damage (Coutts and Philipson 1987),
- Roots do not grow more than 1 to 5 cm into waterlogged soils (Coutts and Nicoll 1990c),
- Active roots dieback, soon after submergence by the water table (Coutts and Philipson 1978a) and
- Sinker roots have the potential to penetrate anaerobic soils by growing into fissures and cracks (Pyatt and Smith 1983).

The water table lay within 0.1 m of the soil surface from January to March. Despite this, the effect of anaerobic conditions on root growth would be minimal, as soil temperatures were consistently below 6 °C and roots were dormant. The initial drop in the water table, at the end of March coincided with an increase in soil temperature from 4 to 6 °C, inducing higher activity in the root apices and the initiation of growth. In June the water table rose to within 0.2 m of the soil surface. However extensive root damage was unlikely as waterlogging was brief (less than one month) and soil temperatures were comparatively low (between 7 and 9 °C). Growth rates of roots would be highest in the summer, when mean soil temperatures were over 12 °C peaking at 17 °C in August. As water tables are generally low at this time, root extension would only be impeded by physical obstructions, including tree roots, old stumps and anaerobic soil peds. However during dry weather, fissures and cracks form in the anaerobic O horizon through which vertical root growth can occur until encountering further obstructions. In summer 1995, extreme conditions in the upper soil horizons may have inhibited growth or caused root damage. For example, precipitation from June to September was low and temperatures within the litter layer attained maxima of 40 °C in clear plots within

the top 1.5 cm of soil. Coutts and Philipson (1987) observed decreases in growth rate at temperatures above 30 °C. Therefore reductions in root extension were possible, while damage to the root tips may have been caused by desiccation and high substrate temperatures. In September, water tables rose and soil temperatures fell to 10 °C. Extensive dieback of sinkers to between 0.1 and 0.15 m depth was probable as roots were still actively respiring and requiring oxygen. By November soil temperature decreased, reducing root activity and increasing tolerance to anaerobic conditions. While further decreases in December to between 6 and 1 °C, resulted in root dormancy.

5.4.4 Future root growth at Site 1

After four growing seasons, exploration of the upper soil horizons by lateral roots remained uninhibited, while vertical development of Sitka spruce roots was restricted by the seasonally high water tables and anaerobic soil peds. As a result a flat root plate, lacking deep sinker roots will develop. It is expected that future surface growth will continue unless limited by physical barriers such as stumps (from the previous rotation) and roots. Coutts (1983) observed that the major surface roots of Sitka spruce established during the first few years, constituted the main structural roots at 34 years. Therefore, the laterals present at the time of excavation have the potential to provide tree stability and exploit large areas of soil (up to 4 $m^2 tree^{-1}$) for nutrients and moisture throughout the rotation.

Fine root distribution at the time of soil sampling was extremely variable between cores, horizons and treatments. Continued root growth would be expected to increase the biomass per unit volume, and decrease variation across the site. Eventually a localised fine root capacity will be reached, increases in root weight will steady and turnover will equilibrate. Ford and Deans (1977) observed this dynamic state in Sitka spruce after 11 years growth on a ploughed site.

Until canopy closure, seasonally high water tables will be common. Annual waterlogging of the upper horizons after the summer causes the sinker root tips and distal parts below the aerobic/anaerobic boundary to die back. Subsequent regeneration initiates at the onset of favourable conditions, by the production of new root tips which branch from the end of the surviving fraction. The repeated and persistent pruning effect of the water table will eventually produce 'shaving brush' ended sinkers (described by Coutts 1989).

Direct precipitation input to the soil reduces considerably after canopy closure. Anderson and Pyatt (1986) recorded interception losses of 29 and 49 % for pole stage and mature Sitka spruce, respectively, growing at Kielder Forest. The majority of the water penetrated the

canopy as throughfall while stemflow accounted for the remainder. Spatial modification of incoming water causes the roots to distribute accordingly, so that increased below ground biomass is recorded at the stem base and upper surface horizons. Reduced inputs result in smaller fluctuations of the water table between seasons and increases in the depth of aerobic soil during the autumn and winter months. Additional soil water loss arises through greater evapotranspiration from the increased foliar biomass of the tree canopy. Under these conditions, more vigorous roots may open up drainage channels in the soil (Adams *et al.* 1972). The combined effect of these factors is to increase the available rooting depth for sinkers and reduce dieback during wet periods.

The results obtained during the current study suggest that residue and herbicide treatments are unlikely to affect the distribution of root growth. However, the logging debris affords more favourable conditions of soil temperature and moisture (*Chapter 3.3.1*), which enhance rates of net mineralisation (*Chapter 3.3.2*) and may increase root activity, nutrient uptake and tree growth. If the onset of canopy closure is advanced by the presence of residue, larger treatment differences will follow. Watertable depth will increase earlier than in clear areas due to reductions in precipitation inputs by interception and increased evapotranspiration. Consequently, penetration of the soil by sinker roots will be deeper, while the release of nutrients for plant uptake may be enhanced.

5.5

SUMMARY

At the end of the fourth growing season, the length of the first order lateral roots from the tree stump to the root tip ranged between 0.68 and 1.64 m, and sinkers penetrated the soil to a maximum depth of 0.18 m. Within the sample cores, the distribution of fine root biomass was greatest in the L and FH horizons (77 to 92 %) and was unaffected by treatment. However, the proportion of root growing in the O horizons, was significantly greater in the herbicide treated plots compared to the + R and - R treatments ($P = 0.016$). The difference probably arose due to lower mean watertable and anaerobic soil depths in the herbicide plots, and was attributed to across site variation, rather than the influence of treatment. Extensive growth of second order roots within the upper soil horizons, where rates of net mineralisation are most rapid, favours the uptake of nutrients. Although residue retention did not significantly affect the distribution or biomass of root growth, the activity of roots and the rate of turnover may have been affected. However, neither of these variables was assessed during the current study.

Patterns of subsequent root growth and the implications for the tree growth are discussed with respect to site conditions and treatment.

Chapter 6

GROWTH RESPONSES OF SITKA SPRUCE FOLLOWING CON AND WT HARVESTING

6.1 INTRODUCTION

Above ground responses of Sitka spruce to different edaphic factors vary. Physical conditions including air and soil temperature, exposure, photon flux density and photoperiod affect growth. While chemical influences acting below ground include nutrient and moisture availability. This chapter details experiments investigating growth of Sitka spruce in + R, + RH, - R and + H treatment plots. The variables observed included;

- phenology (bud burst, leader shoot elongation and cessation of extension and the occurrence of lammas shoots),
- morphology (tree height and total biomass (including roots), leader length and needle weight) and,
- nutrient concentrations and contents (whole tree (including roots) and top whorl N, P, K, Mg and Ca).

6.1.1 *Sitka spruce phenology*

Northern conifer species display a mode of shoot growth that involves annual complements of new foliage arising from predetermined primordia formed in the previous year (Pollard and Logan 1977). After bud burst and extension of this complement, the pattern may be modified in one of two ways. Where edaphic factors permit, precocious expansion of the buds (lammas growth/prolepsis) or supplementary initiation and emergence of foliage after the spring flush (free growth) may occur (Pollard and Logan 1976).

Bud flush

The timing of bud flush depends on the initiation of growth processes and the rate at which this growth proceeds. Sorensen and Campbell (1978) observed that the rate of development rather than the time of initiation had a greater influence on bud burst. Many factors are thought to contribute to the development process. Genetics is considered to play a role in controlling phenological events of young trees (Pollard and Ying 1979), while Irgens-Moller (1958) attributed variations to the age of the tree. Environmental factors may determine phenological differences in older trees and within populations (Irgens-Moller 1967). These include nutrient availability (Benzian *et al.* 1974; Chandler and Dale 1990), interactions

resulting from water stress (Lieffers and Rothwell 1987) and photoperiod (Wareing 1956; Flint 1974; Campbell and Sugano 1975). However, the major influences are air and soil temperature.

Flushing in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco.), was delayed by cold soils below 5 °C (Lavender *et al.* 1973). While, shoot phenology of tamarack (*Larix laricina* (Du Roi) K. Koch.) and dwarf birch (*Betula pumila* L.) was advanced after site drainage and subsequent increases in soil temperature (Lieffers and Rothwell 1987). Although Timmins and Worrall (1974) observed no differences between cold and warm rooted Douglas fir, Sorensen and Campbell (1978) recorded earlier flushing dates with increased air and soil temperatures (by 5.7 and 0.45 days per 1 °C, respectively). The importance of temperature in regulating bud burst is supported by Cannell and Smith (1983), Thomson and Moncrieff (1982) and Bloomberg (1978). They used expressions of temperature as functions to explain variability in flushing dates of Sitka spruce and Douglas fir. However, the relationship may be limited by inadequate chilling or short photoperiods (Flint 1974; Campbell and Sugano 1975). Exposure to temperatures of 7 °C or less for periods of four weeks or more, meets chilling requirements in *Picea* species (Nienstaedt 1967). However, interruption of this period during the early phase of dormancy release counteracts the action induced by previously experienced low temperatures (Nienstaedt 1967). In cases where the chilling requirement is not satisfied, long photoperiods can compensate (Pollard and Ying 1979). Although Cannell and Smith (1983) concluded that in the British uplands, where over 60 winter days record mean air temperatures ≤ 5 °C, photoperiod plays a minor role in regulating bud burst.

Shoot growth

The number of needles resulting from predetermined growth in *Picea* species is controlled by the primordia present in the bud at the beginning of the growing season. Therefore leader or lateral shoot length and biomass may be influenced by;

- modifying the numbers of primordia in the bud set the previous autumn,
- altering stem unit extension and needle expansion and/or
- stimulating additional free growth (lammas).

Primordia initiation towards the end of the growing season is considered to be influenced by temperature (Bollman and Sweet 1976; Pollard and Logan 1977), nutrition (Linder and Rook 1984), photoperiod (Cannell and Cahalan 1979), light quality (Morgan *et al.* 1983) photosynthetic photon flux density and soil water deficit (Pollard and Logan 1977). The number of stem unit primordia set and their extension the following year, also depends on the prevailing environmental conditions (von Wuehlisch and Muhs 1991). Research investigating

the influence of nutrition on growth of Norway spruce demonstrated threefold increases in predetermined leader length depending on the timing of nutrient application (von Wuehlisch and Muhs 1991). Whereas, mineral nutrient deficiencies reduced shoot length, bud length and needle dimensions (Chandler and Dale 1990).

Predetermined stem elongation continues until all primordia are extended, and is completed early enough for the shoots to harden off before early autumn frosts (von Wuehlisch and Muhs 1991). Cessation of leader growth is thought to be regulated by photoperiod (Longman 1991) night length (Pollard and Logan 1976) and temperature (Heide 1974).

In young trees of Norway spruce (*Picea abies* L. Karst.), predetermined extension may be followed by proleptic growth (von Wuehlisch and Muhs 1986, 1991; Longman 1991) which initiates shortly after bud initiation (von Wuehlisch and Muhs 1986). In Sitka spruce lammas growth is observed after long day treatments in juvenile material. However, this is replaced by a single flush in adult plants (Longman 1991). The secondary extension is dependent on a surplus of carbohydrates that cannot be utilised by the annual increment of predetermined elongation. Additional factors including environmental conditions (soil moisture, nitrogen availability, physical bending and photoperiod (Coutts and Philipson 1976, Newton and Preest 1988, von Wuehlisch and Muhs 1991, Hallgren and Helms 1992, Millard and Proe 1992)), genetic variation (Walters and Soos 1961; Hallgren and Helms 1992) and tree size, age and vigour (Walters and Soos 1961) contribute to the regulation of lammas growth.

Provided there is low risk of early autumn frosts, trees demonstrating secondary growth tend to have a competitive advantage. The precocious extension of primordia benefits the trees because stem units are displayed more efficiently (Cannell and Johnstone 1978), the length of the current growing season is prolonged (Ununger and Kang 1988) and the foliage is less prone to deer browsing (Newton and Roth 1996). In addition, lammas growth increases the subsequent initiation of needle primordia and predetermined growth the following year (Ununger and Kang 1988). However, no relationship has been found between predetermined and lammas growth attained in the same growing season for Norway spruce (von Wuehlisch and Muhs 1991) or Sitka spruce (Cannell and Johnstone 1978).

6.1.2 Tree morphology and nutrient concentrations

Height and biomass

Early stand development and establishment of trees is influenced by handling during restocking. South and Mason (1993) observed that small differences in height at initial planting caused appreciable modifications in height at age 6 to 10 years.

After planting, tree growth and partitioning (Cannell 1989) is affected by nutrient availability, soil moisture, photon flux density, temperature and exposure. For example, Benson *et al.* (1992) observed smaller dry matter production after periods of poor nutrient supply, low temperatures and water stress. In addition, Raison *et al.* (1992) estimated that 80 % of the variation in annual foliage production of Radiata pine could be explained in terms of the water and N availability during the previous summer (when primordia were initiated) and during the period of needle extension (Raison *et al.* 1992). Extreme temperatures and severe drought reduce efficiency of light use and increase respiration and foliage loss (Cannell 1989). Although annual precipitation inputs (1300 mm) are not considered to limit growth at Kielder Forest, roots present in the upper soil horizons may become moisture stressed during periods of low rainfall, high air temperatures and solar radiation. Nutrients may also become limit growth if low moisture reduces mass flow to the root. High winds and exposure are common in the uplands of Britain and can cause damage and reduced growth. Symptoms are detailed in *Chapter 2.9.*

Nutrient concentrations

Nutrient concentrations of Sitka spruce grown in Britain are well documented for N, P, K and Mg. However, Ca and micronutrients are less well researched. Levels recorded in different ages of Sitka spruce and originating from a number of locations are presented in *Table 6.1.2.* Although the absolute values are good indicators of nutrient deficiency in younger crops, the proportion of macronutrients present is also important. The optimal ratio for nutrients in Sitka spruce is;

N	*P*	*K*	*Mg*	*Ca*	
100	2-15	50-100	5-10	5-10	(Van den Burg 1985).

Within individual trees the nutrient concentrations vary, depending on nutrient availability at the site, the age of the foliage, the time of year and the mobility of the nutrient within the plant. The N and P contents generally decrease as the needles age increases (Beaton *et al.* 1965; Hom and Oechel 1983). Hom and Oechel (1983) recorded the highest N contents in current foliage of Black spruce (*Picea maria*), with the first 8 age classes maintaining high values before declining to 70 % of the maximum in the oldest (13 years) needles. In addition, the P content was higher in the the current tissue with a gradual decline after 1 year, to 55 % of the maximum values after 13 years (Hom and Oechel 1983). At the beginning of the growing season, the concentrations of macronutrients in buds of trees demonstrating predetermined growth are high (except for Ca, which tends to accumulate during the season). As shoots extend, dilution reduces concentrations, whereas contents continue to rise. Nambiar

and Fife (1987) observed nitrogen content of Radiata pine needles to decrease throughout the growing season. The nutrient was remobilised to support new needle growth later on in the same year. It is likely that the multiple flushes that occur during free growth of *Pinus* species, lead to modified nutrient translocation within the shoot compared to that of *Picea* species. During the winter, storage of nutrients is observed to occur in the foliage of spruce, with no translocation to the stem, as found in broadleaved trees (Chapin and Kedrowski 1983).

Table 6.1.2: A summary of nutrient concentrations (dry weight of top whorl foliage, unless otherwise stated) of Sitka spruce growing in North America, Britain and Europe. Different qualities of growth at different stages throughout the rotation are represented. (n.m = not measured; nat. regen. = naturally regenerated; deficient * = values less than this threshold show deficiency; optimal ** = values greater than this show optimal growth.)

Authors	*Year*	*Area*	*Tree age*	*Notes*	*Nutrient concentration (%)*				
					N	*P*	*K*	*Mg*	*Ca*
Beaton *et al.*	1965	British Columbia	110 years	observed	1.10	0.14	0.83	0.09	0.64
			7 years	levels	1.15	0.18	0.82	0.09	0.42
Binns *et al.*	1980	Britain	young stands	deficient *	1.20	0.14	0.50	0.03	n.m
				optimal **	1.50	0.18	0.70	0.07	n.m
Coutts *et al.*	1995	Britain	30 -50 years	national average	1.30	0.17	1.00	0.09	0.32
Farr *et al.*	1977	Alaska	nat. regen. seedlings	observed aboveground	0.80	0.10	0.50	0.07	0.50
Benzian and Smith	1973	Britain	seedlings	observed aboveground	1.50	0.20	1.00	0.10	0.70

6.1.3 Objectives

The responses of Sitka spruce growth to CON and WT harvesting at Kielder Forest have been researched during the past two decades at a site established in 1981 (Proe and Dutch 1994; Proe *et al.* 1994; Proe *et al.* 1996). Trees grown on WT harvested areas possessed consistently smaller heights and diameters than trees planted where residue was retained. Foliar N, P and K concentrations were also lower in the WT treatments, although the effect became less apparent for N and P after 12 years (Proe and Dutch 1994). Proe and Dutch (1994), suggested that the differences in growth may arise from a combination of factors including nutrition, shelter and weed suppression.

The objectives of the experiments detailed in this chapter were to;

- determine whether growth (height and biomass) of Sitka spruce is affected by harvesting intensity or suppression of weeds during the first four growing seasons after restocking,
- assess the influence of treatment on tree phenology, nutrient concentrations and contents, and
- ascertain whether treatment differences, if any, are being sustained, increasing or decreasing.

6.2 METHODS

6.2.1 Sampling procedure

During the 1994 and 1995 growing seasons (May to mid October), morphological and phenological observations were recorded and top whorl foliar samples collected from the buffer zones of + R, - R, + RH and + H treatment plots (see *Figure 2.7a* and *b*). The biomass and nutrient content of four whole trees (including roots) from each assessment area (+ R, - R, + RH and + H treatments) were determined by the MLURI in autumn 1994. In addition, top whorl foliar nutrient concentrations were measured annually (in October) by the FC, using ten trees selected from the assessment plots of each treatment.

The number of trees sampled per plot (excluding measurements by the MLURI and FC) differed according to the variable measured and the year. In 1994 eight trees were considered for each measurement, whereas 1995 sample sizes increased to 16 for phenological measurements. This increase was deemed necessary, as assessment of tree phenology involved observing the presence or absence of a particular characteristic. When expressed as a percentage, individual trees represented a large proportion of the total (12.5 % during 1994, n = 8 per plot). However, increasing samples per plot to 16 reduced the percentage accounted for by each tree to 6.25 % and facilitated investigation into differences between treatment over time.

Phenological and morphological measurements were performed on the same set of randomly selected trees (permanent sample trees). If a chosen tree had a broken leader, damaged leader terminal bud or forked main stem the nearest neighbour within the buffer zone was selected. Damage to the leader sometimes occurred after tree selection, through frost injury of the newly flushed bud or wind damage. In these cases, another neighbouring tree was used. Depending on the time at which the damage occurred, data was discarded. For example, at the beginning of the season a replacement tree could be selected without influencing the growth trends throughout the season. However, if leader damage occurred during the latter stages of growth, all height data from that tree was discarded so that trends would not be altered by the inclusion of values with missing data. As few trees were injured late in the season, within plot variation was not affected. Foliar samples for nutrient and biomass analysis were collected randomly, from different sets of trees on each occasion. Individual trees were sampled once during a growing season.

6.2.2 Phenology (bud-burst and secondary proleptic growth (lammas))

In 1994, leader buds from the eight permanent sample trees per plot were observed for flushing. Measurements were repeated on four occasions, from 5 May to 7 June (*Appendix 6.2*), in order to observe 0 to 100 % buds burst. During 1995, recording intensity increased to 6 times between 1 May and 2 June (*Appendix 6.2*) and included 8 extra permanent sample trees per plot. In addition, the date of flushing was recorded in the terminal buds of the top and second top lateral shoots growing in a northerly direction from the stem. Swollen buds were considered to have burst once the scales had broken and green needles were visible ('stage 3', Lines and Mitchell 1965). Intermediate flushing stages were not considered. The height of each bud above the soil litter surface (to the nearest 5 mm) was recorded.

Occurrence of lammas growth was recorded in leader shoots of permanent sample trees towards the end of the 1994 and 1995 growing seasons. Identification of lammas was aided by clear differences in needle distribution and colour. The determined growth of spring and early summer is dark green with densely spaced needles at the tip where the new bud is set. In comparison, lammas growth is lime green with widely spaced needles at the base (*Plate 6.2.2*). For trees demonstrating secondary growth, the extra length was determined in millimetres.

