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SEASONAL PATTERNS OF NITROGEN MINERALIZATION AND NITRIFICATION FOLLOWING HARVESTING IN THE WHITE SPRUCE FORESTS OF INTERIOR ALASKA

University of Alaska, Fairbanks PH.D. 1986

SEASONAL PATTERNS OF NITROGEN MINERALIZATION AND NITRIFICATION FOLLOWING HARVESTING IN THE WHITE SPRUCE FORESTS OF INTERIOR ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfillment of the Requirements

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DOCTOR OF PHILOSOPHY

By

Andrew MacLean Gordon, Bsc.F., R.P.F.

Fairbanks, Alaska

May 1986

SEASONAL PATTERNS OF NITROGEN MINERALIZATION
AND NITRIFICATION FOLLOWING HARVESTING
IN THE WHITE SPRUCE FORESTS OF
INTERIOR ALASKA

RECOMMENDED:

Chairman, Advisory Committee

Dean, School of Agriculture
and Land Resource Management

APPROVED:

Director of Graduate Programs

May 6, 1986

Date

When I smell those spruce trees

I'll feel young....

the late Stan Rogers (1983)

ABSTRACT

The effects of commercial timber harvesting upon nitrogen transformations were evaluated for the forest floor and mineral soil of mature white spruce (Picea glauca (Moench.) Voss) forest sites in interior Alaska. Analyses of forest floor and mineral soil incubated in situ in mature forest and two recently harvested areas of different ages indicated an ammonium-dominated soil system for the unharvested area.

Statistically, logging had no effect upon mineralization, nitrification or on the average NH_4-N or NO_3-N produced on incubation in the forest floor. In the mineral soil the same patterns were apparent with the exception that the NO_3-N produced on incubation was significantly greater in the harvested areas. However, the lack of a large number of incubation periods (n=8), over the entire course of study (22 months of continuous incubation) likely contributed to this result. While mineralization (ammonification) rates did not differ between areas, there were times in mid-summer when nitrification rates in the clearcut areas far exceeded those in the control area. Thus, although the net amount of NH_4-N produced was not different between areas, the amount of nitrogen moved from the organic pool into available pools (net nitrogen mineralization) was greater in the harvested areas, primarily because of mid-summer nitrification in the

latter. Increased soil moisture and temperature regimes due to harvesting were thought to be the prime factors responsible.

Nitrogen cycling in the mature white spruce forest was typical of a steady-state system; cycling was very tight. Field estimates of mineralization for the forest floor (2.48 $g/m^2/yr$) and the mineral soil (0.48 $g/m^2/yr$) fit well into a schematic cycle developed around other estimates of N-pools and fluxes derived from the literature. This was also true of nitrification rates which were very low in both horizons. In the cleared areas, mineralization rates in the forest floor varied from 0.11 to 3.59 $g/m^2/yr$ and in the mineral horizon from 0.42 to 0.54 $g/m^2/yr$. Nitrification rates varied from 1.49 to 3.01 $g/m^2/yr$ in the forest floor and from 0.24 to 0.27 $g/m^2/yr$ in the mineral soil.

The effects of changes in abiotic and biotic controls on nitrogen mineralization and nitrification due to harvesting, and the implications of whole-tree vs. conventional logging are also discussed.

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ACKNOWLEDGEMENTS

The sun was setting on Old Baldy in the interior of Algonquin Park, Ontario. It was a hot August night in 1974 and myself and Dave Gauthier had just slogged through a mile and a half of black spruce swamp in our summer search for timber wolves. As we rested on the logged-off hill high above the surrounding landscape, Dave rambled on about the science of biology and nature. For his thoughts that night, I'd like to thank Dave, now a wildlife biologist in the Yukon, for I feel it was there that the seed was planted.

Since then, on my way to Alaska, many have helped and advised. Dr. John Theberge, University of Waterloo, Mr. Mac McLean, Ontario Ministry of Natural Resources, Dr. Helmut Krause, University of New Brunswick, Dr. Harald Piene, Canadian Forestry Service and Mr. George Marek (some say he's retired) all honed my thoughts on the science of forest ecosystems. For the opportunity to listen to these people and for their help I will be forever grateful.

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INTRODUCTION

The circumpolar boreal or taiga forest extends in North America from Newfoundland to interior Alaska. In the latter, on well-drained, warm sites white spruce (Picea glauca (Moench.) Voss)[a], white or paper birch (Betula papyrifera Marsh.), and trembling aspen (Populus tremuloides Michx.) predominate. On cooler, poorly-drained sites black spruce (Picea mariana (Mill.) B.S.P.) and occasionally larch (Larix laricina (Du Roi) K. Koch) are the dominant species. White spruce and balsam poplar (Populus balsamifera L.) dominate the flood plains of interior rivers. The two interior species of Picea differ in their growth habits and ecological associations over much of their respective ranges. While black spruce in eastern Canada and parts of the northern United States is the principal pulpwood species due to its uniform growth rate and stature (Gordon, 1983), black spruce in Alaska is, more often than not, relegated to the poorest sites, is of low stature and is essentially non-commercial at the present time. White spruce, on the other hand, is one of the more productive species in interior Alaska, often occurring in pure stands. This phenomenon is rare in the eastern boreal forest where white spruce is found often only in mixed-wood situations.

---

[a] vascular flora follows Hultén (1968)

The interior forests of Alaska comprise approximately 44 million hectares; of this, 14 million hectares are classified as commercial forest land (Hutchison, 1967). Since the beginning of development in the interior around the turn of the century, these forests have traditionally supplied local residents with a variety of wood products. In recent years, however, an exponential rise in this demand has seen increased utilization of forested areas primarily in the form of timber extraction not only for lumber but also for fuelwood (Richmond, 1981). White spruce particularly has been used to supply houselogs and medium quality sawtimber, making up 81% of the commercial board-measure harvest (Farr, 1967).

Until recently, forest ecologists have considered one of the most important consequences of forest harvesting to be the removal of a large portion of the site nutrient capital in the harvested trees and many past studies have been concerned with the effects of clear-cutting upon soil biological, chemical and physical properties. For example, the effects of clear-cutting on chemical changes in forest floor organic matter (Covington, 1981), woody litter decomposition (Abbott and Crossley, 1982; Gadgil and Gadgil, 1978), soil microbiological properties (Smith *et al.*, 1968; Sohlenius, 1982; Theodorou and Bowen, 1981) and soil solution chemistry (Dyck *et al.*, 1981; Hart *et al.*, 1980, 1981) have been documented. With whole-tree logging, and consequently, the removal of branch material and potential needle litter, a

substantial fraction of the nutrient pool formerly present on the site will be lost to subsequent generations of trees. Recent studies at the ecosystem level in a variety of forest site types have evaluated nutrient losses and changes in site productivity resulting from whole-tree harvesting (Adams and Boyle, 1980, 1982; Johnson et al., 1982; Silkworth and Grigal, 1982, and many others). With any type of logging, replacement of these losses will largely arise from the remaining stock of nutrients. Under summer whole-tree harvesting, it is likely that this reserve will be taxed severely (cf. Burger and Pritchett, 1984). A certain proportion of branches and needles remain on the site during winter-harvesting operations due to cold weather breakage of branches. The rate at which nutrients, especially mineral nitrogen, are supplied from this reserve will undoubtedly have a substantial effect, in conjunction with other stand parameters, upon not only the re-establishment of the stand but also upon the growth rate of young trees.