Plate 6.2.2: Photograph of Sitka spruce demonstrating lammas growth at the end of the third growing season.

Duration of leader shoot elongation

Duration of leader growth in 1994 and 1995 was derived for each tree using estimates of leader bud flush date and the date on which shoot elongation was complete. Shoot growth cessation was determined as the first date maximum leader length was recorded. A maximum error of 21 days was associated with each tree, due to the intervals occurring between each observation date. However, it was assumed that this error would be standard for all treatment plots.

6.2.3 Tree height and leader extension

Tree height (the distance from the soil surface (top of the litter layer) to the leader terminal bud) was recorded at the end of 1993, 1994 and 1995 on the eight permanent sample trees selected in 1994. In addition leader growth occurring throughout 1994 and 1995 was measured fortnightly, from mid May to August and less frequently (every 3 to 4 weeks) from August to the beginning of October. Total sampling occasions decreased from eleven to nine in 1994 and 1995, respectively. *Appendix 6.2* lists sampling and measurement date details. All heights were recorded to the nearest 5 mm.

6.2.4 Biomass, nutrient concentrations and contents

Annual foliar nutrient concentrations were measured in mid October, from 1992 to 1995 by the FC (see *Chapter 6.2.1*). Additional destructive samples were collected at fortnightly intervals during the 1994 and 1995 growing seasons. On each occasion a whole, top whorl lateral shoot, growing north of the main stem was taken. Shoots were oven-dried for 48 hours at 80°C (until constant weight). The samples collected each fortnight were separated into needles and stem, before quantifying stem weight, total needle weight and weight of 100 needles. Total shoot weight and the number of needles per shoot (n) were calculated. Where w was the weight of 100 needles and W the total weight of needles (*6.2.4*).

$$n = \frac{W * 100}{w} \qquad 6.2.4$$

Foliar concentrations of N, P, K, Mg and Ca were determined for oven dried needles, using a modified micro-Kjeldahl, wet digestion procedure (Allen *et al.* 1974). Replicated foliar samples were bulked according to treatment plot and date of collection, and ground using a 0.5 mm mesh centrifuge mill. From each bulked sample, two 0.1g samples of ground material were weighed (to 3 decimal places) into Pyrex digest tubes. Additions of 2 ml of concentrated H_2SO_4 and two volumes of 0.75 ml of H_2O_2 (30v/v) were made to each

replicate. Samples were placed in a heating block at 350 °C for 6 hours, or until all organic material had digested and the solution had cleared. After cooling, the digests were transferred to 100 ml volumetric flasks. One 0.5 ml measure of 10 % lanthanum solution was added to each, before making the solution up to 100 ml using distilled water. Blanks and standards were run with each set to allow calibration. Total N and P were determined using a Perstop Analytical continuous flow analyser. Total K, Mg and Ca were assessed using a Pye Unicam SP9 atomic absorption spectrometer.

Foliar nutrient contents were calculated from needle nutrient concentrations and biomass data for each sample.

Four trees were selected randomly from within the + R, - R, + RH and + H assessment plots in autumn, 1994 by the MLURI. Aboveground growth was sampled and roots excavated. Total oven dried biomass, nutrient concentrations and contents were determined (as above).

6.2.5 Data presentation and statistical analysis

Treatment means and standard errors were calculated for all data. Analysis of variance tested for significant treatment differences in tree height and biomass data, foliar nutrient concentrations and contents and arcsine transformed phenology measurements. The arcsine transformation converts percentages recorded during bud flush and lammas (*equation 6.2.5a*) observations from 0 to 100 %, to 0 to 90. This method avoids errors which may arise if proportions or percentages are grouped at one end of the scale.

$$Transformation = (arcsine\sqrt{(number\ of\ observations\ as\ d\%\ of\ total\ per\ plot)/100}\ )^{\circ} \qquad (6.2.5a)$$

For some variables recorded in stepwise intervals throughout the growing season, including leader length and foliar biomass, curve fits were performed. Differences between treatments were evaluated through time by comparing linearity and curve parameters (Parallel curves analysis; *Appendix 1.5*). Curve fits were also performed on bud flush data to calculate the date of 50 % bud burst in each + R and - R treatment plot. An exponential (*6.2.5b)* and logistic (*6.2.5c*) equation was fitted to 1994 and 1995 bud burst data, respectively. The logistic equation described 95 % of the variation recorded during 1995. However, due to the small number of sampling dates and buds observed during the previous year, variation accounted for was lower in 1994, (from 70 %) using an exponential curve equation. *Chapter 6.3.1* summarises the values for unknowns in the equations below, where x is the percentage buds burst, y is the date of bud flush (days from January 1) and a, b, c and m are parameters.

1994 $$x = \frac{\log\left(\frac{y-a}{b}\right)}{\log(r)} \qquad 6.2.5b$$

1995 $$x = \frac{\ln\left(\frac{c}{y-a}\right)-1}{-b} + m \qquad 6.2.5c$$

The relationship between bud burst date and air temperature (expressed as thermal time and chill days), wind speed and bud height above the litter surface, were investigated using regression equations. Thermal time (accumulated daily mean temperature greater than 5.6 °C) was calculated using equation *6.2.5d* from Cannell and Smith (1983), where $T_{5.6}$ is day degrees with a base temperature of 5.6 °C, n is the total number of spring days with a mean temperature greater than 5.6 °C and t_m is the mean daily temperature on those days taken as (max. + min.)/2.

$$T_{5.6} = \sum_{m=1}^{n} (t_m - 5.6) \qquad 6.2.5d$$

The number of days with a mean temperature (max. + min.)/2 less than 5.6 °C from January 1 was expressed as chill days.

6.3 RESULTS

6.3.1 Phenology

Bud burst

In 1994, flushing initiated between May 2 and 10, and was complete within a three week period. Of the four observations, treatment differences were investigated on two occasions only (May 10 and 22). Before and after these dates 0 and 100 % buds had flushed, respectively (*Figure 6.3.1a*). On May 10 a significantly higher proportion of buds from residue retained plots had flushed than in clear (P = 0.015). Treatment differences were not significant on May 22.

The following year bud burst initiated between May 1 and 7, and finished before June 7. There was no significant effect of treatment on the flush date of leader, top whorl or second top whorl buds. Individual trees demonstrated acropetal development. Shoot terminal buds present on the lower branches burst before those higher in the tree crown (*Figure 6.3.1b*). Completion of flushing in the lower branches was earlier (mid May) compared to that of the leader shoots (beginning of June).

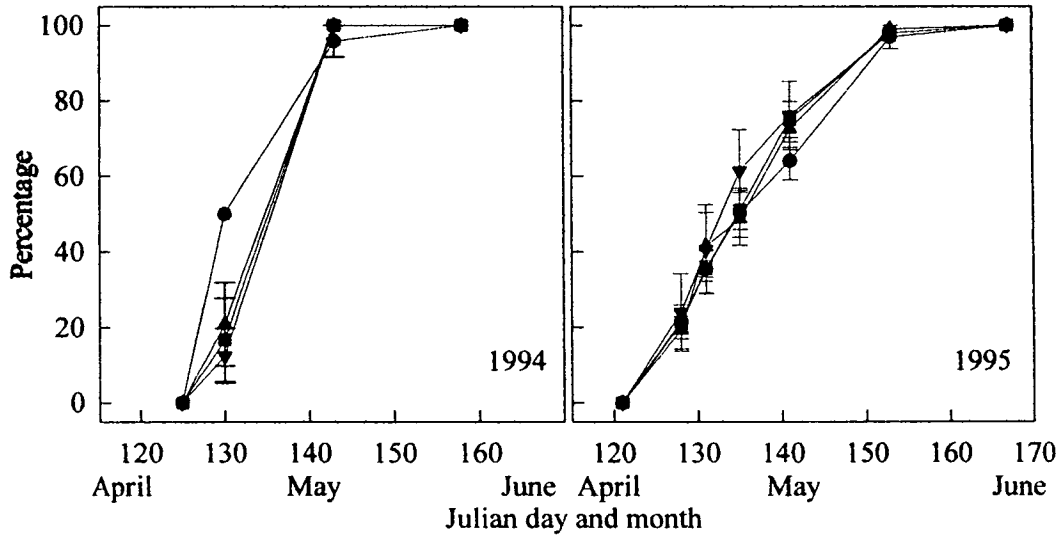


Figure 6.3.1a: Mean percentage number (± standard errors) of leader buds flushed in 1994 and 1995 for treatments, + R (●), + RH (▲), - R (■) and + H (▼) (n = 3).

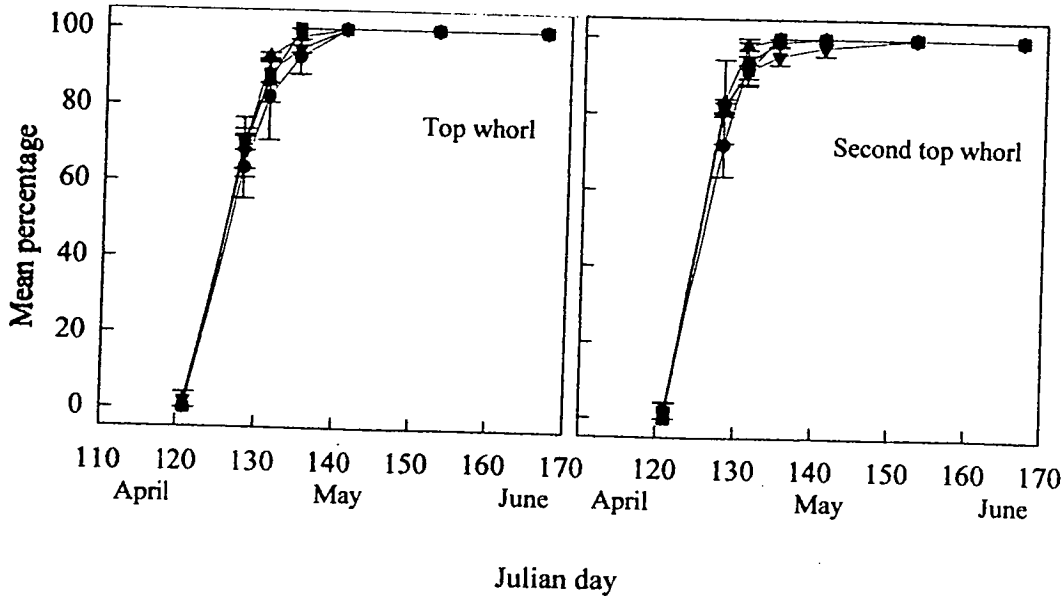


Figure 6.3.1b: Percentage flushing in second top and top whorl branch terminal buds in 1995. Means and standard errors are shown from + R (●), + RH (▲), - R (■) and + H (▼) treatments (n = 3).

The number of days to 50 % bud burst (estimated using equations *6.2.5b* and *c*) ranged from 130 to 138 and was not significantly influenced by treatment or year (*Table 6.3.1a*).

The relationship between 50 % leader bud burst (combined data from 1994 and 1995) and thermal time, number of chill days and tree height was poor (*Table 6.3.1b*). However, multiple regressions using the variables chill days and accumulated temperature resulted in a R-squared value of 0.68 (*Table 6.3.1b*).

The analysis was repeated independently for each year. In 1994, relationships between the each variable and bud flush date were not significant. The maximum R-squared value (0.45) resulted from a multiple regression using all three variables. However, in 1995 the relationships improved. The number of chill days was the strongest predictor ($R^2 = 0.97$; $P < 0.001$) (*Figure 6.3.1c*). Inclusion of tree height and accumulated temperature improved the relationship slightly ($R^2 = 0.99$; $P < 0.05$).

Table 6.3.1a: A summary of parameter values used in *equations 6.2.5b* and *c* to estimate days to bud flush from January 1 in + R and - R treatment plots. The percentage variation in actual flush dates accounted for by each equation and the estimated number of days to 50 % buds burst are presented. The estimated number of chill days and accumulated temperature recorded from January 1 to the calculated date for 50 % of buds burst are listed.

1994		*Parameter*			*% variance*	*Days to*	*Chill*	*Accum.*
Treatment	*block*	*a*	*b*	*r*	*accounted*	*50% flush*	*days*	*temp.*
+ R	*1*	102.6	-89287824	0.89635	99.9	131	103	66.8
	2	106.2	-3.09E+08	0.8878	96.9	130	105	46.6
	3	101.0	-11875828	0.9107	94.1	132	104	48.2
- R	*1*	111.7	-9971221	0.9130	91.3	132	104	67.7
	2	130.4	-172530	0.9446	70.2	135	105	64.7
	3	119.5	-946441	0.9310	82.2	133	104	50.0

1995		*Parameter*				*% variance*	*Days to*	*Chill*	*Accum.*
Treatment	*block*	*a*	*b*	*c*	*m*	*accounted*	*50% flush*	*days*	*temp.*
+ R	*1*	-245	0.0869	350.0	111.1	97.9	130	94	117.9
	2	-53.5	0.0932	160.9	127.7	96.8	134	101	96.3
	3	-18.9	0.1054	125.8	136.1	98.1	138	105	98.0
- R	*1*	-29.3	0.1441	132.1	128.9	95.0	132	96	123.8
	2	-10.9	0.1563	113.9	133.1	95.5	134	100	95.2
	3	-69.7	0.0952	175.7	125.3	98.3	133	96	89.8

Table 6.3.1b: R-squared values indicating relationships between 50 % bud burst and thermal time, number of chill days, tree height and the interaction expressed using linear and multiple regression analysis. Apical buds are represented. The significance of each relationship is given after the R-squared value, n.s. = not significant, '*' $0.05 \geq P > 0.01$, '**' $0.01 \geq P > 0.001$, '***' $P \leq 0.001$.

Predictor	*Year*		
	1994 & 1995 (n = 24)	*1994 (n = 12)*	*1995 (n = 12)*
Thermal time (a)	0.024 n.s.	0.044 n.s.	0.382 n.s.
Number of chill days (b)	0.116 n.s.	0.094 n.s.	0.970 ***
Tree height (c)	0.690 n.s.	0.388 n.s.	0.600 n.s.
a and b	0.683 **	0.205 n.s.	0.981 **
b and c	0.534 *	0.450 n.s.	0.974 **
a and c	0.093 n.s.	0.391 n.s.	0.734 n.s.
a, b and c	0.691 *	0.452 n.s.	0.987 *

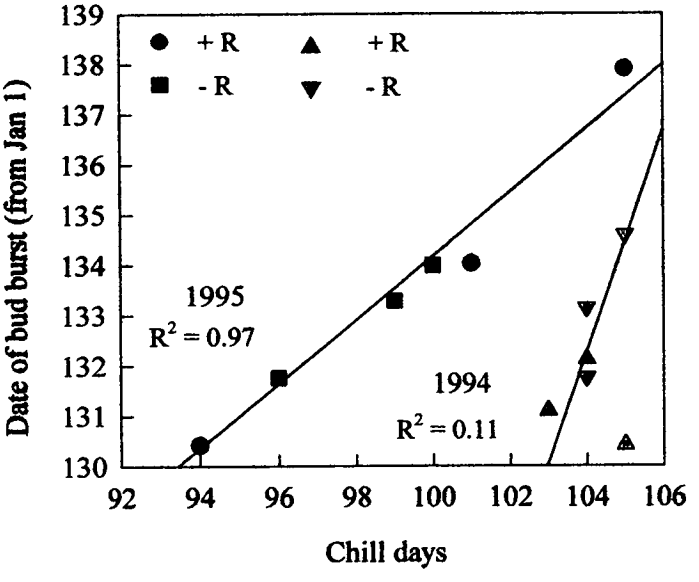


Figure 6.3.1c: The relationship between the number of chill days (temperature < 5.6 °C) and date of leader bud burst in + R and - R treatments for 1994 (■) and 1995 (■). Each point represents a separate treatment plot.

Lammas growth

In October 1994, terminal buds of leader shoots from all treatments demonstrated secondary growth. The proportion of permanent sample trees exhibiting lammas was not significantly affected by treatment. Values ranged from 0.13 to 0.29 in + H and + R, respectively (*Table 6.3.1c*). However, of the trees demonstrating additional lammas, the retention of residue significantly increased the length grown (F = 30.18; P = 0.002)(*Figure 6.3.1d*).

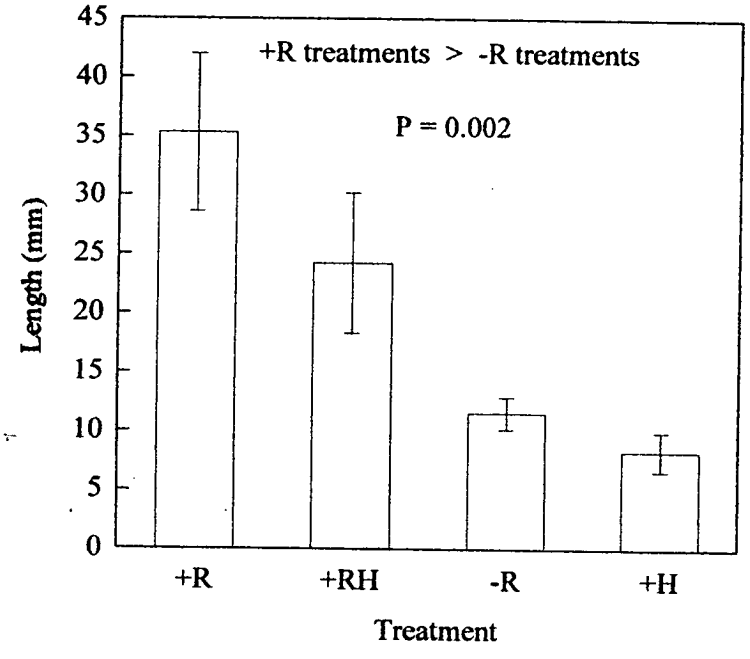


Figure 6.3.1d: Mean length (± standard errors) of lammas growth (mm) recorded in + R, - R, + RH and + H treatments at the end of the 1994 growing season (n = 3).

The following year, lammas growth was observed occasionally in trees from + R, - R and + H treatment plots. The maximum proportion recorded per treatment was 0.04, for + R and + RH plots. Treatment differences in lammas occurrence and additional length grown were not significant.

Table 6.3.1c: Proportion of assessed trees demonstrating leader shoot lammas growth in 1994 and 1995 for + R, + RH, - R and + RH treatments (n = 3).

	Proportion of shoots			
Year	*+ R*	*+ RH*	*- R*	*+ RH*
1994	0.29	0.29	0.29	0.13
1995	0.04	0.00	0.02	0.04

Duration of shoot growth

In 1994, cessation of leader growth occurred earlier than in the following year, resulting in a significantly shorter period (approximately 24 days) of shoot elongation (P = 0.001). Residue retention significantly increased the number of growing days recorded in 1994 (P = 0.046) (*Table 6.3.1d*), whilst no treatment effects were detected in 1995. The duration of leader elongation was not related to number of chill days or thermal time (greater than 5.6°C), either from the time of bud burst or January 1.

Table 6.3.1d: The number of days during which leader shoot growth was detected during the 1994 and 1995 growing seasons. Year and treatment means are listed (± standard errors) (n = 3).

	Duration of leader shoot elongation (days)				
Year	*Year mean*	*+ R*	*+ RH*	*- R*	*+ H*
1994	98.1 (± 1.5)	104.9 (± 3.6)	109.5 (± 5.6)	85.7 (± 5.0)	96.2 (± 7.8)
1995	123.5 (± 2.6)	124.2 (± 4.0)	122.6 (± 10.7)	122.2 (± 2.2)	124.0 (± 2.4)

6.3.2 Tree heights and leader extension

Tree height

Tree heights recorded at the end of the three growing season (1993 to 1995) were not significantly affected by treatment. Residue retained (+ R and + RH) and - R treatments exhibited similar relative growth rates. Within these treatments, annual increases in height represented 45 and 55 % of the total tree height for 1994 and 1995, respectively. However, percentage increases in height of trees from + H treatments were considerably higher. During 1994 and 1995, height at the start of the growing season increased by 60 and 63 %, respectively, over the previous year (*Figure 6.3.2a*).

Although, residue and herbicide treatments did not significantly influence tree height recorded at the end of each year (1993 to 1995), mean values were generally greater in residue retained plots in 1993 and 1994. At the end of the 1995 growing season, differences between the residue retained and + H plots diminished. A maximum of 0.05 m separated the + R, + RH and + H, whereas - R grown trees were at least 0.12 m shorter (*Figure 6.3.2a*). Percentage differences between treatments decreased through time, from means of 15 % in 1993 to 7 % in 1995.

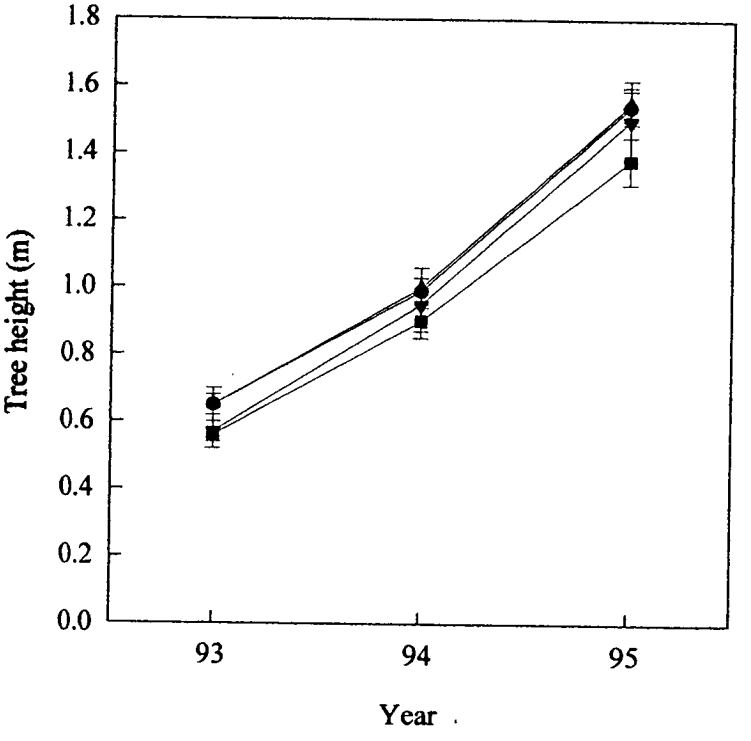


Figure 6.3.2a: Mean (± standard error) tree height at the end of 1993, 1994 and 1995 for treatments + R (●), + RH (▲), - R (■) and + H (▼) (n = 3).

Leader length

In 1994, leader growth was recorded from mid May until the end of August. The effect of treatment varied through the growing season. At the start of June, mean leader lengths in residue retained treatments were significantly greater than those from the clear ($P = 0.013$). However by August, trees grown in herbicide treated plots possessed significantly longer leaders ($P < 0.017$) (*Figure 6.3.2b*). Total leader extension differed by approximately 40 mm in herbicide and non-herbicide treatments (0.37 m and 0.33 m, respectively) at the end of the growing season.

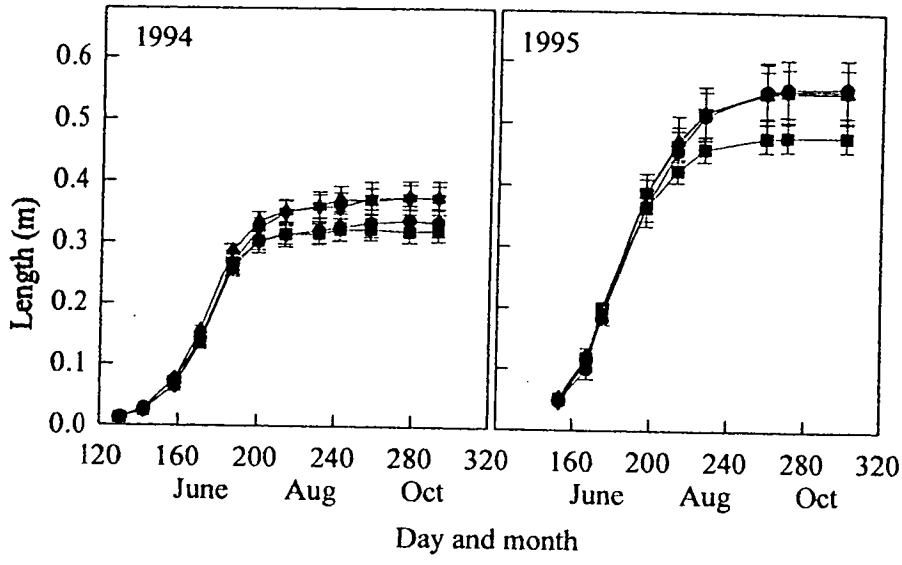


Figure 6.3.2b: Leader extension throughout the 1994 and 1995 growing seasons. The means (± standard errors) for treatments + R (●), + RH (▲), - R (■) and + H (▼) are plotted (n = 3).

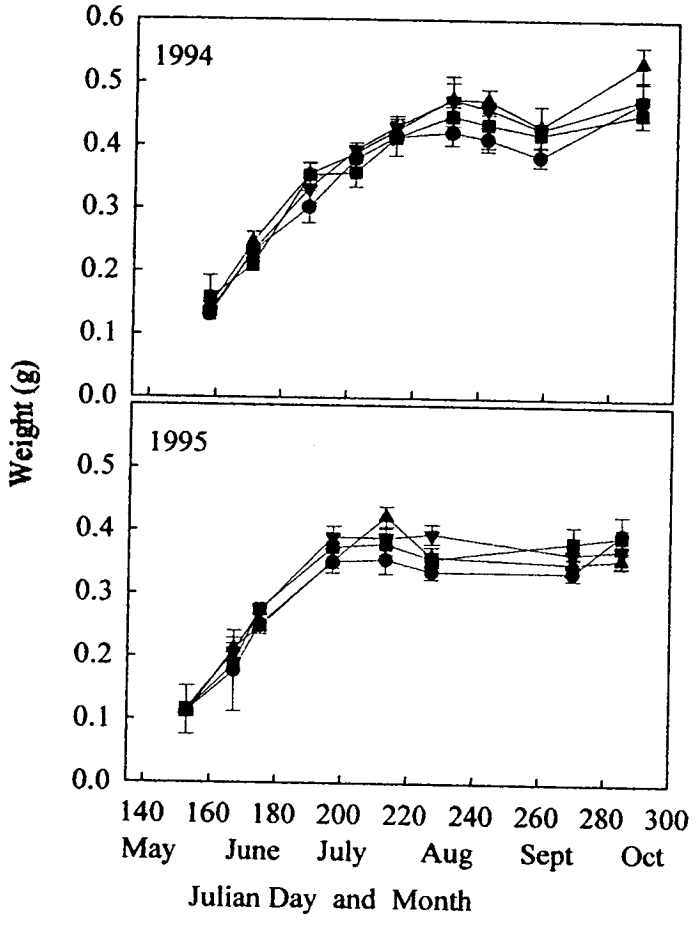
Leader growth in 1995 initiated in mid May and continued for an additional two weeks (compared to the previous year), until mid September. There was no significant effect of treatment, although mean leader length in - R plots was consistently lower from the beginning of August (*Figure 6.3.2b*).

A logistic equation accounted for the greatest amount of variation in leader length data recorded in 1994 and 1995. Comparisons between the curves demonstrated that herbicide application resulted in significantly greater overall leader heights in 1994 (P = 0.02). However, there were no significant treatment effects recorded during 1995.

6.3.3 Biomass, nutrient concentrations and contents

The weight of 100 needles increased rapidly from the first measurement dates in June until August. After a period of little weight change or a slow decline at the end of August and in early September, an additional gain was recorded in October. Needles collected in 1995

obtained a maximum weight approximately 20 days earlier than those from the previous year. In 1994, the initial peak occurred at the end of August and experienced a steady state before the final increases. Weights recorded in October, at the end of the growing season demonstrated that the mean value for all treatments was approximately 0.06 g greater in 1994 (*Figure 6.3.3a*)



Figures 6.3.3a: Graphs demonstrating biomass increases for weight of 100 needles. Both growing seasons, 1994 and 1995 are represented. Mean values (± standard errors) from each treatment, + R (●), + RH (▲), - R (■) and + H (▼) are plotted (n = 3).

In 1994, there were no significant differences in weight of 100 needles between treatments. The following year, the retention of residue significantly increased weights on July 16 ($P = 0.009$). However, no other significant differences were recorded at the $P < 0.05$ level. Curve fits indicated no effect of treatment throughout the 1994 or 1995 growing seasons.

Numbers of needles per top whorl lateral shoot increased at the beginning of the season and were associated with large error bars, due to the small size of the shoots and needles (*Figure 6.3.3b*). From the beginning of July, needle numbers remained constant. However, in 1994 a further small increase was observed at the end of August, which corresponded with the initiation of lammas growth. In 1995 the number of needles per top whorl shoot was approximately 100 greater than in the previous year ($P < 0.001$). Treatment differences throughout the growing season were inconsistent. On the final measurement date of each year there was no significant effect of residue retention or the application of herbicide.

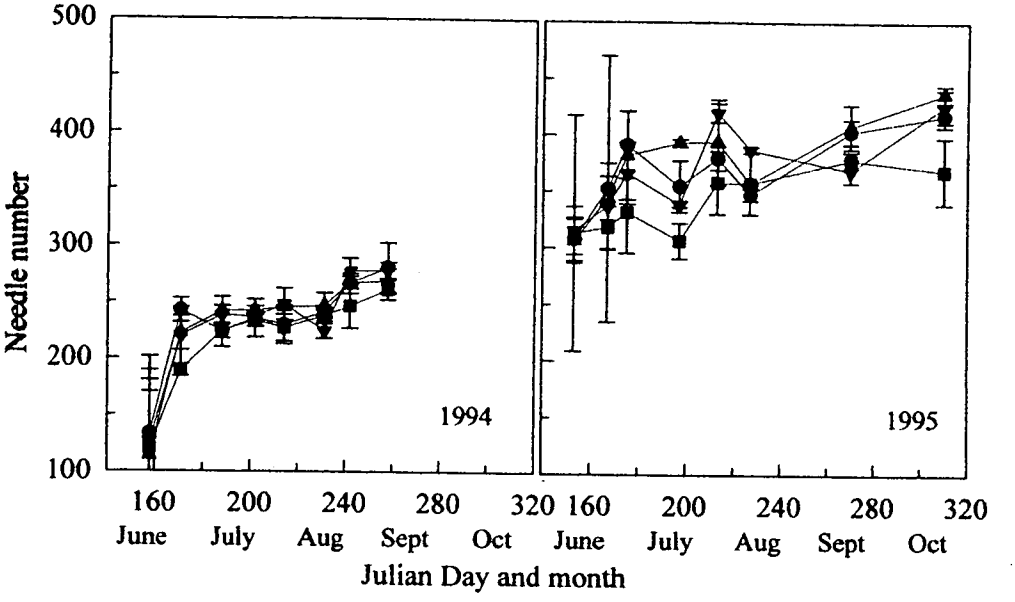


Figure 6.3.3b: Needle number of top whorl lateral shoots sampled in 1994 and 1995 from + R (●), + RH (▲), - R (■) and + H (▼) treatment plots. Means (± standard errors) are presented (n = 3).

The biomass of whole trees destructively harvested at the end of 1994 varied from means of 407.5 to 553.4 g, for - R and + H plots respectively (*Table 6.3.3*). Biomass was not significantly affected by treatment although means were greater in the presence of herbicide application.

Table 6.3.3: Biomass (g) and nutrient contents (N, P, K, Mg and Ca) (g) of whole trees sampled at the end of the 1994 growing season. Means and (± standard errors) are summarised for all treatments.

Treatment		*Nutrient content (g)*				
	Biomass (g)	*N*	*P*	*K*	*Ca*	*Mg*
+ R	438 (± 64)	5.42 (± 0.76)	0.66 (± 0.09)	2.38 (± 0.34)	0.34 (± 0.06)	0.94 (± 0.09)
+ RH	466 (± 89)	6.14 (± 1.07)	0.70 (± 0.11)	2.76 (± 0.51)	0.37 (± 0.05)	1.00 (± 0.16)
- R	407 (± 25)	5.28 (± 0.11)	0.59 (± 0.02)	2.43 (± 0.05)	0.36 (± 0.01)	0.58 (± 0.05)
+ H	553 (± 37)	6.76 (± 0.19)	0.79 (± 0.05)	3.38 (± 0.26)	0.45 (± 0.01)	1.00 (± 0.15)

Foliar nutrient concentrations

Annual foliar nutrient concentrations (N, P, K, Mg and Ca) measured in October, 1992 to 1995, were above levels thought to be limiting for all nutrients except Ca. At the end of 1992, all treatments demonstrated Ca levels below the national average (0.32 % (Coutts *et al.* 1995)). Low levels were also observed in 1994 and 1995 for treatments cleared of residue (*Figure 6.3.3c*). Significant treatment differences were occasionally observed. In the first year after planting, K levels were greater in the presence of residue ($P = 0.004$). At the end of the 1995 growing season, P concentrations were significantly greater in herbicide applied plots ($P = 0.041$), whereas residue retention increased Ca concentrations ($P = 0.001$).

Foliar nutrient concentrations in the top whorl shoots fluctuated during the growing season. Concentrations of all nutrients except Ca were high at the beginning of the season. However as shoot biomass increased, N, P, K and Mg levels dropped to less than half the initial value by mid July. Towards the end of the growing season a rise in concentration occurred for N, P and K, whereas concentrations of Mg remained relatively constant after July. In contrast, Ca concentrations were low at the beginning of the season and increased steadily to three times the initial value at the end of the growing season. Treatment differences were inconsistent between nutrients and years (*Figure 6.3.3di and ii*). However, concentrations of Ca were greater in residue retained grown trees at the end of both years ($P \leq 0.041$).

Nutrient concentrations of whole trees were low compared with those from foliar samples (*Figure 6.3.3d*). Significant treatment differences were apparent for calcium only. Levels were higher in trees from residue retained plots ($P = 0.022$).

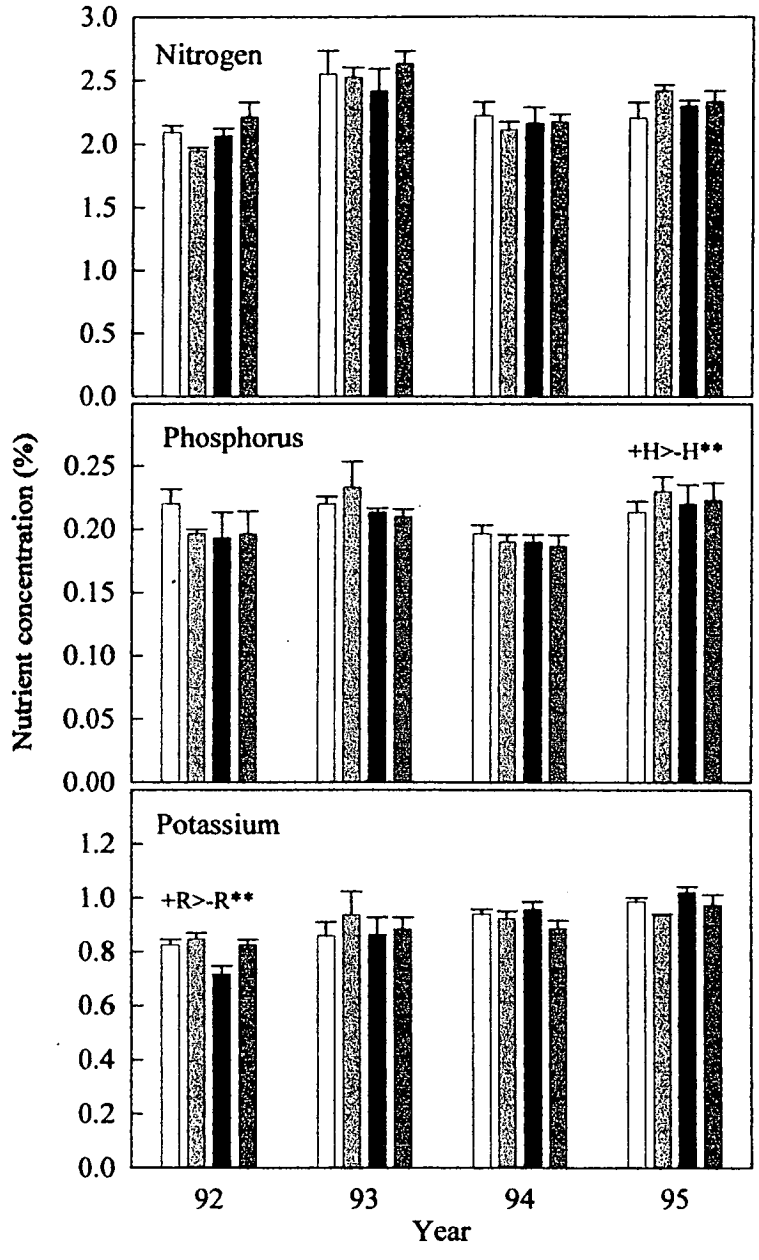


Figure 6.3.3ci: Foliar nutrient concentrations (N, P and K) of top whorl shoots measured in October from 1992 to 1995. The mean percentage (+ standard error bars) are shown for + R (white), + RH (light grey), - R (black) and + H (dark grey) treatments (n = 3). Significance levels are shown. '*' and '**' represent $0.05 \geq P > 0.01$ and $0.01 \geq P > 0.001$, respectively.

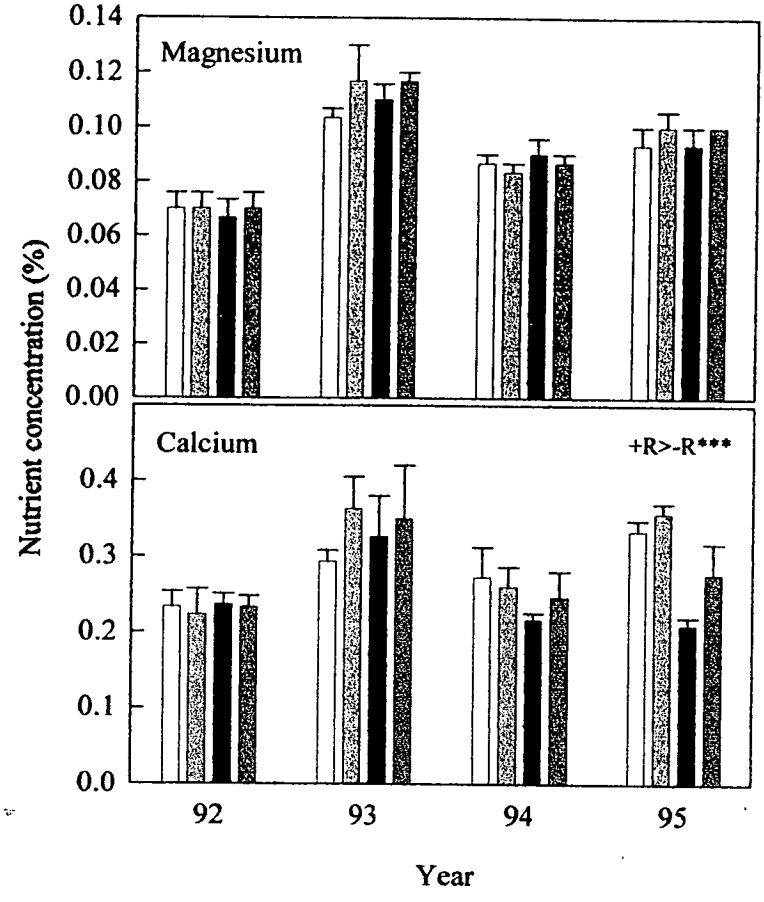


Figure 6.3.3cii: Foliar nutrient concentrations (Mg and Ca) of top whorl shoots measured in October from 1992 to 1995. The mean percentage (+ standard error bars) are shown for + R (white), + RH (light grey), - R (black) and + H (dark grey) treatments (n = 3). Significance levels are shown. '***' represent $P < 0.001$.