Soil temperature and moisture content are the important factors controlling the mineralization of nitrogen. It follows that, in cold-dominated soils such as those found in portions of interior Alaska, the processes of organic matter decomposition and nitrogen mineralization may occur at slower rates than in warmer, temperate-latitude soils. The underlying question to be asked is: if physical variables controlling nitrogen mineralization are affected by the removal

of forest cover, what can the mineralization and nitrification rates be expected to do? Rapid short-term increases in the rate due to increased surface temperature and available moisture may be offset by excessive leaching. Over a longer period of time, the mineralization rate may decline as the forest floor dries and/or supplies of organic material decline. Competition for mineral nitrogen reserves by undesireable tree, shrub or herbaceous "weed" species may further limit the nitrogen available for uptake by more immediately desireable species such as white spruce. As well, upon decomposition the remaining mass of primary root tissues with its typically high C/N ratio will likely become a carbon source for microbial activity. Thus, soil nitrogen reserves may become temporarily unavailable while supplying these microbial demands.

I am not suggesting that intentional disturbance will disrupt soil nitrogen processes to such an extent that successful forestry could never be realized. Vegetation succession following disturbance in white spruce forests is testimony to the fact that plants respond rapidly to disturbance, capturing newly-available nutrients. The micaceous loess upland and alluvial bottomland soils found in interior Alaska are adequately resilient and have a strong chemical buffering capacity. Indeed, a plantation of white spruce established on either an upland or valley-bottom site would probably do fairly well. In terms of our present

utilization of white spruce forests then, our knowledge of forest soil chemistry may actually be fairly adequate; physical controls on forest growth may be more important at these latitudes than chemical controls. I would like to suggest, though, that with the increased planting densities, mechanical site manipulations, shortened rotations and increased tree growth due to genetic improvements that are all part of intensive forestry, our knowledge may be abysmally short-sighted. Demand for electrical energy, for example, may stimulate interest in short rotation wood-energy plantations in the interior for chip production (Smith, 1980). Under this type of cropping the resilient sites of the past may not be the continuously productive sites of the future.

Recently, state legislation has created the Tanana Valley State Forest, 0.6 million hectares centered around Fairbanks in the Tanana River drainage. Both Federal and State forestry agencies are urging the implementation of intensive forest management in order to support sustained yield, as mandated by the Alaska Statehood and Forest Practices Act, on forest lands (subject to increased extraction pressure). While intensive forest management practices such as whole-tree harvesting, chipping and intensive site preparation have helped to realize "more volume on fewer acres in less time" in some areas of the eastern boreal forest, the implementation of these practices is by no means widespread.

Certainly in Alaska forest management is in its infancy; the advent of full-fledged intensive, or even good, forest management is still to be realized. Interestingly enough, this implementation lag in Alaska may eventually manifest itself as a long-term benefit to state foresty as more knowledge becomes available from other North American and Scandinavian experiences.

Increasing development of Alaska's interior forests for a variety of wood products dictates the need for an understanding of changes in productivity of the land base with use and time. The study of nutrient cycles in natural forests in interior Alaska (Van Cleve et al., 1983) and elsewhere have enhanced our basic knowledge about the structure and functioning of ecosystems, giving us cause to reflect on our ability to regenerate forests after harvesting. Similarly, process-level studies in disturbed areas shortly after harvesting, in conjunction with basic knowledge about tree biology, will give us information on the ability of these areas to continually grow forests. There is presently a lack of such information. The effects of forest management activities upon nutrient reserves and processes in Alaska need to be explored. While we do not yet manage forests at this latitude (or perhaps anywhere) on the molecular level at which nutrient cycling studies are conducted, it is just conceivable that some day we might.

This study, then, addresses the hypothesis that commercial timber harvesting in the upland mature white spruce forests of interior Alaska affects soil nitrogen mineralization and nitrification rates. Within the context of the above, the following four objectives were formulated and subsequently evaluated:

1) to quantitatively assess and model the effects of timber harvestingdisturbance upon the seasonal breakdown and transfer of organically-bound nitrogen to available forms within the forest floor and surface mineral soil of mature white spruce stands;

2) to determine, using these mineralization rates and other estimates of N-pool sizes for system components, the short-term and potential long-term effects of fluctuations in these rates due to disturbance upon the site and system nitrogen balance;

3) to provide a predictive mechanism for the potential replenishment and/or depletion of nitrogen supplies with disturbance; and

4) to elucidate and test, in conjunction with the above, methodology associated with the use of polyethylene bags in field incubation experiments, through a variety of laboratory and field experiments.

LITERATURE REVIEW

NITROGEN MINERALIZATION

The mineralization of organic nitrogen in soil is a biochemical reaction mediated by many soil organisms whereby proteins and amino and nucleic acids are converted in the presence of oxygen to carbon-dioxide, water and ammonia (Figure 1). The latter is usually considered a waste-product of this reaction. Many species of bacteria, fungi and actinomycetes may synthesize the extracellular, proteolytic enzymes required for protein decomposition (Alexander, 1971). In general, proteinic material is readily decomposed under neutral or alkaline conditions by bacteria of the genera Pseudomonas, Bacillus, Clostridium, and Micrococcus, and by actinomycetes. Under acid conditions ammonifying fungi may also play a large role. Fungi are also important as nitrogen releasers in some deciduous forests (Kohler and Kunze, 1979).

In acid forest soils the ammonia is rapidly protenated and the ammonium ion (NH_4^+) is the dominant nitrogenous end-product. The biochemistry of the process is well understood and many excellent reviews on the topic are available (cf. Harmsen and Van Schreven, 1955; Jansson and Persson, 1982; Paul and Juma, 1981). The former indicate that, partially because of historical interest in nitrate (NO_3^-) as the