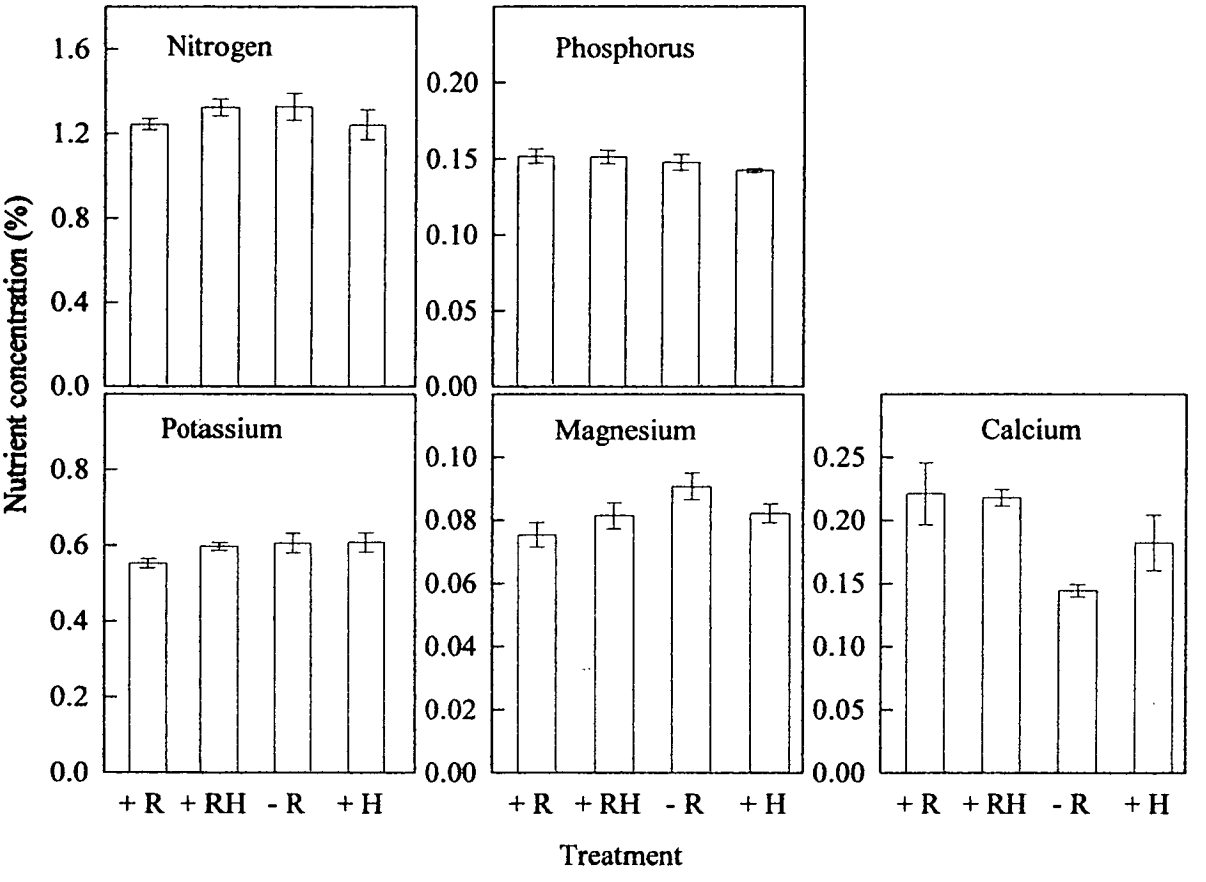


Figure 6.3.3d: Nutrient concentrations (N, P, K, Mg and Ca) of whole trees destructively sampled at the end of 1994. Means (± standard errors) from + R, + RH, -R and + H treatment plots are presented (n = 3).

Nutrient contents

Foliar nutrient contents increased during the growing seasons of 1994 and 1995, for all nutrients measured (*Figure 6.3.3ei and ii*). In 1994, a trend for linear increases continued to the final harvest in all nutrients except Ca. Calcium contents peaked at the end of August, remaining constant in September. Similar increases were observed in 1995. However, increases continued to the final harvest for N, P and Ca contents, only. Rises in K were rapid during the initial part of the growing season, before decreasing in August and increasing again

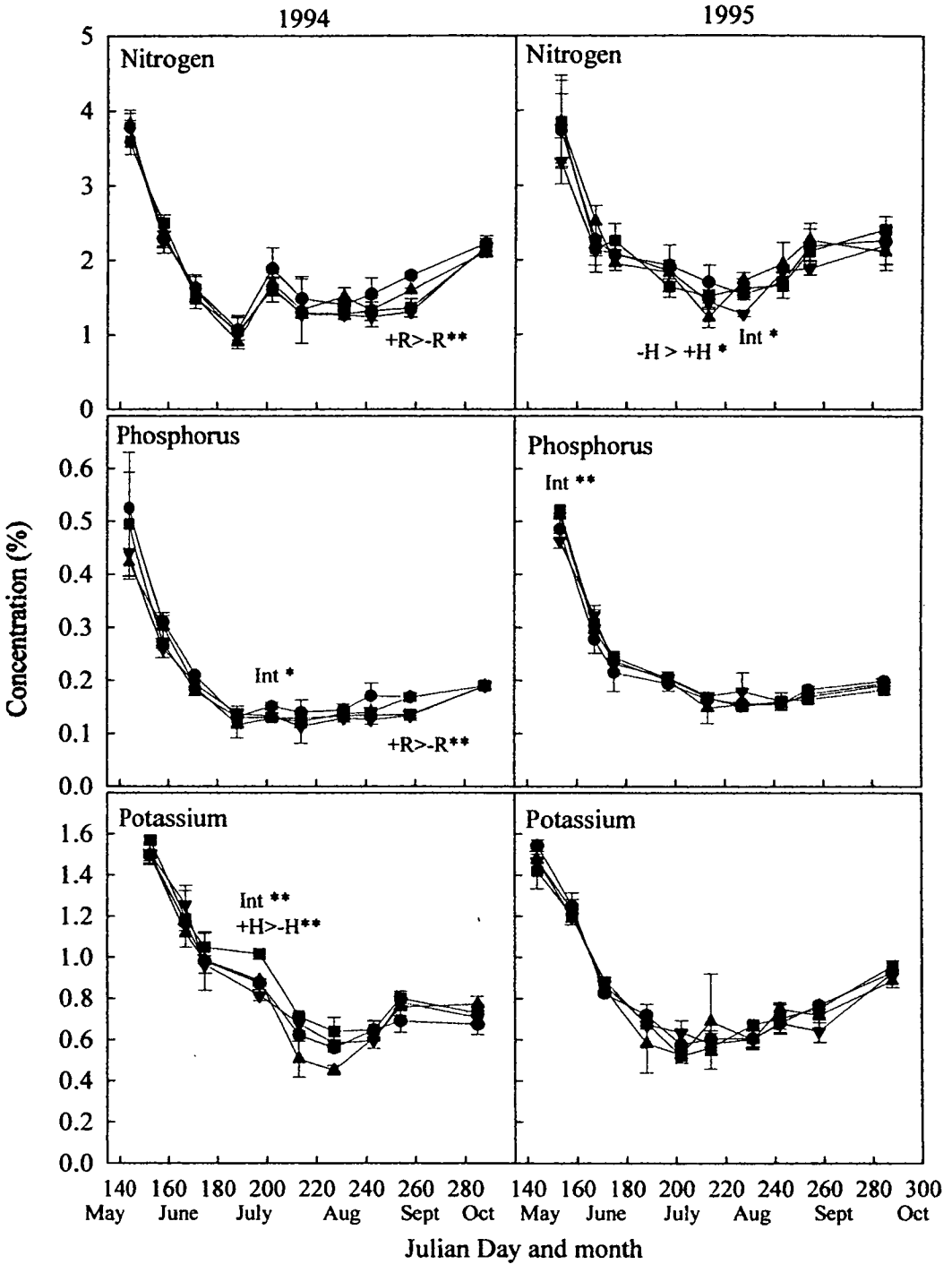


Figure 6.3.3di: Foliar concentrations (N, P and K) in top whorl shoots collected during the 1994 and 1995 growing seasons. Treatment means (± standard errors) are plotted for + R (●), + RH (▲), - R (■) and + H (▼) (n = 3). Significance levels are presented from analysis of variance between horizons and treatments; '*', '**' and '***' indicate $0.05 \geq P \geq 0.01$, $0.01 \geq P \geq 0.001$ and $P \leq 0.001$, respectively. Int signifies an interaction between residue and herbicide treatments.

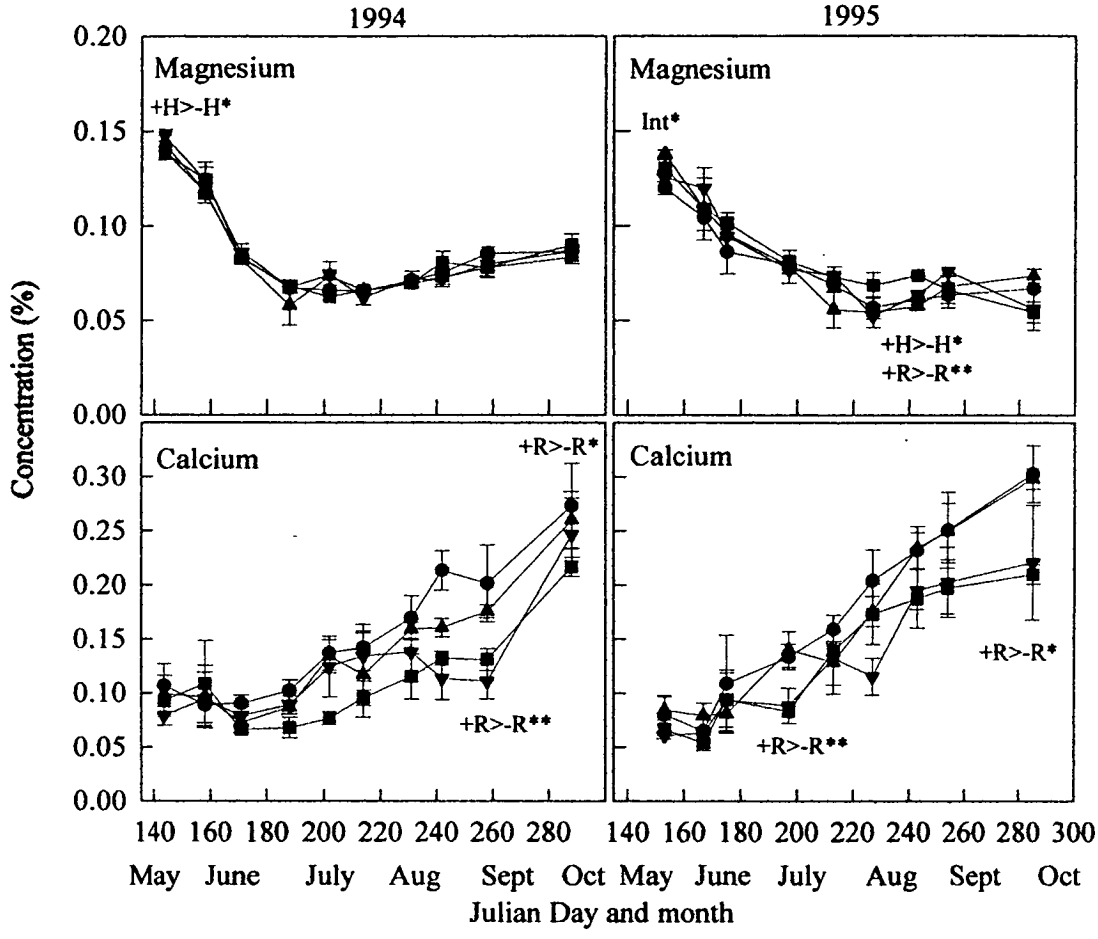


Figure 6.3.3dii: Foliar concentrations (Mg and Ca) in top whorl shoots collected during the 1994 and 1995 growing seasons. Treatment means (± standard errors) are plotted for + R (●), + RH (▲), - R (■) and + H (▼) (n = 3). Significance levels are presented from analysis of variance between horizons and treatments; '*', '**' and '***' indicate $0.05 \geq P \geq 0.01$, $0.01 \geq P \geq 0.001$ and $P \leq 0.001$, respectively. Int signifies an interaction between residue and herbicide treatments.

to October. Similar rapid increases were observed for Mg. However, levels remained constant after mid July. Residue retention significantly increased contents of N ($P = 0.036$), P ($P = 0.050$) and Ca ($P = 0.015$) at the end of 1994. Whereas, the following year Mg ($P = 0.037$) and Ca ($P = 0.012$), were greater in foliage from residue grown trees.

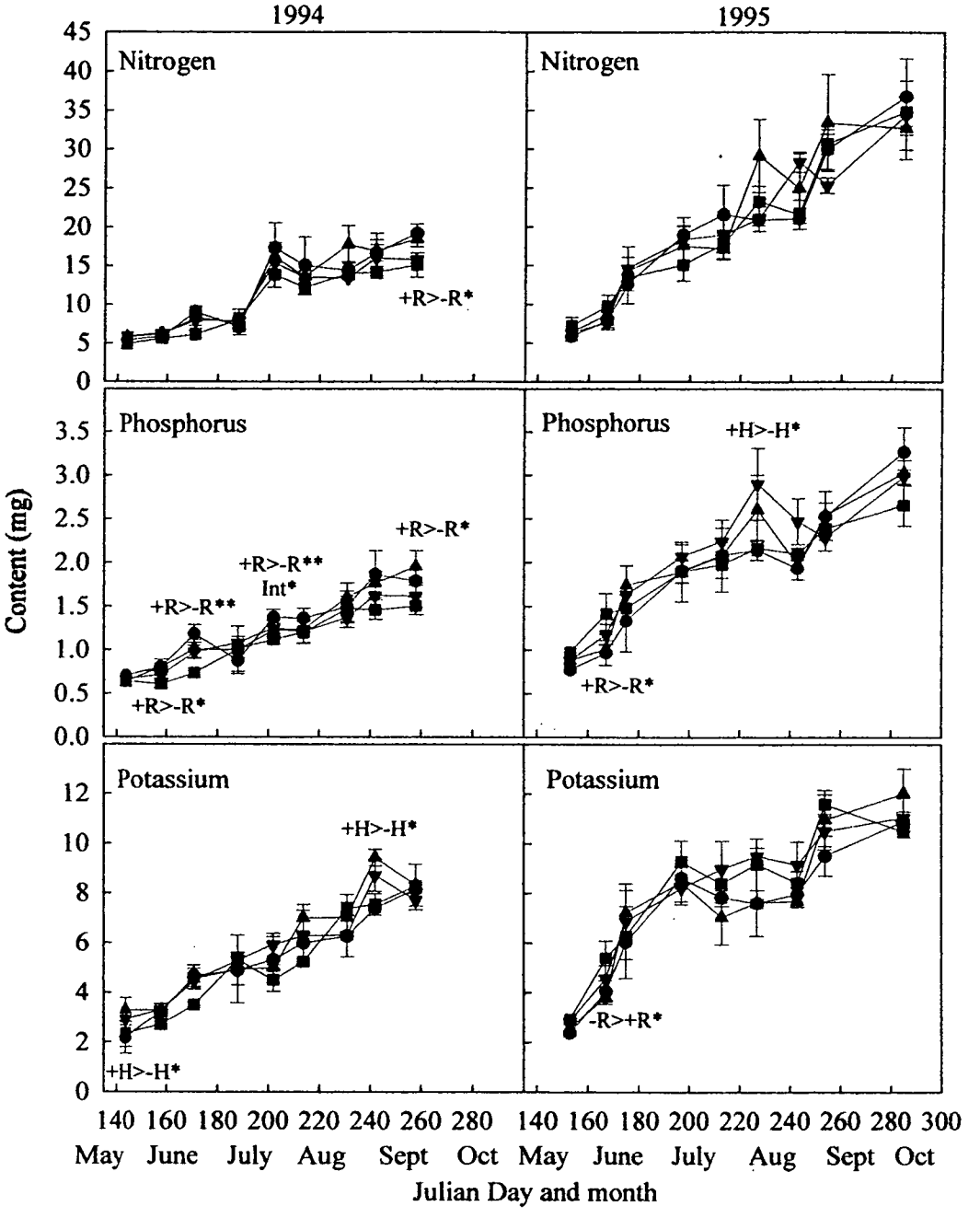


Figure 6.3.3ei: Foliar contents (N, P and K) in top whorl shoots collected during the 1994 and 1995 growing seasons. Treatment means (± standard errors) are plotted for + R (●), + RH (▲), - R (■) and + H (▼) (n = 3). Significance levels are presented from analysis of variance between horizons and treatments; '*', '**' and '***' indicate $0.05 \geq P \geq 0.01$, $0.01 \geq P \geq 0.001$ and $P \leq 0.001$, respectively. Int signifies an interaction between residue and herbicide treatments.

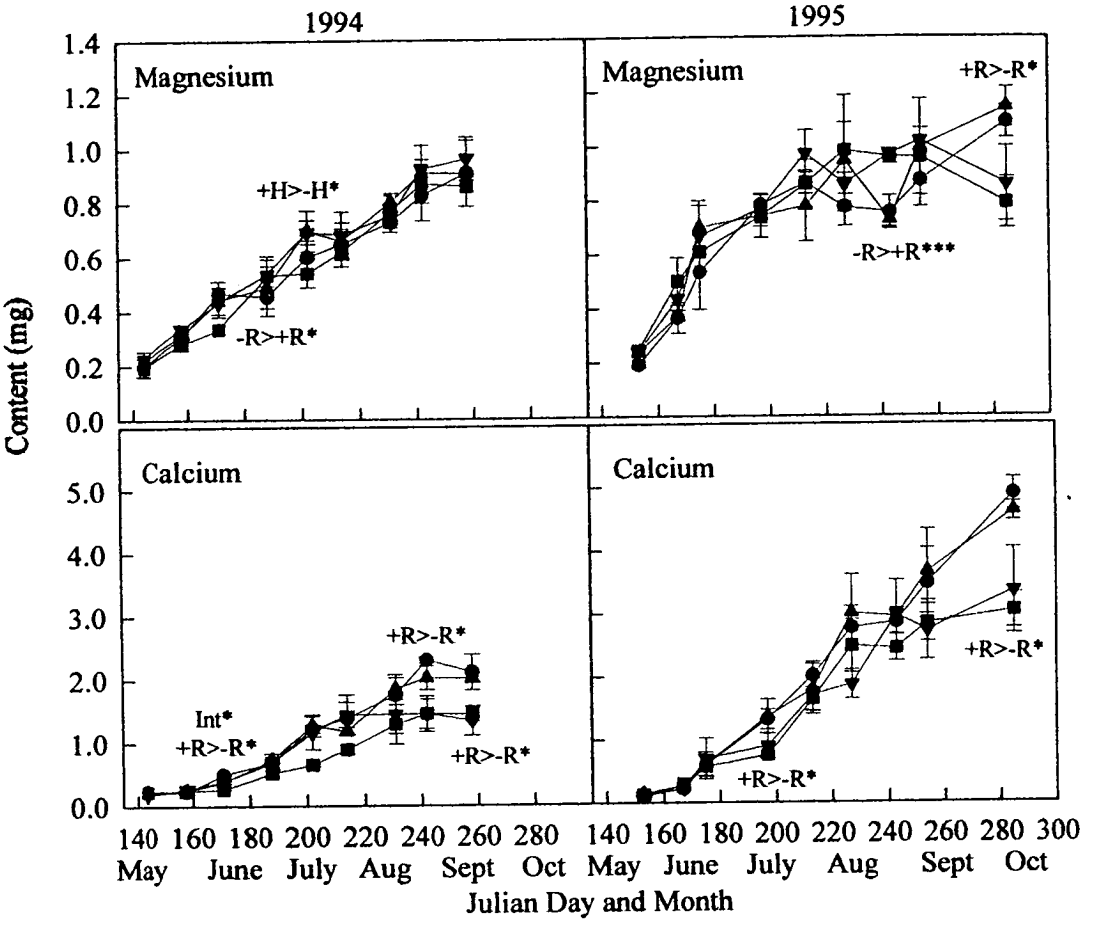


Figure 6.3.3eii: Foliar contents (Mg and Ca) in top whorl shoots collected during the 1994 and 1995 growing seasons. Treatment means (± standard errors) are plotted for + R (●), + RH (▲), - R (■) and + H (▼) (n = 3). Significance levels are presented from analysis of variance between horizons and treatments; '*', '**' and '***' indicate $0.05 \geq P \geq 0.01$, $0.01 \geq P \geq 0.001$ and $P \leq 0.001$, respectively. Int signifies an interaction between residue and herbicide treatments.

Contents measured in whole trees (*Table 6.3.3*), were not significantly affected by treatment, although trees grown in herbicide treatments contained increased mean values of all nutrients.

6.4 DISCUSSION

Retention of residue at *Site 1* benefited the newly planted Sitka spruce seedlings by reducing wind speed and modifying the soil temperature (Proe *et al.* 1994). The sheltering influence afforded by the woody debris diminished as tree height increased and the residue settled. Therefore, measurements of leader phenology performed in spring 1994 (mean seedling height 0.6 m) were more likely to demonstrate a physical treatment effect than those recorded in 1995 (mean seedling height 1.0 m). Additional observations of lower whorl shoots recorded during the second year allowed comparison of buds still influenced by the residue. However, determination of the treatment influence on bud phenology is confounded by the effects of increasing tree crown diameter and height in lessening wind speed and modifying air and soil temperatures.

6.4.1 *Phenology and leader extension of Sitka spruce at* Site 1

Bud burst

Residue retention advanced flushing in May 1994 resulting in earlier 50 % bud burst dates. Unlike observations by Cannell and Smith (1983), there was no significant relationship between flush date and chill days or accumulated temperature. In addition, tree height was poorly correlated with bud burst. The presence of woody residue reduces wind speed at *Site 1* (Proe *et al.* 1994) and slows the movement of air around the shoots. Therefore, warmer conditions are probable as the stiller air is more readily heated by solar radiation, and lower chill factors result from the effects of cold air and high winds. However, the air temperatures recorded within the residue retained plots may not truly reflect those occurring within the buds. Additional discrepancies may arise from the heating effects of direct sunlight, which can raise internal bud temperatures by, for example, an additional 5.6 °C on cool spring days (Wellington 1948).

Although Cannell and Smith (1983) observed relationships between environmental factors and bud burst in Sitka spruce seedlings (aged 2 years), Irgens-Moller (1958), Silens (1962) and Pollard and Ying (1979) suggested that genetics were more important in determining flushing in young trees. Therefore, a combination of factors, including wind speed, air temperature, solar radiation, photoperiod and genetics, may play a role in determining bud burst date. Inaccuracies associated with the small sample size used to calculate 50 % flushing, may also have influenced the relationships observed at *Site 1* in spring 1994.

In May 1995, the physical effect of treatment diminished as increased tree heights exposed leader terminal buds to air temperatures unaffected by residue. As a result, control of flushing was determined by environmental conditions. The strongest relationship occurred between the number of chill days and 50 % flush date ($R^2 = 0.97$), with slight improvements when accumulated air temperature and tree height were included. Cannell and Lines (1983), suggested that the chilling requirement of Sitka spruce growing under British conditions was at least 140 days. However, all buds flushed within 106 days at the current site. The strong correlation between the date of 50 % bud flush and the number of chill days, suggests that the chilling requirement had been met 34 days before that anticipated by Cannell and Lines (1983).

Within individual trees, buds flushed at different times depending on their location. In agreement with previous work (Sweet 1965; Walters and Soos 1963; Lavender 1980), lateral buds burst before leaders, progressing from the base of the crown to the uppermost shoots. Irgens-Moller (1967) observed that buds in warm locations flushed first. This suggested that at *Site 1* the laterals growing lower in the crown experienced warmer temperatures, due to reduced exposure. In addition, increases in tree crown diameter across the site reduced the influence of treatment on microclimate and suppressed differences in bud flush date between + R and - R plots.

Shoot growth (predetermined)

In 1994, predetermined growth was largely complete by early August. However, additional leader extension was observed later that month. The significantly longer leaders recorded at the beginning of June in the presence of residue, probably arose due to the earlier bud flush dates of trees grown in these plots. At the end of the growing season the total length attained was significantly greater in herbicide treated plots ($P = 0.02$). Despite this, the number of needles present on each lateral shoot (approximately 240) remained constant until August, and was unaffected by treatment. As needle number is dependent on the prevailing conditions of the previous autumn (von Wuehlisch and Muhs 1991) the results suggest that treatment did not affect environmental conditions in 1993. Additional increases in leader length and needle number observed in late August and September were attributed to lammas growth.

The following year growth was not significantly affected by treatment, although residue retained and herbicide plots demonstrated greater extension than - R trees. Total lateral shoot needle number increased by approximately 100 in 1995, and was not influenced by treatment. However, numbers at the end of the growing season were lower in - R samples. Increases in tree size probably account for the greater number of needles compared to that of 1994.

Although favourable conditions at the end of the previous growing season (indicated by the presence of lammas growth) may have promoted greater initiation of primordia (Ununger and Kang 1988). Reductions in needle number and unit extension of shoots from - R plots suggest that growing conditions from the middle of 1994 to the end of the 1995 growing season were less favourable in this treatment.

Positive responses of leader stem extension to residue retention and herbicide application probably result from reductions in competing vegetation and increases in available nutrients (*Chapter 3.3.2* and *3.3.3*). However the significantly greater leader lengths attained in herbicide applied plots during 1994 may be in response to lower water table (*Chapter 2.8*) and greater aerobic soil depths (*Chapter 5.3.3*). Improved tree growth is common after drainage of peatlands, due to greater substrate aeration and increased available rooting depth (Boggie 1972). In addition, associated decreases in the soil heat capacity and thermal conductivity can increase maximum temperatures at 10 cm depth from 15 - 16 °C to 18 - 20 °C (Lieffers and Rothwell 1987). Consequently, rates of nutrient mineralisation in the herbicide applied plots would be enhanced, the volume of soil available for exploration by the roots increases and competing vegetation is removed. In 1995, high summer temperatures and solar radiation increased the water table depth in all treatment plots. Therefore the effect of water table depth would be minimal.

Shoot growth (lammas)

In 1994, trees from all treatment plots exhibited additional free growth indicating the presence of favourable growing conditions (von Wuehlisch and Muhs 1991; Hallgren and Helms 1992; Millard and Proe 1992). Lammas length was significantly greater in residue retained plots ($P = 0.002$). Therefore conditions experienced during the second flush were conducive either to more rapid extension, or a longer duration of growth. Detailed measurements of elongation rate were not made. However, estimates of the growing period were significantly greater in residue retained plots ($P = 0.001$), suggesting that a longer duration of growth was responsible. Although many factors are thought to control the cessation of lammas and predetermined growth, including photoperiod, night length and temperature, only microclimatic variables are influenced by treatment.

Fewer trees demonstrated lammas growth in 1995 and treatment did not significantly affect the length attained. Prolific secondary growth may have been inhibited by increases in tree size or age (Walters and Soos 1961), unfavourable environmental conditions or extended periods of predetermined elongation. Estimated duration of leader growth was 25 days greater in 1995 than 1994. Therefore environmental conditions in late August and September

were unlikely to have limited secondary growth. In addition, nutrients were unlikely to be restricting further growth as N and P concentrations were similar in both years. Increases in the number of lateral shoot needles in 1995 resulted from more primordia being set the previous year. Assuming that leader shoots demonstrated similar increases, secondary growth may be reduced as extra time is required to extend the additional primordia during predetermined elongation. Once extended, shortening photoperiods would inhibit further secondary growth.

6.4.2 Tree heights

Annual tree heights increased exponentially from 1993 to 1995. Treatment did not significantly influence the height. However, the differences between the smaller - R plot means and the remaining treatments increased towards the end of the measurement period. At a neighbouring site, Proe and Dutch (1994) observed greater height increases and an influence of treatment after three growing seasons. Trees growing in residue were taller (0.85 m) than those from WT harvested areas (0.69 m). Unfortunately, subsequent height measurements at the neighbouring site were not performed again until year 6, therefore further direct comparisons cannot be made.

Proe and Dutch (1994) explained the initial differences in tree height as the response to the retention of residue. Two factors may be acting; an increase in shelter and a reduction in weed competition. At the current site, sheltering by brash reduced wind speed at 0.3 m above ground level by approximately 30 % during 1992 and 1993 (Proe and Dutch 1994). Despite the increased exposure in clear plots, tree height was not significantly reduced. In addition, advantages are transient as trees had grown sufficiently for the crown to be above the sheltering influence of brash by 1995. The differences in height reported by Proe and Dutch (1994) may have arisen due to increased exposure in the absence of protection from surrounding stands. Differences in substrate quality of the organic soil horizons may also be present as logging residue was left for an additional year before restocking.

6.4.3 Biomass and nutrient concentrations

Oven dried weight of 100 needles increased from mid May to mid August, during acropetal development (Chandler and Dale 1990) of lateral shoots. Small weight decreases occurred at the end of August before further weight gains to the middle of October. This trend was more pronounced in 1994, probably due to the initiation of lammas growth. Previous research recorded similar changes in needle weight of spruce. For example, needle mass of Black spruce (*Picea mariana* Mill.) fell during the summer, before increasing in autumn (Chapin and Kedrowski 1983). Fluctuations were attributed firstly to translocation of carbon and

nutrients to other plant parts during periods of rapid growth, and then to the winter storage of carbohydrate in the current year's needles (Chapin and Kedrowski 1983). Current lateral shoots are major storage areas of nitrogen and phosphorus (Millard and Proe 1993, Proe and Millard 1995a and b) and remobilisation of nutrients from these sites can support future growth (Chapin and Kedrowski 1983). Recent evidence advocates this. Proe and Millard (1994) observed that labelled ^{15}N originally found in the current shoot needles, is detected in new lammas shoots. Therefore a combination of modified respiration rates and remobilisation of cell contents influence current shoot needle weight before, and during the initiation of free lammas growth. In 1995, lateral shoot needle weight increased from May to mid July and remained relatively constant until October. The decline in weight at the beginning of August was minimal compared to the previous year.

Annual concentrations of macronutrients (N, P, K and Mg) recorded in mid October were above Sitka spruce deficiency levels (Binns *et al.* 1980). However, concentrations of base cations (K, Mg and Ca) were below the national average (Coutts *et al.* 1995). In addition, treatment differences observed in 1995 showed significantly greater amounts of Ca occurring in foliage from residue retained plots. The immediate source of base cations is from the exchangeable pool. However, after disturbance cation leaching is accelerated by greater mineralisation of litter and soil organic matter exposed after clearfelling. Increases in nitrification acidify the drainage water and the H^+ ions displace exchangeable Ca^{2+}, Mg^{2+} and K^+ which balance the greater NO_3^- concentrations (White 1987) and render the cations available for plant uptake. Although net nitrification was significantly increased in the LFH horizons of residue retained plots during 1994 (see *Chapter 3.3.2*), actual concentrations in the soil were low compared to that of NH_4^+. Therefore, it is considered unlikely that increased foliar Ca concentrations result from enhanced nitrification in + R and + RH plots. Additional sources of nutrients after CON felling include the needle and woody residue. Fahey *et al.* (1991b) recorded total foliar nutrient release after 4 years of approximately 6.2, 1.1, 8.2 and 1.5 g m^{-2} for N, P, K, and Ca respectively. Compared to other macronutrients, the needles are slow to act as a source of Ca (Maheswaran and Attiwill 1987). However, release from aboveground woody residue, where the proportion of Ca is higher than in the foliage, is more rapid (Fahey *et al.* 1991b). Although Ca is not generally considered to limit growth of trees in Britain (Binns *et al.* 1980), disturbance at harvesting and the removal of above ground residue may reduce availability and have long term implications for site productivity. In addition, other studies from Britain and North America (Mann *et al.* 1988; Stevens *et al.* 1988; Federer *et al.* 1989; Hornbeck *et al.* 1990) have emphasised the susceptible nature of Ca to depletion after intensive harvesting.

Nutrient concentrations throughout the growing season exhibited similar annual trends regardless of year. Percentage N, P, K and Mg dropped sharply from bud burst to late July, due to the dilution of nutrients present at flushing (Chapin and Kedrowski 1983). After a stable period during August, concentrations of all nutrients except Mg levels in 1995, increased to mid October. Millard and Proe (1992) observed an increase in foliar N concentrations during the autumn and winter, when soil temperatures were low and concentrations of soil mineral N were minimal. Some of the mobile nutrients (P, K and Mg) move to the current foliage for winter storage (Chapin and Kedrowski 1983). Calcium concentrations increased throughout the growing season. The immobile nature of Ca (Pritchett 1979) prevents concentration in the bud prior to flushing. In September 1994, additional free growth initiated in all treatment plots. During this period, N, P and Ca contents were significantly larger and percentage concentrations were up to 50 % higher in samples grown in residue. The favourable nutrient status of current foliage prior to and during lammas extension may be responsible for the greater lengths grown in residue retained plots.

Lateral shoot nutrient content was greater in 1995 than 1994, indicative of the exponential rate of growth observed in the young Sitka spruce trees. Contents increased linearly with increasing biomass of the shoot in 1994. Similar increases were observed in N and Ca content in 1995, whereas P, K and Mg accumulated rapidly at the beginning of the season before a period of slower increases during August. At the end of the 1994 growing season, contents of N, P and Ca were significantly greater in trees grown in the residue retained plots. In contrast, Mg and Ca contents were significantly larger in + R and + RH treatments, in October of the following year. As concentrations of all nutrients (except Ca) were unaffected by treatment at the end of the growing season, the differences in contents observed arose due to an interaction between greater concentrations and lateral shoot weight.

Aboveground stand characteristics, especially net primary production, have been observed to be positively correlated with available soil N (Myrold *et al.* 1989). Therefore, the absence of significant treatment differences at *Site 1*, in tree biomass and nutrient content at the end of 1994, suggest that N availability in the organic soil horizons was not sufficiently influenced by herbicide application or residue retention to affect growth. However, leader shoots of trees grown in herbicide treated plots were significantly greater than those from - R and + R plots during the third growing season. Possible explanations for the enhanced leader extension in + H and + RH plots include reductions in competition for resources by weeds and increased soil aeration. By the end of the third growing season, the biomass of competing ground vegetation in treatments without herbicide was relatively low (*Chapter 3.3.3*), and was not considered to

affect nutrient availability to trees. However, increased watertable depths were recorded during the 1994 growing season in + H and + RH plots (*Chapter 5.3.3*), and have been attributed to site variation rather than treatment influences. The greater depths of aerobic soil permit more extensive exploration by roots (*Chapter 5.3.2*) and may have increased nutrient uptake.

6.5 SUMMARY

Phenology of Sitka spruce seedlings is influenced by the presence of logging residue. In the third growing season trees from CON harvested treatments demonstrated advanced 50 % bud flush dates, a greater duration of shoot extension and longer leader growth attributable to lammas. As tree size increased, the physical effects of shelter afforded by the residue decreased and were limited to the lower branches of the tree crown. Consequently, phenological characteristics of shoot growth including flushing dates and duration of the growing season were determined more closely by general aboveground conditions. In 1995, the strongest relationship occurred between time of leader bud burst and the number of chill days ($R^2 = 0.97$).

In 1994, leader length and biomass of destructively harvested trees were greater in herbicide applied plots. An interaction between reduced competition for resources from vegetation, and greater depths of aerobic soil during the spring and summer may favour growth. From studies performed in autumn 1995 (*Chapter 5*), it was demonstrated that the proportion of root biomass in the O horizon of herbicide treated plots was significantly greater than that in the + R and - R treatments. Increased depths of aerobic soil may enhance nutrient uptake in the herbicide treated plots. The effect was not recorded in 1995 leader length, possibly due to the very high summer air temperatures and solar radiation that increased water table depth in all treatment plots.

Needle weight and foliar nutrient concentration of N, P, K and Mg were not consistently affected by treatment. However, levels of foliar Ca in samples collected at the end of 1994 and 1995 and concentrations in trees harvested at the end of 1994, were significantly lower in WT harvested plots. Of the nutrients analysed, Ca deficiency in trees grown without residue retention may be detrimental to long term site productivity.

Chapter 7

DISCUSSION

7

The following chapter discusses the results obtained from *Site 1*, suggests ways in which the methods could have been improved and considers the implications of the observations recorded for long term management and productivity.

7.1 Discussion of results

Results from the preliminary study established at an adjacent site (Falstone) within Kielder Forest (see *Chapter 1.9*), demonstrated that the height, d.b.h., dry matter biomass and nutrient content of Sitka spruce trees from 3 to 10 years after planting was significantly reduced by residue removal (Proe and Dutch 1994). In order to identify the factors causing the differences in the initial rates of tree growth, an additional study was performed at a proximal site (*Site 1*). Climate and soil type were thought to be similar and the responses to the intensity of harvest were expected to demonstrate the same trends. However during the first 4 years after planting, differences in height increment between the CON and WT treatments could not be detected (*Chapter 6.3.2*). Other variables measured in 1994 and 1995, including whole tree biomass and nutrient content (*Chapter 6.3.3*), were unaffected by the retention of residue.

The absence of large treatment effects at *Site 1* indicated that the conditions afforded by logging debris were not sufficient to significantly alter early growth of trees, or different factors interacted to negate the effects of individual influences. Possible differences between the two sites (Falstone and *Site 1*) that might account for the variable responses observed include;

- *the duration between felling and planting.*

  At Falstone the first rotation was felled in autumn 1979 and trees were replanted in spring 1981, whereas *Site 1* was harvested in autumn 1991 and restocked in spring 1992. Consequently, the first site remained bare for 18 months compared to 6 months at *Site 1*.

  Nutrient release from the litter and logging residue occurs in distinct phases (*Chapter 1.5* and *Chapter 4.4.3*), characterised by rapid leaching losses, a period of N immobilisation during partial decomposition, and the initiation of net mineralisation. Therefore, the availability of nutrients to newly planted seedlings

may be greatly affected by the time of restocking. It is suggested that the planting of spruce at *Site 1* coincided with the microbial immobilisation of N, whereas the delayed restocking at Falstone avoided the period of low inorganic N availability and allowed differences between treatments to be expressed after three years growth.

- *the quantity of residue retained at the site.*

  The biomass of residue remaining on site at Falstone was estimated by Titus (1985) from an adjacent site felled in a 'herring bone' fashion (see *Chapter 1.1*) during January 1981, as 49 371 kg ha^{-1}. In comparison, at *Site 1* the logging debris from trees felled within each treatment plot was retained. Although the biomass of logging debris cannot be calculated, as the numbers of stems felled at *Site 1* was not evaluated, it is expected that the quantity of residue per hectare would be less.

  The biomass of residue retained at the site may influence the level of response exhibited by the tree. Greater differences between CON and WT harvested areas would be expected in areas with greater quantities of biomass retained per unit area of soil.

- *tree height at planting.*

  Restocking clearfell sites is often hindered by the presence of residue which makes planting to a constant depth difficult. Tree heights at the two sites may have been affected by the different quantities of biomass retained and the duration between felling and replanting during which the debris could settle. In addition, the measurement of initial heights through residue is difficult. However, results from an adjacent site established in 1989 (M. F. Proe and J. Dutch, unpublished data, 1989) showed there to be no significant difference in heights between trees planted on bare soils and through logging debris.

- *the exposure at each site.*

  The height above sea level (a.s.l.) was unlikely to be responsible for influencing the degree of exposure experienced, as both sites were approximately 300 m a.s.l. However, differences in the aspect of each site and shelter afforded by neighbouring stands of trees might have modified exposure. For example, the experimental area at Falstone was situated within a large clearfelled area and sloped in a south easterly direction, whereas *Site 1* was surrounded by thicket or mature spruce stands on three of the four edges and had a westerly aspect (*Chapter 2, Figure 2.7b*). As the newly planted seedlings at *Site 1* would have experienced greater shelter, the benefits associated with residue retention may have been small relative to those at Falstone.

- *and the pattern of residue retention.*

  At Falstone, the CON treatment consisted of residue bands (approximately 8 m wide) separated by clear strips (approximately 4 m wide). Within these plots, differences in the growth rates of seedlings were not detected during the initial 10 years, except in the third year after planting. In comparison, growth in WT areas was significantly reduced. The absence of differences between the clear and residue retained areas of CON plots may be attributed to the proximity (2 m maximum) of all trees to the beneficial influences of logging debris. On peaty gley soils, moisture and nutrients often move laterally through the L and FH horizons due to the low hydraulic conductivity of the O horizon. Poor vertical movement is more evident during the early years after replanting due to the high watertable depths and low formation of drainage channels. As moisture and nutrients can flow across the site, treatment plots are unlikely to be 'nutrient tight'. The majority of the measurements reported in this thesis were performed in the buffer zones at *Site 1* (5 m wide see *Chapter 2*). Therefore the trees grown in WT harvested (- R and + H) plots adjacent to CON (+ R and + RH) areas may experience favourable interference from residue and inputs of nutrients from treatment plots upslope.