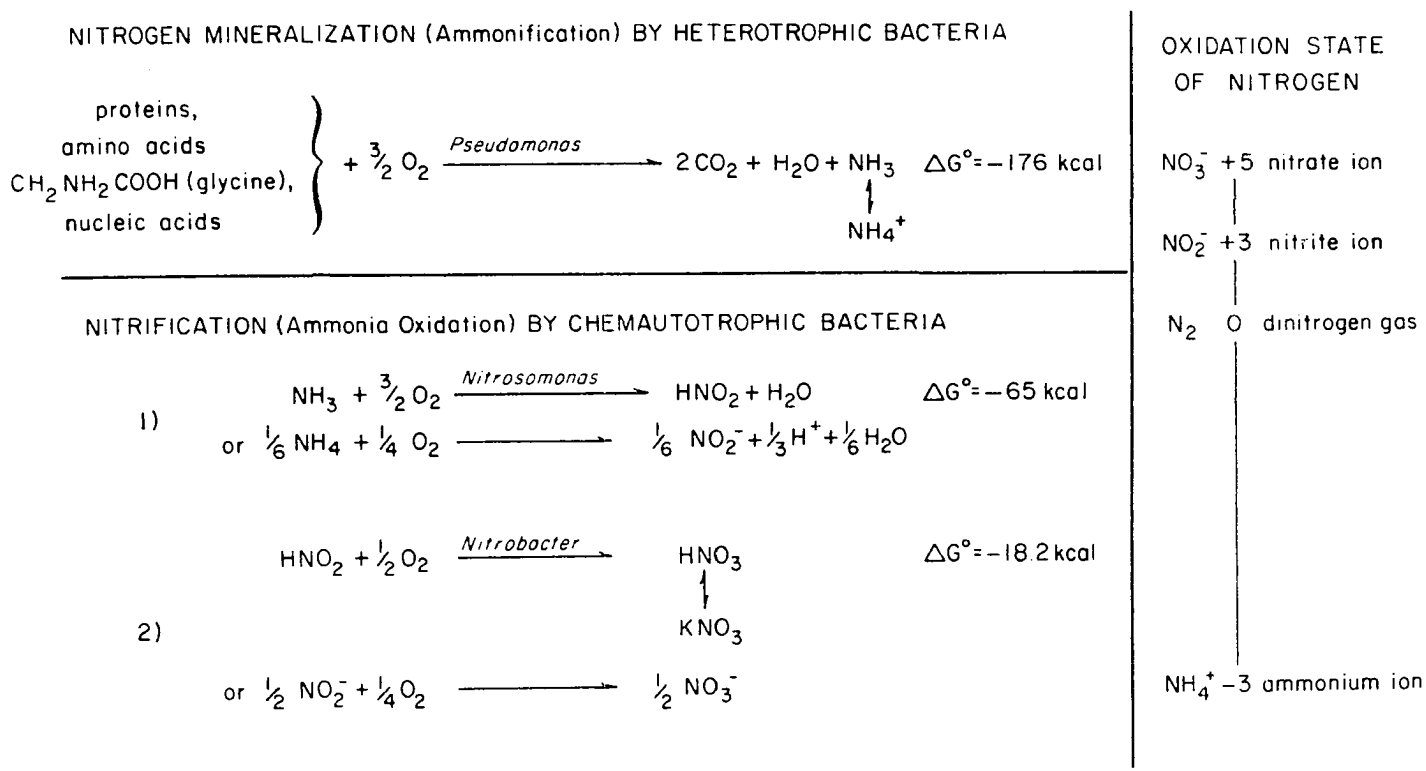

Figure 1. Biochemical reactions for nitrogen mineralization and nitrification in forest soils.

preferred source of nitrogen uptake by many plants, many workers persist in referring to "not only the oxidation of NH_4 to NO_3 but the whole process of mineralization of organic nitrogen as `nitrification'". In this study "nitrogen mineralization" will refer solely to biochemical ammonification, described above. The term "net nitrogen mineralization", where used, will indicate the net amount of nitrogen converted from organically bound nitrogen to NH_4-N, but will also include that portion of the NH_4-N pool converted to NO_3-N by nitrifiers. "Nitrogen immobilization" will refer to the process which occurs through microbial incorporation of ammonium or nitrate and "nitrification" will refer to the two-step biochemical process whereby NH_4^+ is oxidized to NO_3^- by chemautotropic bacteria.

Soil temperature and moisture content are the primary environmental factors governing the mineralization of nitrogen in soil. The complex interactions of these two factors leads to a large variation world-wide in nitrogen mineralization rates (Table 1). Judging by the contradictory information in the literature on the effects of temperature and moisture on nitrogen mineralization, the interaction of these two factors and/or the chemical nature of the soil itself, may be a more important control on nitrogen mineralization than either temperature or moisture content by itself. For example, Smith *et al.* (1981) showed that forest soils in Washington mineralized less nitrogen under anaerobic as com-

Table 1. Soil nitrogen mineralization rates from some selected ecosystems.[a]

Nitrogen Mineralization Rate (kg/ha/yr)	Forest Soil or Type	Location	Study
	Forest Floor		
14[b]	Abies balsamea (L.) Mill.	Maine	Federer, 1983
25	Picea glauca	Alaska, interior	This study
17[b]	Picea mariana	Alaska, interior	This study
67	Picea sitchensis (Bong.) Carr.	Scotland	Williams, 1983a
72	Picea spp.[c]	Germany	Glavac and Koenies, 1978a
29[b]	Picea spp.	Sweden	Popovic, 1971
13	Pinus nigra var. maritima (Ait.)Melv.	Scotland	Miller et al., 1979
31	Pinus resinosa Ait.	Massachusetts	Aber et al., 1983
44	Pinus resinosa	Wisconsin	Bockheim et al., 1983
26	Pinus resinosa	Wisconsin	Pastor et al., 1984
43	Pinus strobus L.	Wisconsin	McClaugherty et al., 1985
44[d]	Pinus strobus	Wisconsin	Pastor et al., 1984
29	Tsuga canadensis (L.) Carr.	Wisconsin	McClaugherty et al., 1985
29	Tsuga canadensis	Wisconsin	Pastor et al., 1984
~6[b]	Tsuga mertensiana (Bond.) Carr.	Oregon	Matson and Boone, 1984
~11[b]	Tsuga mertensiana (dieback)	Oregon	Matson and Boone, 1984
88	Acer saccharum Marsh.	Wisconsin	McClaugherty et al., 1985
100	Acer saccharum	New Hampshire	Melillo, 1977
74[d]	Acer saccharum	Wisconsin	Pastor et al., 1984
85[b]	Betula papyrifera	New Hampshire	Federer, 1983
25[b]	Betula papyrifera	Alaska, interior	This study
35[e]	Fagus spp.	Germany	Glavac and Koenies, 1978b
103[c,e]	Fagus spp.	Germany	Glavac and Koenies, 1980
84	Fraxinus americana L.	Wisconsin	Pastor et al., 1984
23	Populus tremuloides	Wisconsin	McClaugherty et al., 1985
75	Quercus alba L.	Wisconsin	McClaugherty et al., 1985
64[d]	Quercus alba	Wisconsin	Pastor et al., 1984
41	Quercus rubra L.[f]	Massachusetts	Aber et al., 1983
63[d]	Quercus rubra	Wisconsin	Pastor et al., 1984
81[d]	Tilia americana L.	Wisconsin	Pastor et al., 1984
100	northern hardwoods	New Hampshire	Aber et al., 1983
	Mineral Soil		
47	Picea glauca	Wisconsin	Nadelhoffer et al., 1983[g]
5	Picea glauca	Alaska, interior	This study
26[b]	Picea spp.	Sweden	Popovic, 1971
53	Pinus resinosa	Massachusetts	Aber et al., 1983
32	Pinus resinosa	Wisconsin	Nadelhoffer et al., 1983[g]
9	Pinus strobus	Wisconsin	McClaugherty et al., 1985[h]
80	Pinus strobus	Wisconsin	Nadelhoffer et al., 1983[g]
2	Pinus sylvestris L.[i]	Sweden	Popovic, 1980
~9	Pinus sylvestris[c]	Germany	Rodenkirchen, 1984
50	Pinus resinosa-P. strobus	Wisconsin	Nadelhoffer et al., 1983[g]

Table 1. Continued

	Mineral Soil (cont.)		
~1[b]	Tsuga mertensiana	Oregon	Matson and Boone, 1984
~3[b]	Tsuga mertensiana (dieback)	Oregon	Matson and Boone, 1984
62	Acer saccharum	Wisconsin	Nadelhoffer et al., 1983[g]
36	Acer saccharum	Wisconsin	McClaugherty et al., 1985[h]
51	Betula papyrifera	Wisconsin	Nadelhoffer et al., 1983[g]
24	Populus tremuloides	Wisconsin	McClaugherty et al., 1985[h]
9	Quercus alba	Wisconsin	McClaugherty et al., 1985[h]
54	Quercus rubra	Massachusetts	Aber et al., 1983
17[b]	Quercus rubra	New Hampshire	Federer, 1983
71[b]	Quercus rubra	Connecticut	Federer, 1983
100	Quercus rubra	Wisconsin	Nadelhoffer et al., 1983[g]
111	Quercus velutina Lamb.	Wisconsin	Nadelhoffer et al., 1983[g]
91	Quercus velutina-alba	Wisconsin	Nadelhoffer et al., 1983[g]
	Clear-cut/Cultivated		
19	Picea glauca (forest floor)	Alaska, interior	This study
5	Picea glauca (mineral soil)	Alaska, interior	This study
200	Picea spp. (forest floor)	Germany	Glavac and Koenies, 1978a
94	Picea spp. (forest floor)	Germany	Glavac and Koenies, 1980
167	Pinus nigra-fertilized	Scotland	Miller et al., 1979
~27	Pinus sylvestris[c]-fertilized	Germany	Rodenkirchen, 1984
~9	Pinus sylvestris[c]-fertilized/tillage	Germany	Rodenkirchen, 1984
~47	Pinus sylvestris[c,j]	Germany	Rodenkirchen, 1984
550	cultivated histosol	New York	Guthrie and Duxbury, 1978
675	cultivated histosol	Florida	Reddy, 1982
37[d]	old field[k]	Georgia	Stinner et al., 1984
128[d]	no-tillage[k]	Georgia	Stinner et al., 1984
150[d]	conventional tillage[k]	Georgia	Stinner et al., 1984
	Other		
130	Acacia senegal-humus	Senegal	Bernhard-Reversat, 1977
156	Rumex alpinus[l]	Bavarian Alps	Rehder, 1982
80	Senecio cordatus[m]	Bavarian Alps	Redher, 1982
19	coastal tundra	Alaska, arctic	Chapin et al., 1980
2	cushion plant-lichen	Devon Is, Canada	Babb and Whitfield, 1977
21	hummocky sedge-moss	Devon Is, Canada	Babb and Whitfield, 1977
128	marsh forest-humus	Brazil	Pfadenhauer, 1979
8	ombrotrophic bog-peat	Sweden	Rosswall and Granhall, 1980
<1	polygon tundra[n]	Alaska, arctic	Norrell and Johnston, 1974
634	swamp forest-peat	Brazil	Pfadenhauer, 1979
1062	virgin histosol	Florida	Reddy, 1982
554	wet meadow[o]	Alaska, arctic	Gersper et al., 1980