Despite the absence of significant differences in biomass production and height growth, the intensity of residue retention affected phenological characteristics and the duration of leader extension in trees growing at *Site 1*. In 1994, the length of leader growth attributed to lammas and the total period of leader extension were significantly greater in the residue retained plots (*Chapter 6.3.1*). Possible reasons for the occurrence of treatment differences during the third growing season but not the fourth, include the;

- greater influence of shelter afforded by woody residue,
- improved soil nutrient availability, and
- increased or more favourable soil moisture content within the upper organic horizons.

During the first 2 years after restocking *Site 1*, Proe *et al.* (1994) recorded that the removal of residue increased wind speeds at 30 cm above the litter surface by 40 % compared to CON felled areas. The shelter afforded by the logging debris provides an environment more favourable for tree growth (*Chapter 2.9*), and is most pronounced during the first 3 years. As the logging debris settles, and the tree crowns increase in diameter and emerge above the woody debris, the effect slowly diminishes. Surplus carbohydrate (Longman 1991) and high nutrient status (Millard and Proe 1992; *Chapter 6.1.1*) also favour secondary growth. In September 1994, concentrations of nutrients including N, P and Ca were significantly greater in the needles of trees in residue retained plots than those in WT harvested treatments.

However in October, when foliar analysis is conventionally performed, differences in nutrient concentration were absent, except for Ca. The concentration of foliar nutrients throughout the 1995 growing season, demonstrated few treatment differences. However where residue retention affected the results, concentrations were greater in the + R and + RH plots. The influence of treatment was most evident for Ca, although all levels of the cation were greater than those thought to limit growth (Binns *et al.* 1980).

In situ studies performed during the third growing season after felling, indicated that net mineralisation of N was greater in the LFH horizon than the O layer (*Chapter 3.3.2*). The presence of residue dramatically altered the bulk density, moisture content and temperature of the organic horizons which were considered to increase total release of N and significantly enhance net nitrification (*Chapter 3.3.2*). In addition, rates of net mineralisation and indices of potential mineralisation measured after incubation of soil under controlled conditions were greater in material from + R and + RH plots. This provides evidence that residue retention increases nutrient availability by providing favourable physical and chemical conditions.

Increased levels of NH_4^+ and NO_3^- in the soil are not necessarily indicative of greater tree N contents. In young plantations the concentration of N in the root zone may have a greater effect on growth than overall N mineralisation rates (Smethurst and Nambiar 1990b), as uptake by the tree is determined by the abundance and activity of roots, their distribution, and the presence of competing vegetation. At the end of the 1995 growing season, more than 75 % of the oven dried biomass of fine root sampled in the top 15 cm of soil grew within the nutrient rich LFH horizon (*Chapter 5.3.2*). The effect of residue retention did not influence root abundance or distribution, however the mulch present in the + R plots insulates the soil against fluctuating conditions of moisture (*Chapter 3.3.1*) and temperature (*Chapter 2.8*), and may therefore increase the root activity and duration of nutrient uptake. Unfortunately, it was not possible to assess these variables. The biomass of root occurring in the O horizon was thought to be determined by the depth of anaerobic soil during periods of seasonally high water tables. From September to April, the watertable lay closer to the soil surface in + R and - R plots. Consequently, root growth was restricted to the LFH horizons. In the herbicide treated plots a greater proportion of the root biomass was measured in the O layer. However, this difference was considered to result due to site variability, rather than the effect of treatment.

In the + R and - R treatment plots, ground vegetation competed with spruce seedlings for available nutrients in the soil. However, the trees did not demonstrate deficiency symptoms and foliar nutrient concentrations in the top whorl lateral shoots were above those thought to

limit growth (Binns *et al.* 1980; *Chapter 6.3.3*). Therefore, the availability of nutrients at the site during the third and fourth growing seasons was sufficient to support tree and ground vegetation growth. Accumulation of vegetation biomass was greater in the clear areas (*Chapter 3.3.3*), due to the accelerated invasion and establishment of seedlings in the absence of residue. However, the diversity of species present during the third growing season, including high proportions of *Chamerion angustifolium*; suggested that soils underneath residue mats contained greater available inorganic N (*Chapter 3.4.2*).

7.2 *Future growth of Sitka spruce and implications for management at* Site 1

Further growth of Sitka spruce at *Site 1* is unlikely to be affected by aboveground physical factors. However, influences below ground including altered soil temperatures and moisture content may continue. As the tree crown expands, these effects will slowly diminish due to reductions in direct and incident solar radiation and interception of precipitation inputs. However, if the timing of canopy closure is influenced by treatment, secondary effects may be observed as physical conditions in the soil will be temporarily modified.

As the influence of physical factors declines, the importance of nutrient availability in determining rates of tree growth increases. From biomass data and nutrient contents measured during 1993 and 1994, the annual uptake of nutrients was determined (*Table 7.2*) for trees planted at a density of 4 100 trees per hectare. However, total nutrient contents were analysed using samples from assessment plots (restocked at double the density). As the spruce roots were not greatly intertwined at this stage and competition for nutrients was low, the figures are thought to reflect the nutrients taken up during the 1994 growing season, despite differences in the number of trees per hectare.

Table 7.2: Nutrient uptake by Sitka spruce during the third growing season after restocking. (Data from whole tree harvests (above and below ground) performed by MLURI)

Treatment	*Nutrient (kg ha^{-1} y^{-1})*				
	N	*P*	*K*	*Mg*	*Ca*
+ R	16.6 (± 0.3)	2.08 (± 0.33)	7.50 (± 1.33)	1.04 (± 0.22)	3.00 (± 0.37)
+ RH	18.4 (± 2.7)	2.11 (± 0.29)	8.53 (± 1.48)	1.12 (± 0.11)	2.98 (± 0.27)
- R	14.7 (± 0.6)	1.69 (± 0.07)	7.16 (± 0.34)	1.07 (± 0.02)	1.62 (± 0.25)
+ H	18.6 (± 1.1)	2.26 (± 0.19)	9.89 (± 1.19)	1.27 (± 0.06)	2.72 (± 0.33)

The demand for nutrients is not constant through time. Models suggest that maximum requirements accompany rapid uptake during foliage formation and fine root production, at or

just before canopy closure (Miller 1986), and Ibrahim (1990) recorded exponential increases in nutrient contents of Sitka spruce from years 4 to 12. Once the tree crown is fully formed, declines in foliar biomass and needle litter production may occur (Gholz *et al.* 1985), the mass of needles reaches a steady state condition and the uptake of nutrients falls sharply (Miller 1981). Retranslocation then becomes a major process in supplying resources for current growth (Miller 1986), providing up to 90 % of N used for leaf growth in some species (Millard 1996).

Internal cycling of nutrients from the old to new shoots is advantageous as leaching losses from decomposing needle litter are reduced (Helmisaari 1992) and the trees become less dependent on fluctuations in soil nutrient availability (Carlyle 1984; Helmisaari 1992). For example, retranslocation supplied 30 to 50%, 23 to 37 %, 17 to 31 % and 7 to 20 % of the N, P, K and Mg, respectively, required for annual biomass production of sapling, pole stage and mature stands of Scots pine (Helmisaari 1992). In comparison, Ca is an immobile nutrient which does not undergo internal retranslocation (Miller 1986), is often taken up in excess of growth requirements and may limit the growth of subsequent rotations (Ericsson 1994). Evidence of the depletion of Ca after intensive harvesting has been obtained from studies in North America (Mann *et al.* 1988; Federer *et al.* 1989; Hornbeck *et al.* 1990) and Beddgelert Forest, Wales, where the removal of Ca during WT harvest was approximately equal to the soil reserves in the rooting zone (Stevens *et al.* 1988).

The occurrence of Ca deficiencies in the upland forests of Britain may become more common in subsequent rotations. During the initial establishment of conifer plantations, 2 to 3 applications of rock phosphate (a Ca containing compound) were generally applied. This probably met the crop's demand for Ca and led managers to believe that the cation was not a limiting nutrient. However in the second rotation, requirements for P are usually less and fertilisation at planting is often unnecessary (Taylor 1990). The absence of an application of rock phosphate at restocking may lead to Ca deficiencies during subsequent growth. Although Ca contents in the soil at *Site 1* were not significantly affected by treatment, foliar concentrations during the third and fourth growing seasons were significantly greater in + R and + RH treatments. Therefore, in the absence of fertilisation, new foliage of trees growing on sites with low Ca reserves in the rooting zone may exhibit deficiency symptoms.

Late rotation N deficiency may occur in some infertile forest soils, if immobilisation of N occurs in the humus underneath old conifer crops (Miller 1981). Although this process has been observed under British conditions for pine (McIntosh 1984), similar mechanisms have not yet been recognised in spruce forests. Miller and Miller (1987) suggested that either

mineralisation in spruce litter is relatively rapid under British conditions, or the stands are not of sufficient age to exhibit this phenomenon.

7.3 Predicting future yields from current knowledge

Unlike the results recorded at Falstone (Proe and Dutch 1994), rates of tree growth at *Site 1* during the initial four growing seasons were not modified by the intensity of harvesting. Similarly, short term (first 4 years) growth of Radiata pine was not detrimentally affected by the removal of woody residue or litter at felling (Smethurst and Nambiar 1990b), whereas Scots pine and Norway spruce exhibited inconsistent responses during the first 5 years of a study to investigate the effects of WT removal of thinnings (Jacobson *et al.* 1996). The variety of growth rates obtained after harvesting or thinning, emphasise the importance of continued measurements to fully characterise responses through time. Broader ecosystem features should also be considered when predicting growth, as site and tree characteristics alter through time. For example, at *Site 1* the watertable is expected to fall as evapotranspiration and loss of precipitation inputs through interception increase with canopy closure. During the drying of peaty gley soils characteristics may be irreversibly altered if cracks appear in the O horizon which form drainage channels, while rates of nutrient mineralisation and greater aerobic soil depths may favour greater penetration of soil by roots and higher nutrient availability to trees. On sandy soils in southern Australia long term benefits of residue retention may become evident when the N leached from the surface soil becomes available to trees as roots exploit deeper parts of the soil profile (Smethurst and Nambiar 1990b).

Prediction of yield from current rotations is further complicated because recent studies performed in Europe have indicated that the growth of trees is generally better today than during the past 2 to 3 decades (Becker *et al.* 1990; Ericsson and Johansson 1993; Nilsson *et al.* 1995). Consequently, existing yield tables and site classifications may become obsolete or require modification. The increased forests yields have been attributed to greater deposition of atmospheric N (Becker *et al.* 1990; Ericsson and Johansson 1993) and nutrients (Becker *et al.* 1990; *Table 7.3a*), higher CO_2 concentrations and a more favourable climate (Becker *et al.* 1990). Increased deposition of pollutants may be beneficial at some infertile sites and could be viewed as a positive result if vitality and sustained production are desirable. However, Emmett and Reynolds (1996) predicted that between 45 and 97 % of the coniferous forest in Wales received N in excess of the critical load (the threshold value for pollutant deposition, which will not cause chemical changes leading to long term ecological damage (Bull 1991)). Consequently, eutrophication of freshwater courses and declines in ecological health may result. In addition, Rosen (1989) recorded greater cation leaching in the presence of increased

availability of anions of strong acids (sulphate (SO_4^{2-}) and NO_3^-) and high N inputs to forest ecosystems can lead to an increase in the N/Mg ratio and cause a Mg deficiency (Evers 1994). Magnesium deficiencies may also be caused in rare cases on Ca rich sites, or on loamy sites where a K excess causes an antagonistic relationship (Evers 1994). However the introduction of measures to suppress emissions of air pollutants, will reduce levels of nutrients currently obtained from atmospheric sources and may increase the necessity for use of suitable management procedures to maintain forest productivity.

Table 7.3a: Estimates of annual precipitation inputs and losses in some forest soils (from Malcolm and Moffat 1996).

	Ranges of values (kg ha^{-1} y^{-1})						
Element	***NH_4^+***	***NO_3^-***	***PO_4^{2-}***	***K^+***	***Na^+***	***Ca^{2+}***	***Mg^{2+}***
Precipitation input	3.9 - 6.0	1.9 - 7.4	0.03 - 0.15	1.5 - 5.5	22.6 - 58.0	2.9 - 12.5	2.6 - 11.2
Average annual export in Sitka spruce at harvesting	2.6		0.3	0.8	-	3.0	-
Flux from litter layers after harvest (0 to 7 years)	0.8 to 41.0	0.59 to 14.1	0.04 to 2.2	1.8 to 43.0	11.7 to 186.0	2.8 to 42.3	1.85 to 28.7

Ideally, models and indices used to estimate the growth of successive rotations should incorporate many site variables. *Table 7.3b* lists some of the factors which should be considered and briefly describes the modifications which occur after WT and CON harvesting.

Table 7.3b: Factors to be considered when designing models to predict future timber production and planning harvesting.

Variable	***Influence and responses***
Exposure	Strong winds slow the height growth of newly planted seedlings. As wind speed increases, reductions in height increment become larger. Therefore, on exposed sites the retention of residue affords shelter which should enhance growth rates.
Air temperature	Aboveground temperatures may affect the duration of the growing season and rates of photosynthesis, especially in seedlings. As the residue reduces wind speeds and allows warming of the air surrounding the newly planted seedlings, the duration of the growing season may be extended by secondary growth and rates of photosynthesis increase. However, later growth may be detrimental if early autumn frosts occur before bud set and cessation of shoot extension.

Soil moisture and temperature	Moisture and temperature affect mineralisation in the soil, influence root activity, growth and uptake of nutrients. Logging debris acts as a mulch, which reduces fluctuations in soil temperature and moisture providing an environment more favourable for root growth and microbial activity. However delays in soil warming during the spring may slow microbial turnover, and lead to a lag period before the net mineralisation of nutrients at the beginning of the growing season.
Soil physical characteristics	Depending on soil type, compaction, horizon mixing and poor drainage may result after disturbance at felling which may detrimentally affect subsequent growth of seedlings. The soils (described by Pyatt 1982) may be ranked into broad risk categories; low, medium and high (Anon. 1997, *in press*), as follows; *Low risk*; brown earths, podzols, rankers, skeletal soils, limestone soils and littoral soils except and with shallow or very shallow water tables, *Medium risk*; shallow peaty soils (peat < 45 cm deep), surface water gleys, ground water gleys and ironpan soils, and *High risk*; peatland soils (peat > 45 cm deep) and littoral soils with shallow or very shallow watertables. On high or medium risk soils, damage by heavy machinery can be reduced by driving over residue mats.
Total nutrient capital and chronic nutrient additions	The total nutrients available to the tree are restricted to those present in the rooting zone. Additional low level additions result from atmospheric deposition and weathering of underlying rock (*Table 7.3a*). On infertile sites or on soils with low organic matter content, logging debris should be retained as a high proportion of nutrients are present in the foliage and small woody tissues. In addition, the capacity to prevent nutrient losses from the site through immobilisation is enhanced by increased organic matter with a high C/N ratio. In cases where Ca deficiencies are a potential problem, retaining the bark on site may alleviate symptoms. In addition, physical soil characteristics are improved by the incorporation of organic matter to the upper horizons.
Environmental sensitivity	Depending on the forest site and the intensity of residue removal, harvesting may cause degradation of the habitat or landscape, pollute watercourses and cause fresh water eutrophication (see Anon. 1997, *in press*).
Tree species and genetic stock	Genetically improved planting stock and the greater diversity of tree species being planted to meet multiple objectives place different demands on the site. Therefore, choice of harvesting method should be made after assessing the requirements of the subsequent rotation of tree species.

7.4 Forest management at clearfelling

Although the total area harvested by WT methods may increase if the combustion of biofuels is adopted as a viable method of energy production, only 10 % of current clear felling programmes in the Forest Enterprise (Forestry Commission) are achieved by this method (Anon 1997, *in press*). Sixty percent of this is performed by cable crane, 40 % by skidder working and a small proportion by forwarders (Anon 1997, *in press*). In recognition of the potential impacts of WT harvesting to the environment and subsequent growth of trees a 'Guide to Good Practice in Whole-Tree Harvesting' (Anon 1997, *in press*) is to be published. The objectives are to consider the likely risks of harvesting on different soils, to make recommendations to managers and provide operational guidelines to be adopted during felling. Revision of the proposals is expected to occur as current experimental sites in Britain mature

and provide a greater understanding of the processes following harvesting. Six principal threats to the forest environment (beyond those experienced during CON felling), are highlighted. These included;

- soil physical damage, erosion and siltation of watercourses,
- impoverished soil fertility and associated silvicultural implications,
- acidification,
- freshwater eutrophication,
- degraded landscape and
- degraded habitat.

With these potential impacts in mind, recommendations are made depending on site suitability.

If sufficient nutrients are available and soil organic matter is retained, timber yields are expected to be largely sustained. Therefore measures should be taken to prevent losses from the site. For example, the export of soluble ions from the site through leaching may be mitigated by chipping or grinding the needle litter before spreading across the forest floor. The results reported in *Chapter 4*, indicated that grinding needle residues delays the initiation of net N mineralisation. It is thought that the comminution of the substrate allows compounds, such as polyphenols and lignins, to be released which enhance microbial uptake of N. However, this practice may not be economically viable.

If sites are immediately replanted or invaded by ground vegetation, rapid nutrient losses resulting from the assart effect (the flush of nutrients which becomes available immediately after harvesting) may be reduced by plant uptake. However seasonal constraints (including frozen soils and high water tables) and practical limitations (such as the facilitated restocking of bare soils, or areas where the residue is partially decomposed) may hinder early planting with seedlings. Therefore, seeding of clearfell sites with fast growing annuals could prevent excessive nutrients losses and provide a long term fertiliser as the vegetation decomposes. It is likely that this practice would be more successful on WT harvested areas, as the bare soils provide a more suitable seed bed. Losses of Ca from the site may be reduced by retaining cation rich bark on site. Debarking logs helps counterbalance the large removals of nutrients at WT harvesting and is beginning to be common practice in some countries (Ericsson 1994).

If reductions in forest growth occur after clearfelling, various methods may be adopted to alleviate the effects. These include remedial applications of fertiliser (Smith *et al.* 1994; Jacobsen *et al.* 1996) and the planting of N fixing leguminous and non-leguminous vegetation (Jurgensen *et al.* 1992). However the methods have drawbacks and site characteristics should be considered during planning. For example, applications of mineral fertilisers can be

expensive (Smith *et al.* 1990), do not compensate for losses of organic matter, and have little potential to improve long term site productivity (Miller 1981). In order to maintain forest productivity, a variety of the options need to be practised.

7.5 Future research

To determine whether growth rates of Sitka spruce at *Site 1* are affected by treatment later in the rotation, measurements of tree height, biomass and nutrient content should be performed at regular intervals. Quantification of rates of *in situ* mineralisation of N and availability of nutrients should occur regularly until canopy closure, after which retranslocation reduces the importance of the soil as a source of N, P, K and Mg. However, as Ca is not cycled internally, and little is known of the dynamics of micronutrients in British forests (including boron and sulphur), foliar sampling should continue past canopy closure in order to detect deficiencies or imbalances which may affect subsequent growth rates. Additional foliar nutrient analyses should be done through the crown, to detect possible shortages of mobile nutrients including K.

Some European studies have reported increased productivity of forests during the past 2 to 3 decades (*Chapter 7.3*). If similar trends are present in Britain, differences in growth rate of trees which might be expected after CON and WT harvesting may be masked by a general pattern for enhanced yields. Comparison of results from the current study with those from newly established experimental forests in Teindland (North Scotland) and Ae (South Scotland), will reveal whether the lack of significant treatment differences is specific to conditions at *Site 1* or common across much of northern Britain. In the event that productivity is enhanced, it is important to identify the factors controlling the increased yields, such as;

- increased deposition of N or other nutrients,
- more favourable temperature conditions (which influence all enzymatic processes, including photosynthesis, and microbial turnover in the soil),
- higher ambient concentrations of CO_2 (which may affect rates of photosynthesis and release of nutrients in the soil), and
- improved growing conditions resulting from the first rotation (including additions of organic matter, reductions in watertable depth, the suppression of ground vegetation and modifications in the diversity of soil microbes).