[a] A more extensive review of European literature is given in Ellenberg (1971,1977) and Rodin and Bazilevich (1965). Vitousek and Melillo (1979) summarize nitrogen mineralization values (19 to 139) for the major North American watershed studies. Comparisons within this table should be

Table 1. Continued

used with some caution. Major differences in field and laboratory procedures, soil horizon descriptions and terminology (especially involving the use of net nitrogen mineralization and nitrogen mineralization) are very evident. Many of the studies employ net nitrogen mineralization; this study did not employ this concept universally.

[b] corrected to a 6-month growing season

[c] forest floor plus top mineral horizon: for Rodenkirchen (1984), mineral soil depth was 20 cm

[d] average of values presented

[e] no effect of clear-cutting on nitrogen mineralization in these studies

[f] The Quercus borealis reported by the authors of this study has been renamed Quercus rubra (U.S. Department of Agriculture, 1965).

[g] Nadelhoffer et al. (1984) provide additional information on mineralization rates on these stands

[h] mineral soil depth: 10 cm

[i] entire profile

[j] fertilized, tillage and legume underplanted

[k] sandy clay loam

[l] clay on moraine

[m] clay

[n] top 4 cm

[o] buried horizon, 6 cm thick; corrected to a 4-month growing season

pared to aerobic conditions (incubation temperature 35°C). Conversely, Van Schreven and Sieben (1972) found that water-logging soils (incubation temperature 29°C) actually increased the amounts of nitrogen mineralized on incubation. Terry (1980) has indicated that nitrogen mineralization was not affected by soil moisture tension over the range of 0.1 to 3.0 bars. Marion and Miller (1982) found a similar phenomenon in tussock tundra soils: over a much narrower range of moisture tension (0.0 to 0.4 bars), nitrogen mineralization was not affected.

Terry's (1980) work in histosols is in direct conflict with the recent work of Van Cleve (pers. comm., 1984) in mineral soils who found increasing amounts of nitrogen mineralization as moisture tension was decreased from 3 to 0.2 bars. Nonetheless, several researchers have found that nitrogen mineralization is linearly dependent upon moisture content within the available range (Hopmans et al., 1980; Myers et al., 1982), although nitrogen immobilization has also been found to increase with increasing moisture content (Flowers and Arnold, 1983). Slavnina and Pashneva (1976), in certain Russian soils, found ammonification to be highest at a moisture content of 80% full moisture capacity. (The term "full moisture capacity" was not defined). Another well-known moisture-associated phenomenon that stimulates nitrogen mineralization is alternate drying and re-wetting of the soil (Agarwal, et al., 1971a; Enwezor, 1967; Van Schreven, 1967;

and others). The theory is that drying followed by re-wetting will shatter soil particles, and expose new surfaces to microbial action.

Unlike moisture content, fluctuating temperature environments such as normal diurnal patterns seem not to affect the amount of nitrogen mineralized (Stanford et al., 1975), although Campbell and Biederbeck (1972) reported that mineralization was directly proportional to artificially fluctuated temperatures in agricultural soils when moisture was held constant. As well, as pointed out by Stanford et al. (1975), the relationship between temperature and nitrogen mineralization is not linear and so comparison of average mineralization rates between that taking place at a mean temperature and that under a fluctuating temperature is not valid except within a very narrow temperature range (about 10°C). In general, though, increasing temperature increases ammonification and many studies report on this phenomenon (cf. Bernhard-Reversat, 1980). The optimal temperature for mineralization appears to be site-specific ranging up to 50°C in tropical soils (Myers, 1975), although the optimum constant temperature for ammonification in many soils is likely between 25°C and 35°C (cf. Justice and Smith, 1962). In northern soils, it is likely that reduced mineralization takes place at temperatures as low as 2°C (Alexander, 1967). That mineralization occurs over this wide range of temperatures world-wide is indicative not only of the many micro-

organisms that mediate the reaction but also of the biome-specific characteristics that soil nitrogen mineralization possesses.

Temperature coefficients (Q_{10} values) for nitrogen mineralization are often hard to calculate due to irregular net production of mineral nitrogen (cf. Ross and Bridger, 1978c) but a Q_{10} of 2.0 seems to be a good average for many soils (cf. Marion and Miller, 1982; Ross and Bridger, 1978c; and many others). Combinations of high temperature and moisture content often cause maximum nitrogen mineralization (cf. Clarholm et al., 1981) and multiple regression over a large range of these two parameters has been successfully used to predict mineralization (Cassman and Munns, 1980). Freezing and thawing cycles will also stimulate mineralization (Khonnolaynen and Reppo, 1975; Ross and Bridger, 1978b).

Maximum mineralization rates are often found in the summer, probably in response to temperature (Bonneau, 1980; Kovacs, 1978; Pfadenhauer, 1979; Rodenkirchen, 1984; Runge, 1978), although anomalies have been noted. Laudelout and Lambert (1982) were able to correlate nitrogen mineralization to fluctuations in bacterial biomass that corresponded to spring and autumn maxima. Ross and Cairns (1981) on the other hand, found no relationship between bacterial biomass and nitrogen mineralization, no matter at what time during the season sampling was done. It was not certain to what extent fungi may have been playing a role in N-mineraliza-

tion. Ross and Bridger (1978b) were also unable to relate mineralization rates to general ammonifier counts. However, Norrell and Johnston (1974) found good correlations between ammonification and bacterial biomass in arctic tundra soils, finding both to increase as season progressed. Nitrogen mineralization has also been related to the organic biomass in soil and cell-free protease activity (Beck, 1983).

Mineralization almost always decreases with increasing depth in the soil (Bernhard-Reversat, 1981; Federer, 1983; Hendrickson and Robinson, 1984; Roze and Forgeard, 1982). At high latitudes, depending upon aspect, this may simply reflect decreasing soil temperature with depth. On the other hand, this may be partially related to the particle size fractions in respective horizons. Particle size fractions < 0.3 um have been shown to consistently relate to higher releases of mineral nitrogen (Cameron and Posner, 1979; Lowe and Hinds, 1983; Williams, 1983b). In addition, there is usually a reduction in organic matter content and thus organic-N, the substrate for mineralization, as depth increases.

There are important chemical properties of the soil that effect nitrogen mineralization. A lowering of soil pH will generally, but not always (Bosatta, 1982; Johnson and Todd, 1984), bring about a decrease in nitrogen mineralization, an important consideration in nitrogen-stressed ecosystems subject to heavy acid precipitation inputs (Aber et

al., 1982). Interestingly, Popovic (1984) found acidification to increase nitrogen mineralization (through reduction in microbial biomass and subsequent release of microbially-bound N) and Lohm et al. (1984) found that while acidification of coniferous forest soils did not affect mineralization of nitrogen, it did slow the net turnover rate of the NH_4-N pool. Liming of soils with $CaCO_3$ has been found to stimulate nitrogen mineralization (Ross et al., 1979c; Van Praag and Weissen, 1973) but the effect may also be non-existent (Sarathchandra and Upsdell, 1981), short-lived (Nyborg and Hoyt, 1978) or depressive (Lohm et al., 1984; Popovic, 1984). In general, mineral nitrogen (NH_4-N + NO_3-N) can be said to accumulate at higher rates as pH is increased to near neutrality (cf. Ishaque and Cornfield, 1972), presumably because more strains (species) of mineralizers are adapted to neutral conditions.

The pH range for ammonification appears to be between 3.5 and 7.0, with an optimum at 5.0 (Small, 1954, original not seen). However, the effects of soil acidity on nitrogen mineralization are often obscured by acid generation from the nitrogen cycle itself, especially in non steady-state systems. If the rate of nitrogen mineralization exceeds the rate of nitrogen uptake "discoupling" of the nitrogen cycle results and there is a net production of hydrogen protons (Matzner and Ulrich, 1983). It should be noted, though, that steady-state nitrogen cycling, in any system, can be shown to

be a neutral process (Helyar, 1976).

The rate of nitrogen mineralization is proportional to the amount of potentially mineralizable substrate (Sinha et al., 1977) but one problem in quantifying this may be that nitrogen can be mineralized from several pools of total nitrogen (Berg and Theander, 1984; Bosatta, 1981b; Colom and Wolcott, 1967; Frissel and Van Veen, 1982; Ivarson and Schnitzer, 1979; Jones, 1984; Juma and Paul, 1981, 1984; Keeney and Bremner, 1966; Richter et al., 1982; Sollins et al., 1984). Up to eight potentially mineralizable organic substrates have been proposed. Thus, a $Q_{10} > 2.0$ may reflect a higher degree of degradation of the soil organic matter: either smaller fractions or more readily decomposable pools (Campbell et al., 1984). Heng and Goh (1984), for example, found that additions of polyphenol solutions to forest soils lessened nitrogen mineralization. In some tropical systems, nitrogen mineralization may be more closely related to available rather than to total nitrogen (Lamb, 1980).

The production of mineral nitrogen (or nitrogen measured prior to utilization by microbes, plants) is often correlated negatively with soil C/N ratios (Enwezor, 1976; Marion and Miller, 1982; Marumoto et al., 1980; Ross et al., 1979a; Sahrawat, 1983). This means that, typically, at narrower C/N ratios there is more nitrogen available for plant use and exchange reactions. However, there are many examples where no correlation between N-production and C/N

ratio was evident (cf. Marion et al., 1981; Williams, 1983b). Sollins et al. (1984) found the correlation between net nitrogen mineralization and C/N ratio to be negative for the light fraction (<0.25 mm) and positive for heavier fractions, suggesting that the extent of mineralization of the heavy fraction N is not controlled by the C/N ratio. High mineralization rates can also be associated with high C/N ratios in tropical (Thiagalingam and Kanehiro, 1973) and tussock tundra soils (Marion and Miller, 1982). As would be expected, ammonium production also correlates well with soil total nitrogen (Marion et al., 1981; Marion and Miller, 1982; Vlassak, 1970; Winsor and Pollard, 1956; Youngberg, 1978). Sahrawat (1983) found good correlations between nitrogen mineralization and soil total nitrogen and carbon in tropical rice soils but Williams (1983b) was not consistently able to relate mineralization to total nitrogen in peat soils. It would follow from the above discussion, then, that crop residues of high C/N ratio would tend to promote immobilization of nitrogen. Conversely, residues of low C/N ratio would tend to stimulate nitrogen mineralization. There are certain limitations on this concept: it is not possible to say that mineralization rates are not high, just because little NH_4-N is measured. In a situation of high microbial demand for nitrogen, microbial turnover of N may be rapid, and the C/N ratio of residues not all that important. Nonetheless, as Adams and Attiwill (1984) succinctly summarize:

"N added to ... young aggrading forests of high productivity ... appears to be quickly immobilized. Within normal forest rotations, it is apparent that the C/N ratio of soil acts as a strong buffer to perturbation of mineralization patterns."

For certain agricultural residues the critical ratio above which nitrogen mineralization is inhibited appears to be about 20/1. In forest soils, this ratio is higher, although its magnitude is inversely related to decomposition rate (Bosatta and Staaf, 1982). Van Cleve (1974) determined that materials of narrow C/N ratios contain higher proportions of easily decomposed starches and lipids. Similarly, Aber and Melillo (1982b) found that immobilization increased with increasing initial lignin content and decreasing nitrogen content. They found that higher immobilization rates were associated with early forest successional species. Bosatta and Staaf (1982) also noted increased immobilization with litter of low initial nitrogen content and Berg and Staaf (1981) noted that accumulation of nitrogen in systems was directly proportional to the decomposition rate (see also Berg and Theander, 1984 and McClaugherty et al., 1985). Bosatta (1981a) has gone so far as to claim that the decomposer-root system is stable when net nitrogen mineralization is positive but with negative net mineralization the "system evolves in time towards the annihilation of the roots". This is consistent with evidence that C-mineralization is negatively correlated with N-mineralization (Bosatta and

Berendse, 1984; Freytag and Rausch, 1984).

Van Cleve (1974) also indicated that reduced decomposition occurred as the C/N ratio approached 80/1. Berg and Ekbohm (1983) similarly found the critical ratio in a mature Scots pine forest floor to be approximately 110/1. Adjacent clearcuts were found to have C/N ratios of 60/1, suggesting that residues in clearcuts first supply microbial demands for nitrogen, at least in the early stages after cutting. An important consequence of harvesting may be then the immobilization of nitrogen during the decomposition of logging slash with its wide C/N ratio and large biomass. However, as Stone and Will (1963) point out, seedling growth is not often directly correlated to local accumulations of slash. Nitrogen deficiencies have also been known to persist for many years after the time when residues have visibly disappeared from the site and N-additions are from root and stump decomposition only. In addition, Lamb (1975) found that mineralization patterns in soil were not associated with litter nitrogen contents in Monterrey pine (Pinus radiata D.Don) plantations but were associated with the rates of nitrogen withdrawal in aging needles on the ground. He hypothesized that polyphenol complexing in freshly-fallen litter may be a more important control on nitrogen mineralization.

The process of mineralization-immobilization is definitely linked to C/N ratios, but may be more complex than we allow. For example, Sinclair et al. (1981) studied nitrogen

mineralization in carbon and nitrogen limited systems. When carbon was limiting, nitrogen mineralization was primarily by the protozoa Acanthamoeba which grazed populations of Pseudomonas bacteria and released NH_4-N as a waste product. Pseudomonas contributed little to nitrogen mineralization. When nitrogen was limiting, nitrogen mineralization by the grazers permitted the bacteria to proliferate. Bacterial biomass increased but the total amount of carbon used did not! On the other hand, carbon mineralization itself may simply have increased. Novák (1980) has shown this to be the case when carbohydrates are added to soil, in the absence of utilizable forms of nitrogen. The C/N ratio actually represents the balance between potential energy-yielding organic substances and non-energy yielding inorganic elements which may be required for microbial metabolism. Depression of microbial activity in response to inorganic element additions suggests that some systems are energy and not inorganic nutrient limited. Such an energy (carbon) limited system amended with carbon (slash) will increase respiration and immobilization, with a corresponding decrease in net mineralization (Bosatta and Berendse, 1984).