The enhanced growth rates and yield may modify wood characteristics. Therefore, the timber produced should be carefully monitored to detect changes in quality.

From the birch bioassay described in *Chapter 4*, it was evident that the rate of release of nutrients from litter depended on the origin or age of the substrate. For example, litter

collected from underneath residue mats was slow to initiate net mineralisation of N, compared to that from the original forest floor. If similar responses are observed with Sitka spruce seedlings in bioassay, further research could determine the best time to plant seedlings in order to;

- minimise nutrient losses through leaching from residue,
- avoid nutrient stress during periods of immobilisation and competition with ground vegetation, and
- minimise losses from the site following net mineralisation and nutrient release.

In addition, the identification of compounds responsible for the delayed release of inorganic N from ground fresh litter would provide a better understanding of the factors limiting net mineralisation in the field.

Observations from British Columbia (C. Prescott *pers. comm.*) have indicated that rates of mineralisation in the soil differ across a clearcut area. Nutrient release decreased towards the centre of the harvested site and the range of values recorded became greater as felling coupe size increased. In general, aboveground physical influences of neighbouring stands, including shelter, interception of solar radiation and precipitation inputs, extend two tree lengths from the edge of the unfelled area. Below ground effects, such as modified soil temperatures, C exudation from living roots and uptake of moisture decrease with increasing distance from neighbouring stands. Depending on the climate experienced after clearfelling and the fertility of the site, rates of mineralisation may be favoured by the conditions afforded by surrounding stands of trees. At present the influence of each factor has not been identified, and it is unknown whether similar processes occur in soils of British forests. Therefore, investigations should be performed to characterise differences across clearfelled sites in the UK, in order that the most appropriate clearfell size, depending on site factors including climate and fertility, can be evaluated.

7.6 Improvements to the research methods reported in this thesis

In association with the work performed by MLURI and the FC, the research detailed throughout this thesis aimed to comprehensively characterise *Site 1* and the growth of second rotation Sitka spruce during the first 4 growing seasons. Physical or chemical differences arising through the intensity of harvesting were identified and the effects on the growth of trees evaluated during the previous chapters. Any modifications to the experimental procedure and timing of assessments which were considered to improve the results or increase the knowledge of the site have been discussed briefly throughout this section.

Many variables were observed throughout the third and fourth growing seasons, including foliar nutrient concentrations and contents, tree phenology and morphology, *in situ* rates of N mineralisation and root distribution and biomass. However due to the logistics involved, the studies were not performed concurrently. Therefore, direct relationships and comparisons between some of the measurements could not be made. For example, from root distribution studies performed in autumn 1995 it was assumed that trees had had the potential to take up N mineralised *in situ* during the 1994 growing season. However, a better indication of the ability of roots to access inorganic N would have been obtained if the studies had been performed during the same year. In addition, treatment differences in the timing of bud flush might have been detected if observations had been performed more frequently during spring 1994.

As results from covered and open samples can be used to estimate leaching losses and plant uptake (Adams *et al.* 1989), a greater understanding of N dynamics in the soil might have been gained if additional uncapped soil cores had been incubated *in situ*. Also, the flush of nutrients which becomes available during the assart effect could have been determined by initiating soil sampling in the previous year.

Nutrient release from litter collected 6 months after clearfelling was ascertained using a birch bioassay and aerobic laboratory incubations. However, the study was performed towards the end of the research period. Therefore, further investigations prompted by the results obtained could not be undertaken. If the study could have been repeated, the following questions would have been addressed, in order to gain a better understanding of the timing of nutrient release from litter and the factors controlling net mineralisation of nutrients;

- what proportion of nutrients were lost from the freshly fallen litter through leaching?
- was C the driving variable responsible for N release from the litter? If so,
- what fraction of C compound best described mineralisation rates? and,
- how was the availability of C for use by microbes affected by grinding the substrate?

7.7

CONCLUSIONS

The research detailed in this thesis addressed the overall objective (detailed in *Chapter 1.9*);

- *to determine whether the presence of logging residue influenced environmental factors, nutrient availability and the early growth of Sitka spruce and ground vegetation.*

Results from the current study indicated that forest productivity at Kielder was not affected by the intensity of harvesting during the initial four years after planting. The reasons why the responses of trees at this site to CON and WT harvesting should differ from the observations at Falstone are unclear.

Uncertainties arise when predicting long term productivity at *Site 1*, as the small treatment differences present shortly after restocking (including greater inorganic N availability in the soils, extended lammas growth and duration of the growing season during 1994, and significant increases in foliar Ca concentration of trees in + R and + RH plots) may have implications for future growth. In addition, the possible effects of residue removal during WT harvesting on the growth of trees approaching canopy closure, when demands for nutrients are high, cannot be predicted.

A better understanding of the nutrient dynamics occurring after harvesting and the effects of the removal of different intensities of residue will be obtained after sustained monitoring of replicated sites. As the long term implications of harvesting are not fully appreciated, the complete removal of organic matter during felling should only be done with caution and consideration for the surrounding environment and successive forest yield.

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APPENDICES

Appendix 1

App 1.1 Statistical analysis

The majority of measurements reported throughout this thesis were taken from 3 replicated blocks within the experimental *Site 1* described in *Chapter 2*. Due to limitations of time and suitable resources including additional experimental sites pseudo replication was unavoidable. However, future measurements will be replicated at two additional sites which have been established in Teindland (North Scotland) and Ae (South Scotland) Forests with identical treatment combinations.

Depending on the variable measured (such as tree height or net N mineralisation), different numbers of samples were collected to represent intraplot variation (see individual chapters). In forest soils the high degree of spatial heterogeneity requires large numbers of samples to detect changes in soil properties between treatments (Johnson *et al.* 1990). The number of soil samples collected during the current research was largely determined by within plot variation with consideration of logistical constraints including time and resources (see *Chapter 3*).

All statistical analyses were executed using either Minitab Software (Release 8) or Genstat 5 (Release 3.1) Copyright 1994, Lawes Agricultural Trust (Rothamsted Experimental Station). Details of the conditions for each statistical test and the methods adopted can be found in Parker (1991) and Sokal and Rohlf (1995).

App 1.2 Means and standard errors

Treatment means were calculated from the appropriate plot means from the three blocks. For example;

$$mean\ (x) = \quad (x_1 + x_2 + x_3)/n$$

where $x_{1\ to\ 3}$ are the individual plot means and n is the number of blocks.

Standard errors (*s.e.*) described the reliability of a single random measurement in indicating the sample mean. Again the plot mean was used and the sample number was 3;

$$s.e. = \frac{\sqrt{\Sigma(x_i - \bar{x})^2/(n - 1)}}{\sqrt{n}}$$

where x_i is the treatment mean
$\bar{x}$ is the overall mean and
n is the number of blocks.

App 1.3 Analysis of Variance (ANOVA)

Analysis of variance was performed to test for treatment differences. The procedure assumes that;

- the effects are additive (an individual value is considered to be made up of the grand mean + treatment effect + uncontrolled error),
- the error is normally distributed and has equal variance for all treatments.

Before performing the ANOVA the data was assessed for homogeneity of variance using the F_{max} test. The ratio of the largest variance in the set to the smallest was calculated and compared with a tabulated value of F_{max} for the number of treatments in the set and (n - 1) degrees of freedom, where n is the number of replicates in the sample (3 blocks). The distribution of each data set was checked for normality. Where data was non normal or significantly different variance occurred, transformations were applied. Residual plots were also used to check the assumptions underlying the ANOVA procedure, typically normal probability plots and plots of residuals against fitted values.

The ANOVAs were performed as follows. The data set is taken from the tree heights recorded at the end of the 1993 growing season;

Block	***Treatment***				
	+ R	***+ RH***	***- R***	***+ H***	***Block totals***
1	746	596	518	518	2378
2	634	703	516	567	2420
3	606	569	616	632	2423
Treatment totals	1986	1868	1650	1717	7221
Treatment means	662	623	550	572	602

From this table the (grand total)^2 is divided by the total number of plot means

= 4 345 237

calculate;

the total sum of squares = 4 402 167 - 4 345 237 = 56 930

treatment sum of squares (TSS) = (13 104 209)/3 - 4 345 237 = 22 832

block sum of squares = (17 382 213)/4 - 4 345 237 = 316

error sum of squares = 56 930 - (22 832 + 316) = 33 782

The treatment sum of squares can then be partitioned to test the effect of each factor separately together with the interaction effect;

+ R sum of squares (+R SS) = $(3\ 854^2 + 3\ 367^2)/6 - 4\ 345\ 237 = 19\ 763.8$

+ H sum of squares (+H SS) = $(3\ 585^2 + 3\ 636^2)/6 - 4\ 345\ 237 = 216.5$

+R * +H interaction sum of squares = (TSS) - (+R SS) - (+H SS) = 2 851.7

Sources of variation		*Sum of squares*	*Degrees of freedom*	*Mean squares*	*F*
Treatment		22 832	3	7 611	1.35
	+R	19 764	1	19 764	0.11
	+H	217	1	217	0.85
	+R*+H	2 852	1	2 852	0.50
Blocks		316	2	158	0.03
Error		33 782	6	5 630	
Total		56 930	7		

From significance tables the F ratio may be used to determine whether differences between treatments were significant. In this case none of the F ratios were significant. As significant observations were attributed to all P values < 0.05, there was a 1 in 20 possibility of observing a 'significant' result by chance.

App 1.4 ANOVA (repeated measures; Chapter 2, watertable depths and Chapter 6, shoot characteristics)

For variables recorded in stepwise intervals throughout the growing season, including measures of leader extension, foliar biomass and watertable depth, curves were fitted to the data and treatment differences detected by comparing linearity and curve parameters.

The following steps were taken using plot means rather than individual values ;

1. Genstat procedure REPMEAS was used to check if repeated measures data could be analysed as a split plot. A logarithmic transformation of the data was first used. The test of compound symmetry was accepted, ie. variance-covariance matrix,

pooled over treatments has approximately a common value for diagonal elements and another approximately common value for off diagonal elements.

2. Thus, carried out a split plot analysis on transformed data with treatment as whole plot factor and time as sub-plot factor.

If the assumption of compound symmetry did not hold then we can use a more conservative F-test due to Greenhouse and Geisser for testing the time effect and interaction.

App 1.5 Parallel curve analysis (Nested models) (Chapter 6; leader extension)

In order to test for differences in leader shoot growth between treatments (+ R, + RH, - R and + H), curves were fitted to each set of data. If the rate of shoot extension was influenced by treatment, the parameters used in the equation would differ accordingly. The following steps were used to identify the effects;

1. Fit a single exponential curve to all of the data points;

   ie. $y_i = \alpha + \beta\rho^{xi} + \varepsilon_i$ where y_i = response variable (eg leader length)

   x_i = time of harvest, equally spaced 1, 2, 3

   etc.

   ε_i = random component.

   Assuming that the relationship between y_i and x_i is the same for all four treatments (+R, + RH, - R and + H).

2. Separate exponential curves are fitted to each group, constrained to be parallel, ie they differ only by a constant;

   $$y_i = \alpha_j + \beta\rho^{xi} + \varepsilon_i \qquad \text{where } j = 1, 2, 3 \text{ etc.}$$

   A test is then performed to see whether the fit of the model to the dates is significantly improved by adding in the extra parameters.

   ie. to test hypothesis $H_o : \alpha_j = \alpha_k$ for all j, k with $j \neq k$

   against $H_A : \alpha_j \neq \alpha_k$ for at least one (j, k)

   The test statistic performed is a variance ratio test (F - test),

ie. $$\frac{(RSS_1 - RSS_2)/ df_1 - df_2}{RSS_2 / df_2} \approx F_{df_1-df_2,\ df_2}$$

where $RSS_{1,2}$ = residual sum of squares; models 1, 2

$df_{1,2}$ = degrees of freedom; models 1, 2

If H_o is rejected, go on to the next step.

3. Assume common nonlinear parameters for each group but all linear (α, β) parameters are estimated separately for each group.

ie. $$y_i = \alpha_j + \beta_j \rho^{xi} + \varepsilon_i \qquad j = 1, 2, 3 \text{ etc.}$$

Then use the test statistic to compare this model with that in step 2.

ie. to test hypothesis $H_o : \beta_1 = \beta_2 = \beta_3 = \beta_4$.

If this hypothesis is rejected, go onto step 4.

4. All parameters estimated separately.

ie. $$y_i = \alpha_j + \beta_j \rho_j^{xi} + \varepsilon_i \qquad j = 1, 2, 3 \text{ etc.}$$

Finally use the test statistic to compare this model with that in step 3.

After determining the curve of best fit, the equations may be used to estimate the date of 50 % bud burst or analyse for differences between treatments.

App 1.6 Regression analysis (Chapter 6, bud burst and number of chill days;

Linear regressions were fitted to data to assess the correlation between a dependent and independent variable, where the response and the causal factor have an asymmetrical relationship. There are 4 assumptions which are made during this analysis;

- the independent variable, *x*, is measured withour error,
- for each value of *x* there is a corresponding 'true' value of *y* such that as to fit a rectilinear relationship between *x* and *y*,
- the measurement of *y* show random variation and are normally distrbuted about their 'true' mean, and

- the variance of the values of y about their 'true' mean is the same for all values of x.

The regression equation below was fitted to data describing the relationship between the number of chill days (dependent variable) and the date of bud burst (independent variable).

	Treatment					
	+ R			***- R***		
Variable	***1***	***2***	***3***	***1***	***2***	***3***
Number of chill days	105	101	94	99	100	96
Day of bud burst	137.9	134.0	130.4	133.3	134.0	131.8

The least squares principle is selected to chose the line with minimal sum of squared deviations. The best fitting line is,

$$y = a + bx$$

where

$$b = \frac{\Sigma[(x-\bar{x})(y-\bar{y})]}{\Sigma[(x-\bar{x})^2]}$$

and

$$a = \frac{\Sigma(y) - b\Sigma(x)}{n} = \bar{y} - b\bar{x}$$

where n is the number of observations of y. Therefore for the data listed in the table above;

$$y = 0.647\,x - 69.38$$

To establish the intercept, substitue the computed value of b into the equation;

In order to test the significance of the regression, the variation of y in two components is analysed;

total variation in y (as sum of squares) TSS = $\sum(y_i - \bar{y})^2$

variation accounted for by regression Regression SS= $\sum(\hat{y}_i - \bar{y})^2$

therefore variation not accounted for (residual variance) Residual SS = TSS - Regr. SS.

Residual plots were used to check assumptions used in the procedure.

App 1.5 Paired t-tests

Paired sample tests were used to test the null hypothesis that the mean difference between the pairs of data is zero (see *Chapter 4.3.3*). The following test statistic is used to test this hypothesis;

$$t = \frac{\bar{d}}{S_d/N}$$

where d is the mean difference between the two samples and S_d is the standard deviation of the mean difference ie.,

$$S_d = \sqrt{\frac{\sum(d-\bar{d})^2}{N-1}}$$

Appendix 3

Appendix 3.1 The effect of cold storage on the mineralisation of N

Due to the heterogeneous nature of forest soils, large numbers of replicates are required to obtain representative samples. This causes logistical problems when determining soil characteristics as the material should be 'fresh' at analysis. Therefore, soil cores are often stored at temperatures below 4 °C until processing, at which rates of mineralisation are considered to be minimal. However, Emmer and Tietema (1990) recorded release of inorganic N at 0 °C, which indicated that the cold storage of moist soil could influence estimates of field mineralisation. The following study determined the effect of storage at 2 to 3 °C, on the availability of inorganic N in soils from the buffer zones of + R and - R plots at *site 1*.

Quantities of NH_4^+ and NO_3^- in the L, FH and O horizons were quantified immediately and after 9, 20, 55 and 130 days incubation (using the procedures detailed in *Chapter 3.2*). Results of net mineralisation (expressed per unit of oven dried soil) are presented below (*Figure App 3.2.2,* where 'b' and 'c' represent the + R and -R samples, respectively).

Large intra plot variation masked differences in the release of NO_3^- over time. In comparison there was a trend for increasing values of NH_4^+ in the litter and FH horizons of material collected from - R and + R plots. Therefore it is suggested that chemical extraction occurs as soon as possible after collection of samples from the field. However,

in cases where long periods of time between sampling and extraction are unavoidable, the duration between collection of material and extraction should be kept constant.

Soils sampled throughout this thesis were analysed within 10 weeks, and where possible the duration between collection from the field and extraction solution was kept constant. It is anticipated that the release of NH_4^+ would have been slightly enhanced by cold storage, but rates of NO_3^- would not have been greatly affected.

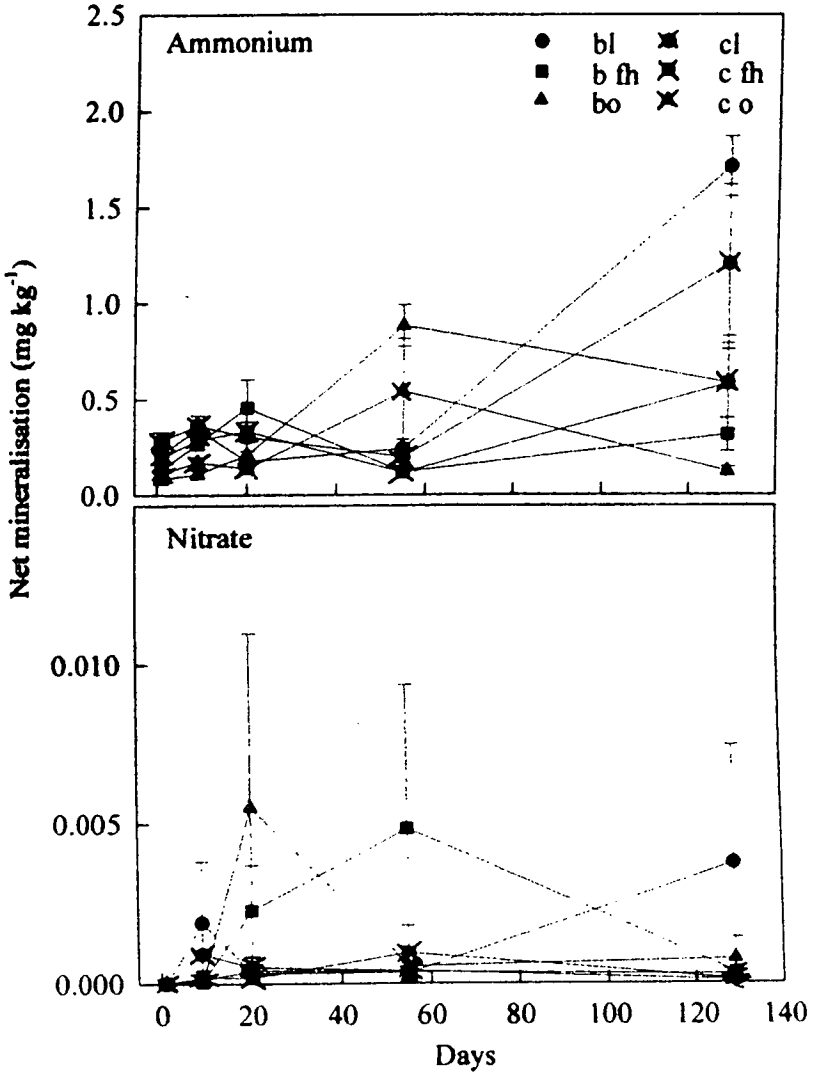


Figure App 3.2.2: Net mineralisation of NH_4^+ and NO_3^- (mg kg^{-1}) through time, at 2 to 3 °C. Results from the L, FH and O horizons are represented.

Appendix 3.2 *Fungal species occurring in + R and - R plots at Site 1*

Table App 3.2.4 lists the 8 species of fungi recorded in + R and - R plots in autumn 1995 (the fourth growing season). Due to the low frequency of fruiting bodies and the collection of samples on a single date only, it was to difficult to determine whether treatment influenced species type, and the total diversity of mycoflora was probably underestimated.

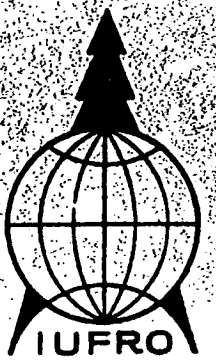
Of the species recorded, *R. emetica* and *H. aurantiaca* are mycorrhizal, whereas the remainder are wood or litter rotting fungi. It was observed that the bracket fungus, *G. sepiarum*, was abundant in all + R plots. This reflected the greater presence of lying dead wood within these treatments compared to the - R plots.

App 3.2.4: Occurrence of fungal species within + *R* and - *R* treatment plots.

	Treatment	
Fungal species	***+ R***	***- R***
Russula emetica	-	✓
Hygrophoropsis aurantiaca	-	✓
Hypholoma marginatum	✓	✓
Hypholoma capnoides	✓	✓
Calocera viscosa	✓	✓
Mycena androsaceus	✓	✓
Clitocybe sp.	✓	-
Gloeophyllum sepiarum	✓	-

Appendix 4

Conference on Effects of Environmental Factors on Tree and Stand Growth



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Nutrient availability in a second rotation Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stand in Britain

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University of Edinburgh, Scotland

1 Introduction

In Britain many first rotation stands planted since the second world war are reaching maturity. Of these, the majority will be felled conventionally (CON) by removing the stems only. However, advances in felling techniques and perceived reductions in re-establishment costs (NELSON and DUTCH 1991) favour whole tree harvesting (removal of all aboveground biomass; WT). Interest in this method is increasing as markets for non-timber residue as a biofuel develop (PROE et al. 1994).

The use of WT harvesting may have implications for the growth of the second rotation crop. During the removal of above ground biomass, large proportions of nutrients are removed in the foliage (CAREY 1980; COMPTON and COLE 1991) and the potential for soil damage increases (Senyk and Smith 1991). In addition, the removal of shelter provided by the residues may reduce height growth of newly planted seedlings on exposed sites (PROE et al. 1994).

The responses of second rotation crops on sites subject to CON and WT harvesting are mixed. Growth reductions after WT harvesting were observed by Compton and COLE (1991), MANN et al. (1988) and PROE and DUTCH (1994), whilst HENDRICKSON (1988) and DYCK et al (1991) reported enhanced growth. It is difficult to draw conclusions from these experiments as observation time, the control of vegetation and other environmental and silvicultural methods were inconsistent between sites.

Two bioassays, performed in 1995 and 1996, to determine differences in soil nitrogen availability between CON and WT harvested Sitka spruce plots under controlled conditions are described here. In addition, the organic soil horizon best predicting growth, and the role of litter as a nutrient source during the first year after clear felling were investigated.

2 Materials and methods

2.1 Site Description

Bioassay material was collected from two proximal sites within Kielder Forest, northern England (55°10'N, 2°30'W). The area has a temperate oceanic climate with a mean annual rainfall of 1300 mm and mean monthly air temperatures ranging between 0 and 15 °C (TITUS and MALCOLM 1992; PROE et al. 1994). The soils are cambic stagnohumic gleys (AVERY 1980), developed on Scremerston Coal Group overlying Carboniferous limestone. Both sites are gently sloping and elevations above sea level range from 300 to 380 m for sites 1 and 2, respectively. The first rotation Sitka spruce stands were planted in 1940 and exhibited an estimated general yield class (EDWARDS and CHRISTIE 1981) of 14 m^3 ha^{-1} y^{-1}. Sites 1 and 2 were felled in 1991 and 1995, respectively, using a mechanical harvester.

Bioassay 1 (material taken from site 1)

At site 1 an experiment was established in 1991 to investigate the effects of logging residue on the growth of the subsequent rotation of Sitka spruce. Compounding effects of soil compaction were avoided by driving machinery between treatment plots.

The experiment was designed as a full factorial, with three factors, each at two levels (present or absent). Each treatment block was randomised and replicated three times across the site. The effects of two factors were investigated; the presence/absence of evenly spread residue (CON/WT, respectively) and the application of herbicide (glyphosate applied annually from autumn 1992). In March 1995, approximately three and a half years after clearfelling, steel can corers (6.5 cm diameter x 16.0 cm depth) were used to extract samples from treatment plots to a depth of approximately 15 cm. The soil cores remained within the cans, were wrapped with cling film to produce an air tight seal at the base and had the tops removed to reveal the uppermost soil horizon. The result was a self contained pot, containing a largely undisturbed soil core. Into each core a single birch (*Betula pendula* Roth.) seedling, approximately 15 mm high, was planted. Each pot received 16 hr day length until mid April when natural day lengths commenced, water as necessary and mean day/night temperatures of approximately 15/8 ^{o}C.

Five harvests were taken at two to three week intervals. The final harvest was performed 82 days after planting. On each occasion, 24 cores were selected randomly (6 from each of four treatments, 2 replicates per treatment block). The cans were sliced open allowing removal of the birch tree and complete soil sample. The seedling was carefully removed and rinsed free of soil. The presence of mycorrhizally infected roots was noted and the fungal species identified. Leaf area was recorded using a projected leaf area meter (LI-COR model LI-3000). Nutrient contents (N, P, K, Mg and Ca) were analysed by wet digestion using a modified micro-Kjeldahl procedure (Allen et al. 1974). Ammonium and phosphorus were measured colorimetrically whilst potassium, magnesium and calcium were analysed by atomic absorption spectrometry. Soils were separated into L, FH and O horizons before estimating the C:N ratio, and recording the oven dried weight of each layer.

Bioassay 2 (material taken from site 2)

Two qualities of litter were collected from a conventionally felled area (site 2). The first formed the original forest floor (equivalent of WT harvesting) whilst the second contained additional material fallen from residue mats (piled six months previously during felling; CON harvested equivalent). All woody material, bark and moss were removed before mixing the litter thoroughly and air drying for 48 hours. From each litter type four quantities (10, 20, 30 and 40 g) were mixed with moist vermiculite and placed in 12 cm square pots. The procedure was repeated with litter ground to pass a 3 mm mesh. Each treatment combination had 4 replicates. After incubating at 20 ^{o}C for 1 week, a single birch seedling of approximately 15 mm height was planted in each pot. The plants were grown under controlled conditions at 20 ^{o}C, 75 % humidity, 16 hour daylength and luminous flux density of 250 μmol m^{-2} s^{-1}.

The C:N ratio was estimated for all litter types at the beginning of the incubation. After 165 days leaf area was measured as above.

Statistical analysis

Analysis of variance was performed on the following results from Bioassay 1; birch nutrient contents, total biomass and C:N ratios. The influence of treatment on leaf area was investigated using REPMEAS analysis of variance (Genstat 5, Release 3.1) and relationships between final leaf area and the oven dried weight of each soil horizon were determined using linear regressions.

Analysis of variance was used to determine significant treatment differences in leaf area and estimated C:N ratios from Bioassay 2.

3. Results

Bioassay 1

Herbicide application did not significantly affect the variables measured during this experiment. Therefore data has been pooled into WT and CON treatments, to investigate the effects of residue retention.

Leaf area

After an initial lag period of 40 days, seedlings from both treatments demonstrated exponential increases in leaf area. Final means of 54.6 and 31.6 cm^2 were attained for CON and WT soil samples, respectively (Figure 1). The retention of residue significantly increased overall leaf area measured throughout the bioassay ($P = 0.026$). However, the effect of treatment on individual harvest dates was significantly greater in CON grown seedlings for harvest 2 only ($P = 0.043$).

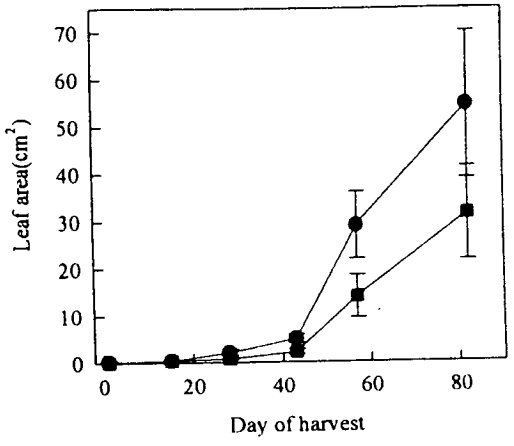

Figure 1: Leaf area of seedlings grown in undisturbed soil samples collected from CON (●) and WT (■) harvested plots. Values represent the means (± standard errors) recorded during sequential harvests (n = 3).

Seedling nutrient concentrations and contents

Nutrient concentrations (N, P, K, Mg and Ca) of birch seedlings at the final harvest were significantly greater in WT plots for nitrogen only ($P = 0.020$) (Table 1) Nutrient contents were not affected by treatment although values were greater in plants grown with residue (Figure 2).

Table 1: Concentrations (± standard errors) of N, P, K, Mg and Ca in birch seedlings from the final harvest. WT and CON treatments are presented (n = 3).

Treatment	Nutrient Concentration (%)				
	N	P	K	Mg	Ca
CON	2.22 (± 0.11)	0.16 (± 0.01)	1.03 (± 0.08)	0.25 (± 0.01)	0.30 (± 0.01)
WT	2.88 (± 0.14)	0.21 (± 0.002)	1.22 (± 0.07)	0.30 (± 0.02)	0.31 (± 0.01)

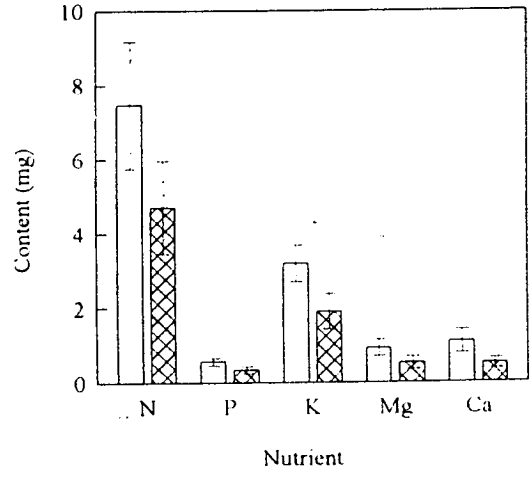

Figure 2: Seedling nutrient content from the final harvest. Means (± standard errors are represented for CON (plain) and WT (cross hatched) grown seedlings (n = 3).

Soil horizon as a predictor of leaf area

Leaf area was positively related to the oven dried litter weight available to the seedling from CON and WT samples (Figure 3). Litter weight predicted leaf area better in CON (R^2 = 0.79) than WT (R^2 = 0.46) grown seedlings. No relationship was observed with the lower soil horizons

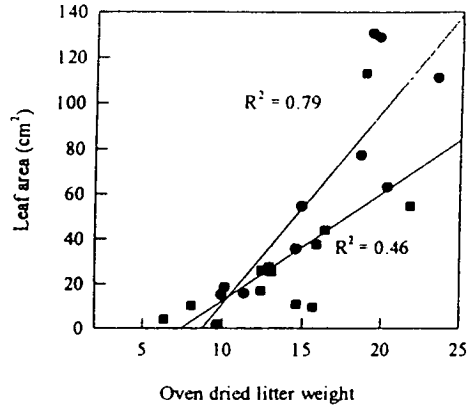

Figure 3: The relationship between litter quantity and leaf area from CON (●) and WT (■) grown seedlings (each point represents one core). The regression equations are indicated by the lines and the associated R-squared values given.

Estimated C:N Ratios

C:N ratios varied little (from 27 to 31) between soil horizon and treatment (Figure 4). Within each soil horizon differences between treatments were insignificant.

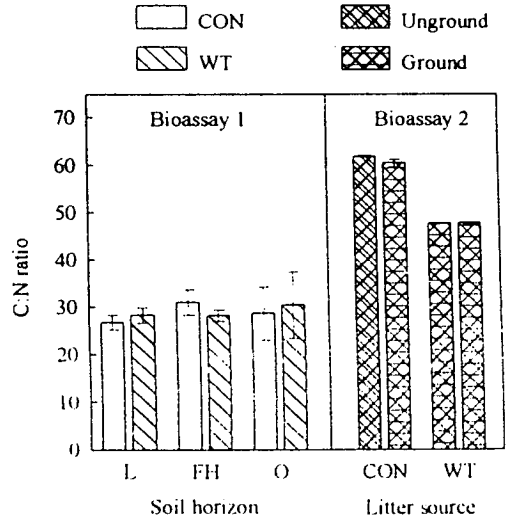

Figure 4: C:N ratios recorded during bioassays 1 and 2. The mean value (± standard errors) are represented for the L, FH and O soil horizons in bioassay 1 (n = 3), and CON and WT areas from bioassay 2 (n = 4).

Bioassay 2

Leaf area

Generally, leaf area increased linearly with stepwise additions of needle litter (Figure 5). WT grown seedlings attained significantly larger leaf areas with 20, 30 and 40 g inputs ($P < 0.05$) than the respective CON plants. Grinding the substrate significantly reduced leaf area ($P < 0.05$) and resulted in small decreases between inputs of 30 and 40 g. Reductions in overall size were especially evident with CON litter. Significant interactions between litter quality and grinding were also observed for all additions except 20 g ($P < 0.05$).

Estimated C:N ratios

The C:N ratio of litter collected from CON mats was significantly greater than that from WT areas ($P < 0.001$). The effect of grinding did not alter the respective ratios (Figure 4).

Further results from this experiment will be presented in a subsequent paper.

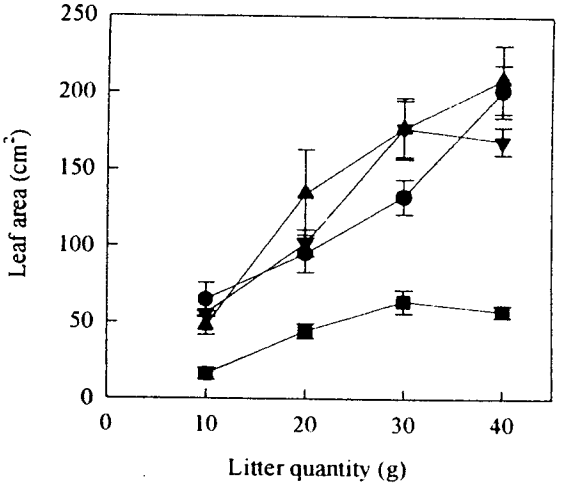

Figure 5: Leaf area growth in response to stepwise increases in litter inputs. Material collected from CON (unground (●)and ground (■)) and WT (unground (▲) and ground (▼)), six months after clear felling the first rotation of Sitka spruce. Means (± standard errors) are represented ($n = 4$).

4 Discussion

The presence of felling residue produced birch seedlings with greater nutrient contents and significantly larger birch leaf areas, indicating greater available nutrients. Concentrations of nitrogen and phosphorus were slightly below foliar levels considered to show deficiency symptoms (N < 2.5 % and P < 0.19 %) (BINNS et al 1983). However, the values recorded in the current study were diluted by the inclusion of the whole plant biomass. Therefore, it is suggested that nutrients did not limit growth of the seedlings in the either treatment. As leaf area continued to increase to the final

harvest, nutrients within the cores of both treatments had not been totally exhausted. Therefore, the treatment effect may reflect temporal differences in release, absolute differences in mineralisable nutrients or an interaction of both factors. Field trials investigating the effects of CON and WT harvested sites have reported similar enhanced growth when residues are retained (SMETHURST and NAMBIAR 1990, PROE and DUTCH 1994; LUNDKVIST 1986). However the physical effects induced by residue retention in the field, modify the local soil environment and complicate identification of factors determining growth.

Assuming that the birch seedlings accessed all mineralised nitrogen in the cores, under controlled conditions 103.6 and 64.9 kg N ha^{-1} y^{-1} became available in CON and WT harvested soils, respectively. These values probably overestimate in situ mineralisation as seasonal fluctuations in temperature and precipitation in the field reduce the period of favourable conditions for microbial action. The lag in leaf area increase observed before the third harvest may have arisen due to a poorly developed root system or a lack of mycorrhizally infected roots. Similar delays in growth have been observed when growing Sitka spruce seedlings as a bioassay. These were attributed to a lack of mycorrhiza (Carlyle 1984). Carlyle (1984) observed that the subsequent growth of mycorrhizal fruiting bodies coincided with a disappearance in the nitrogen deficiency symptoms of the seedlings. Although all seedlings from the final harvest had mycorrhizal associations (with *Thelephora terrestris* (Pers.) and *Elaphomyces sp.*) the timing of infection was not known. If nutrient uptake was reduced by a lack of mycorrhiza or a poorly developed root system, total nitrogen mineralised during the bioassay may be underestimated.

At the end of the first bioassay leaf area was significantly related to the weight of oven dried litter. Various factors may have caused this trend including, direct or indirect effects of litter on the nutrient mineralisation in the core and restricted exploitation of the deeper soil horizons resulting from an under developed root system. However, roots penetrated the entire core depth, therefore an actual influence of litter is possible In addition the relationship was influenced by treatment despite insignificant differences between C:N ratios. The removal of felling residue affects the size of the relatively small pool of young litter that turns over and releases nitrogen faster than the larger pool of old more resistant humus beneath (LUNDKVIST 1986).

The second bioassay demonstrated that WT and CON litter act as a source of nutrients within one year after felling. The significantly higher estimated C:N ratio (61) recorded for material collected beneath residue mats compared to WT harvested areas (48) may be responsible for the smaller leaf areas and the greater lag period recorded before height growth (not presented in this paper). BERG and STAFF (1981) found these delays to be common during the accumulation of relative and absolute nitrogen in decomposing litter material. In addition, BERG and EKBOHM (1983) found that the critical C:N ratio above which there is net immobilisation to be 63 for clearfelled forests. The value recorded during the second bioassay is very similar. Therefore, net immobilisaton during the initial stages of the bioassay was probable.

Grinding was performed initially to enhance the establishment of trees, by increasing the surface area to volume ratio of the litter substrate. However, reduction of litter size reduced growth of plants in CON material and resulted in maximum leaf areas occurring at 30 g of litter, before a slight reduction at 40 g. Grinding was performed by passing material through a centrifuge mill (without a gauze mesh). It is possible that contaminants were acquired during this process which influenced the growth of the seedlings. CARLYLE (1984) found that mycorrhizal fruiting bodies were absent from substrates containing ground litter and speculated that reduced soil aeration

affected fungal colonisation of roots. However the lack of fruiting bodies did not prove that root infection had not occurred. Large differences between ground and unground litter arose only in the CON treatment. As WT substrates were relatively unaffected, grinding alone does not appear to influence mineralisation. An interaction between litter source and particle size may be present.

5 Conclusions

Modification of the forest floor results from the redistribution of felling residue. Retention of aboveground biomass delays nutrient release in the litter layer shortly after clear cutting, probably due to the high C:N ratio of the substrate. Within four years, the C:N ratio of the residue reduces and microbial action enhances nutrient release above that found in WT areas.

As the bioassays were performed under controlled conditions, micro climatic changes resulting from the residue additions were not considered. Therefore these results cannot be applied directly to field conditions. The reversal in trends of nutrient release within four years of felling demonstrates the dangers of drawing conclusions over short time periods.

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Dr Douglas Malcolm and Dr Janet Dutch are gratefully acknowledged for their supervision and comments regarding this research. Funding was provided by the National Environmental Research Council and the Forestry Commission.

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Appendix 6

Table 6.2a: Details of sample size, dates of physiological measurements (leader length) and foliage collection (for biomass and nutrient analysis) during 1994, 1995 and 1996. (✓ indicates that the measurement was performed.)

	1994			**1995**	
	Physiological measurements	*Foliage collection*		*Physiological measurements*	*Foliage collection*
Sample size	8 per plot	8 per plot	*Sample size*	16 per plot	10 per plot
Date			*Date*		
May 22	✓	✓	June 2	✓	✓
June 6	✓	✓	June 16	✓	✓
June 20	✓	✓	June 24	✓	✓
July 6	✓	✓	July 16	✓	✓
July 19	✓	✓	Aug. 1	✓	✓
Aug. 2	✓	✓	Aug. 15	✓	✓
Aug. 19	✓	✓	Sept. 1	✓	✓
Aug. 30	✓	✓	Sept. 12	✓	✓
Sept. 15	✓	✓	Oct. 13	✓	✓
Oct. 5	✓	-		**1996**	
Oct. 20	✓	✓	Feb. 1	-	✓

Table 6.2b: A summary of budburst observation details for 1994 and 1995, including sample size per replicated plot, sample dates and bud position.

Year	*Sample size*	*Observation dates*	*Position of buds recorded*
1994	8 per plot	May 5	Leader terminal
		May 10	
		May 22	
		June 7	
1995	16 per plot	May 1	Leader terminal
		May 7	Top whorl lateral, terminal
		May 11	Second top whorl lateral, terminal
		May 15	
		May 21	
		June 6	