The effects of C/N ratios in residues added to the soil should not be confused with the inhibitory effects of phytotoxic allelochemicals (Lodhi, 1981; Ross and Cairns, 1980) that may also exist in such materials. Other chemical constituents in residues or fertilizers may also affect the

nitrogen mineralization-immobilization process through "priming" (Smith and Douglas, 1971; Westerman and Tucker, 1974). Mineralization of nitrogen in soil is almost always universally increased by the addition of phosphorus (Cornish and Raison, 1977; Ross and Bridger, 1978a; Williams, 1972) and nitrogen as urea (Adams and Attiwill, 1984; Johnson et al., 1980; Popovic, 1977; Williams, 1972). When nitrogen is applied as a salt such as ammonium sulphate, variable results have been found. Williams (1972) indicated a positive effect of ammonium sulphate additions on nitrogen released from Scots pine humus but Flowers and Arnold (1983) found the opposite to be true in an arable clay loam. The ratio of the increase in mineralization (due to N-additions) to immobilization is thought to be soil specific (Maeda and Shiga, 1978).

The quantity of organic nitrogen released to the inorganic pool by application of ammonium and other salts is directly related to the concentration and type of salt solution and the amount of organic-N originally present. Broadbent and Nakashima (1971) found positive results on nitrogen release by ammonium salts and potassium, calcium and aluminum chlorides. Copper sulfate depressed nitrogen mineralization in all cases. Greaves (1916, original not seen) found that salts stimulated ammonifiers but Agarwal et al. (1971b), reporting on the release of nitrogen from soil by a variety of salts, could not find evidence to support this. They did

indicate, however, that potassium sulphate ranked first among sulphates in affecting the release of nitrogen. Ross and Bridger (1978a) also acknowledge enhanced nitrogen mineralization with potassium sulphate additions. Increased salinity in general, however, tends to depress nitrogen mineralization (Laura, 1977).

It is important to realize that the effects of some of these additions may be in changing the N-mineralization rate through physical-chemical and not microbial pathways (Smith and Young, 1984). An example of a physical-chemical effect might be the attraction between positively charged amino acids and negatively charged clay particles. This complex can be extremely resistant to attack from microbial enzymes (Colom and Wolcott, 1967).

The mineralization of nitrogen has been studied in relationship to the mineralization of other elements, most specifically carbon (cf. Bosatta and Berendse, 1984; Bosatta and Staaf, 1982; Ellis, 1974; Freytag and Rausch, 1984; Sinha et al., 1977; Van Schreven, 1967; Winsor and Pollard, 1956) and sulphur (Haque and Walmsley, 1972; Lowe and Hinds, 1983; Maynard et al., 1983; Tabatabai and Al-Khafaji, 1980). At least with respect to sulphur, soil type appears to control which element, sulphur or nitrogen, mineralizes at the faster rate.

Nitrogen mineralization-immobilization is the primary factor controlling nitrogen availability in forest ecosystems

(Keeney, 1980), and many independent studies support various tenets of this concept (cf. Cassmann and Munns, 1980). The possible exception might be those forests with a high component of N-fixing legumes such as Alder (Alnus spp.). Certainly, however, nitrogen mineralization is the principle counter balance to nitrogen losses by leaching in many systems, mineralization almost always being in excess of these losses (Herbauts, 1980 and many others). The desire to quantify soil nitrogen availability has led to a profusion of mineralization models and indices. A variety of chemical extraction and incubation procedures (Castellanos and Pratt, 1981; Fox and Piekielek, 1984; Keeney and Bremner, 1967; Nômmik, 1976; Sahrawat, 1982; Stanford, 1968; Waring and Bremner, 1964a) have been utilized with varying degrees of success to relate "potentially mineralizeable nitrogen" to various soil parameters such as total nitrogen and carbon, carbon release on incubation, pH, temperature, moisture and soil taxonomy (Jones et al., 1982). Stanford and Legg (1968) were able to correlate soil nitrogen availability indices to nitrogen uptake in certain agricultural crops and Powers (1980) was able to correlate mineralizable nitrogen to mean annual increment and foliar nitrogen concentrations in ponderosa pine (Pinus ponderosa L.) stands. He reported that similar correlations were made in European Picea stands by other researchers. Rodenkirchen (1984), for example, found a correlation between nitrogen mineralization and the nitrogen

content in Scots pine needles. Recently, Pastor et al. (1984) found net above-ground production to be strongly correlated with annual nitrogen mineralization for a variety of forest cover types in Wisconsin, and Flanagan and Van Cleve (1983) working in interior Alaska, found a similar correlation between annual foliage production and k, an index of decomposition rate (nitrogen mineralization). It should be pointed out that foliar analysis for N is not always a useful technique for "classifying" sites as to their nitrogen status. Comerford and Fisher (1984), for example, found that volume responses to N-fertilization were as much a function of site quality, stand structure and stand condition as of prior stand nitrogen status.

Nitrogen mineralization models can be classified as either process or ecosystem-type models. The latter will be described in a later section. Most current process-type models tend to build on the classic works of George Stanford and his co-workers (Stanford and Smith, 1972; Stanford et al., 1973a, 1973b; Stanford et al., 1974; Stanford and Epstein, 1974). According to them, cumulative nitrogen mineralized over time follows the first order equation:

$$\log (N_o - N_t) = \log N_o - k/2.303(t) \qquad (1)$$

where N_o = potentially mineralizable nitrogen or N-min potential; N_t = nitrogen mineralized in time, t, and k = the mineralization rate constant. This equation simply states

that the rate of nitrogen mineralization is proportional to the amount of potentially mineralizable substrate. Stanford et al. (1973a) found that k was temperature-dependent and that it doubled for each 10°C upward change in temperature (Q_{10}=2). This nitrogen mineralization potential provides a strong basis for predicting the amount of soil nitrogen mineralized during laboratory incubations and many researchers have utilized such kinetics to model nitrogen mineralization under controlled conditions (Burger and Pritchett, 1984; Campbell et al., 1984; Hendrickson and Robinson, 1984; Herlihy, 1979; Nuske and Richter, 1981; Richter et al., 1980; Sinha et al., 1977). A very broad model of the dependence on temperature by k, the mineralization constant, has emerged (cf. Campbell et al., 1981). These latter investigators also found k to be highly correlated to total soil carbon. The index, kN_o, has also been found to correlate very well with field balance-sheet nitrogen mineralization values (Mary and Remy, 1979). Of particular interest is the fact that Herlihy (1979) found that less than 50% of the potentially mineralizable substrate would become available in a normal temperate (U.K.) growing season, an indication of the strong control exerted on nitrogen mineralization by organic matter "quality".

Many investigators, however, have not been able to apply first-order kinetics to nitrogen mineralization. Addiscott (1983), for example, was forced to use the simple

zero-order relationship, $N_t=kt$, in order to predict nitrogen mineralization. He did, however, find temperature-dependence of k. Molina et al. (1980) openly reject the exponential Stanford model (for the first 12 weeks of incubation), opting for non-linear regression. They indicate that at least two decomposable nitrogenous pools should be considered (see previous discussion). In rebuttal, Stanford et al. (1980) rejected the data manipulations of these authors, but did reiterate that their model generally was not applicable for the first two weeks of incubation, a finding also of Mary and Remy (1979). In support of Molina et al. (1980), however, Smith et al. (1980) and Talpaz et al. (1981) have indicated that non-linear models give more precise and unbiased estimates of N_o and k than the linear models used by Stanford. (The model of Smith at al., 1980 has been recently corrected in the literature by Reynolds and Beauchamp (1984)). Expounding on their earlier ideas, Molina et al. (1983) developed a nitrogen-carbon transformation model (NCSOIL) which utilizes two pools of the active organic phase to mineralize nitrogen. Their work was verified by Jones (1984) and Lindemann and Cardenas (1984). Bosatta (1981b) and Juma and Paul (1981) have also used these type of models with success and Bosatta and Staaf (1982) used a similar approach to describe the nitrogen dynamics of decomposing forest litter of variable C/N ratio. Many other such models

have been re-viewed by Frissel and VanVeen (1982) and Smith (1982).

NITRIFICATION

Nitrification is the two-stage aerobic biochemical process whereby ammonia is oxidized to nitrite (NO_2^-) and then subsequently to nitrate (NO_3^-) (Figure 1). Many chemautotrophic bacteria may mediate these reactions but Nitrosomonas spp. and Nitrobacter spp. are the two most common bacteria in soil associated with the respective step-wise oxidations. The biochemistry of the process is relatively well understood and several excellent reviews are available (Focht and Verstraete, 1977; Schmidt, 1982; Quastel and Scholefield, 1951; Verstraete 1981). Focht and Verstraete (1977) in particular summarize the major nitrification pathways, giving an in-depth listing of the organisms responsible for these at the same time. Melillo (1977) provides a good historical review of early work on nitrification and the primary factors controlling it.

Heterotrophic nitrification has also been shown to exist (Ishaque and Cornfield, 1972; Johnsrud, 1978; Van de Dijk and Troelstra, 1980) although it is generally considered less important than autotrophic nitrification with the exception of truly acid soils, where it has been invoked as the explanation for nitrification in the absence of large autotrophic nitrifier populations (cf. Ishaque and Corn-

field, 1972). The organisms most responsible for heterotrophic nitrification are of the genus Arthrobacter although at least one species of Pseudomonas (aeruginosa: Obatan et al., 1968) has been found to be a heterotrophic nitrifier. The fungi Aspergillus has also been so classified (Focht and Verstraete, 1977). In general, the rate of product formation (ug N/day/g dry cells) is in the range of 12 to 9000 for heterotrophs, but this value may exceed 25,000,000 and 65,000,000 in the two autotrophic genera, Nitrosomonas and Nitrobacter respectively (Focht and Verstraete, 1977), indicating the relative importance of the two processes in many soil systems.

Heterotrophic nitrifiers are apparently sensitive to a different set of environmental controls than their autotrophic counterparts. At least one study (Tate, 1980) found heterotrophs to be directly correlated to soil moisture and populations of aerobic bacteria, relationships that were not evident for autotrophic nitrifier populations. Delwiche (1956) has also indicated that unlike Nitrosomonas and Nitrobacter heterotrophic nitrifiers appear not to be limited by certain chemical compounds such as methionine or ethyl urethane (which is oxidized to nitrate). Focht and Verstraete (1977) hypothesize that the toxic and mutagenic end-products of heterotrophic nitrification (nitrites, hydroxylamines) may be generated to combat or destroy competitors or parasites. On the other hand, one group of end-products (hydroxamic

acids) include a variety of well-known microbial growth factors. Heterotrophic nitrification may also proceed through an organic or inorganic biochemical pathway, in contrast to autotrophic nitrification which proceeds largely in a strictly inorganic fashion. It may also be largely controlled by pH (Ishaque and Cornfield, 1972) or carbon substrate. Indeed, Schmidt (1982) suggests that it proceeds only in substrates with a very narrow C/N ratio (<5). (There is only limited evidence that heterotrophic organisms capable of nitrification in culture can perform the same in the natural environment.) Heterotrophic nitrification, then, might possibly occur in highly acid or alkaline situations with an extremely low C/N ratio. In interior Alaska, the only possible forest ecosystem candidate might be the dry aspen bluffs (alkaline) of south aspect.

Autotrophic nitrification is thus assumed to be the dominant nitrifying process in the areas studied in interior Alaska. The environmental controls on autotrophic nitrification are similar in scope to those on mineralization discussed in the previous section. The temperature range given for both Nitrosomonas and Nitrobacter is 5 to 40°C (Focht and Verstraete, 1977). This range seems to apply even when tropical situations are considered (Bernhard-Reversat, 1980; Myers, 1975), although the latter found a small amount of nitrification at 60°C. Accordingly, Belser (1979) puts the optimum nitrification rate higher at between

35° and 50°C. It would appear that the maximum rate of nitrification is site-dependent and a function of soil climatic adaptation by populations of nitrifiers. Nitrifier populations are enhanced by agricultural tillage practices presumably because of improved temperatures and moisture regimes (Broder et al., 1984). This phenomenon was noted in central Alberta by Malhi and McGill (1982) where the optimum temperature for nitrification was found to be 20°C. Gilmour (1984) found a linear increase in the nitrification rate constant over the range 16 to 28°C. Anderson et al. (1971) also noted that activity of nitrifying bacteria was a function of the metabolic adaptation of the organisms to the climate of origin. Further, Malhi and Nyborg (1979) indicated that nitrification can proceed slowly even at temperatures close to freezing. This may have importance in interior Alaska where cool soil temperatures are often invoked as a control on organic matter mineralization and thus forest productivity (Van Cleve and Dyrness, 1983; and many others). Seasonal periodicity patterns are similar for both nitrification and mineralization (Kovacs, 1978).

The pH range for autotrophic nitrification is from 5.5 to 10 (Focht and Verstraete, 1977) although some authors put the upper range closer to pH 8 (Schmidt, 1982) and the lower range closer to 4.7 (Verstraete, 1981). Generally, a pH below 5 would tend to lead to incomplete oxidation of ammonium, at least in pure culture (cf. Bazin et al., 1982; and

many others). Gilmour (1984), for example, found nitrification to increase linearly over the pH range 4.9 to 7.2. Simulated acid rain studies (pH 3.2 to 4.1) on forest soils also support the view that low pH inhibits nitrification (Klein et al., 1983; Popovic, 1984). Strayer et al. (1981) also hypothesize that acidifying effects would cause a shift in the nitrifying population from autotrophic to heterotrophic, the former being more sensitive to acidification. At high pH (and low cation exchange capacity), NH_4^+ reverts to NH_3 (ammonia) which is toxic to nitrifying populations (Schmidt, 1982). In saline soils, nitrification appears to be more strongly affected by salinity and moisture content than by pH or temperature (Mahasneh et al., 1984).

The effect of moderately high moisture contents in soil (40 to 50% of "full moisture capacity" - term not defined) is to increase nitrification as long as adequate aeration exists (Schmidt, 1982; Slavnina and Pashneva, 1976). This relationship appears to be linear (Tyllova, 1981). Moisture is an important factor controlling nitrification, if only that it governs the gaseous component (O_2 and CO_2) of the soil. Nitrification, being an aerobic process, is limited severely by lack of O_2 caused principally by excessive water occupying soil pores. Oxygen will also be limiting under conditions of high soil moisture content and soil temperature, which tends to reduce its solubility. As well, the presence of readily-oxidized organic matter stimulates heterotrophic micro-organ-

isms, and this in turn will increase O_2 consumption, reducing its availability to the nitrifying population (Schmidt, 1982). An aeration of 15-25% corresponding to a moisture content of 25-35% of full moisture capacity, was found to be optimal for nitrification in certain Russian soils (Slavnina and Pashneva, 1976). "Aeration" (pore space?) and "full moisture capacity" (field capacity?) were not defined. Of the two principal physical factors controlling nitrification, temperature and moisture, the latter may also be the most important. Under anaerobic conditions nitrate will be denitrified to elemental nitrogen. When soil is water-logged and O_2 concentrations are low, for example, very deleterious effects on the nitrifying population occur (Van Schreven and Sieben, 1972). On the other hand, Gilmour (1984) found that below the optimal soil moisture for nitrification, there was a linear decline in the rate as soil moisture decreased.

Another important factor governing nitrification is the availability of the ammonium substrate (Schmidt, 1982). In discussing substrate availability, it should be remembered that even fixed ammonium may become nitrified (Jansson, 1958). In general, ammonium availability is a limiting factor for nitrification although quantities of NH_4^+ above 3000 ug per g of soil will inhibit nitrification (Verstraete, 1981). Furthermore, Strayer et al. (1981), citing unpublished data of Verstraete and Voets, indicated that even 100 ug of NH_4^+ per g of soil could completely inhibit heterotro-

phic nitrification, which is additional evidence for the lack of heterotrophic nitrification in white spruce forest soils in interior Alaska.

Robertson (1982a) attempted to relate pH, C/N ratio and total nitrogen to nitrification. He concluded that these factors, while being important controlling regulators, were not good predictors partially because of the capacity of nitrifiers to adapt to relatively extreme conditions. This adaptation may be rapid. Populations of the nitrifier Nitrosolobus have been shown to double in natural environments in as little as 8 hours (MacDonald, 1979)!

Considering nitrification with depth in the soil profile, many forest floors of mature forest cover types show little nitrification, although some exceptions are noted (Klein et al., 1983). However, the mineral soil often exhibits extensive nitrification and should not be ignored for its ammonium-oxidizing power (Federer, 1983). Nitrification may be inhibited more in the forest floor due to a higher concentration of toxic root exudates and allelochemicals from fine roots in this layer.

Many theoretical (process) models of nitrification in soils have been proposed. McLaren (1969a, 1969b) developed steady-state equations to predict nitrification in soil columns from changes in the available nitrogen pool sizes. He was eventually able to model the kinetics of nitrification in terms of nitrifier population growth (McLaren, 1971).

Seifert (1980) was able to express the temperature dependence of nitrification with a standard Arrhenius equation (c.f. Gilmour, 1984) and the time course of nitrate production (which follows microorganism growth) through the use of the Gompertz function. Duffy and Franklin (1972) have reviewed many of the existing mathematical models of nitrification. They concluded that empirical models of nitrification were of little value in providing insight into physical systems. They suggested that polynomial models based on time, temperature and moisture would be of the most value. Some information on nitrification models in general can be further found in Smith (1982).

NITRIFICATION AND ALLELOPATHY

One of the larger controversies surrounding nitrification today concerns the concept of allelochemical (toxic) inhibition of nitrification by climax vegetation. The cause of the controversy is too complicated to deal with thoroughly here, but since the interpretation of the existing ideas in the literature may have a bearing on the results of this project, a short discussion follows.

Rice (1979, 1984) has reviewed and summarized information on allelopathy and its inhibitory effects on nitrification. Rice, and several co-workers (Lodhi, 1978, 1979, 1982; Rice and Pancholy, 1972) are the principle architects and supporters of the theory that states that climax ecosystems,

through toxic substances released by vegetation, inhibit nitrification. These chemical inhibitors have most often been classed as polyphenolic compounds (Lodhi, 1982) and thiourea analogues (Wood et al., 1981). The toxicity of the latter is due to the presence of a N-C-S group.

Many of the arguments for allelopathic inhibition are based on the relative levels of ammonium and nitrate found in the systems studied (cf. Haines, 1977), the presence of the former and the absence of the latter leading to the coining of the term "ammonium-dominated ecosystem". Other evidence stems from the low levels of both nitrifier populations (Rice and Pancholy, 1972) and the plant enzyme nitrate reductase in climax ecosystems (Smith and Rice, 1983). Nitrate reductase is the first enzyme necessary to reduce nitrate into a plant-useable form (Beevers and Hageman, 1980). One would expect that plants not utilizing nitrate as a nitrogen source would not require high levels of this enzyme.

Much of the work in this camp has been done on western grassland ecosystems. Rice and Pancholy (1972) reported part of their results from the climax tall grass (Sorghastrum mutans - Panicum virgatum) prairie and many others have confirmed the inhibition of nitrification by grass and grass-root extracts (cf. Moore and Waid, 1971; Munro, 1966a, 1966b; Neal, 1969 and many others). However, allelopathic inhibition of nitrification in forest ecosystems has also been documented (Kil and Yim, 1983; Lodhi, 1976; Rice, 1979;

Thibault et al., 1982; Wheeler and Donaldson, 1983).

In the other camp, Vitousek (1977) and Vitousek and Reiners (1975) argue that nitrification rate is a function of ammonium availability and not successional stage. They attribute the high NH_4/NO_3 ratios of Rice and Pancholy (1972) to nitrate uptake rather than inhibition of ammonium oxidation in climax ecosystems. In support of their viewpoint, Purchase (1974) found nitrification in grasslands to be limited by ammonium availability and not by toxic inhibition through root secretions. Robertson (1982b) also found nitrification to be limited by ammonium availability in primary and secondary seres in Indiana and New Jersey respectively. Lamb (1980) and Robertson (1984), working in tropical rainforests, both concluded that nitrification inhibition was not an inevitable result of succession and that ammonium availability controlled nitrification. Conde and Perez (1976) found nitrification to be highly correlated to total soil nitrogen, the substrate for ammonium production and Montes and Christensen (1979) found that enrichment with ammonium stimulated nitrate production in some North Carolina forest soils. Pastor et al. (1984) found both mineralization and nitrification to be highly correlated with humus phosphorus content in Wisconsin, implying a correlation between the two rates. Robertson and Vitousek (1981) found this to be the case in Lake Michigan sand dunes and Adams and Attiwill (1982a) documented the same for some Australian forests.

However, this relationship may be moisture-dependent. Slavnina and Pashneva (1976) found that an increase in moisture content to 80% of full moisture capacity (term not defined) in gray forest soils in Russia resulted in a strong negative correlation between ammonification (high) and nitrification (low). Further, ammonium availability does not always control nitrification in forest ecosystems as shown by the examples of Klein et al. (1983) and Wheeler and Donaldson (1983).

Somewhat in accordance with Smith and Rice (1983), Adams and Attiwill (1982b) found high levels of nitrate reductase in plant tissue associated with high nitrification rates. These rates, however, were associated with mature climax forests. They concluded that the availability of NH_4-N is the primary control on nitrification.

Many studies have indicated that soils from forested ecosystems have consistently higher concentrations of ammonium and lower concentrations of nitrate than those in abandoned pastures or old-field (cf. Vlassak, 1970). Montes and Christensen (1979) also found this to be the case but indicated that nitrification rates may actually be higher in soils from later successional stages. They point out that there is no reason to suggest that nitrogen is less available in more mature stages or that natural selection would favor nutrient conservation adaptations more in one stage than another. The development of mechanisms in climax species,

whether they be plant, shrub or tree, for thriving in ammonium-dominated systems would be "just as advantageous to species in earlier successional ecosystems where mineral nitrogen is limiting". However, this appears to be a blanket statement; the development of NH_4-N nutritional pathways in an early, NO_3-N dominated ecosystem does not really seem to make a lot of sense. In any event, the reader is referred to a good discussion by Haines (1977, p. 301-302) for what could perhaps be called the Rice-Pancholy rebuttal.

Robertson and Vitousek (1981) also echoed these sentiments pointing out that pool size and nitrifier population measurements alone can lead to misleading conclusions. Low nitrate concentrations do not necessarily imply low nitrification rates. For example, if on a certain site plant uptake and/or denitrification and leaching were active processes, such a site could actually have a high rate of nitrification. They also point out that there are several problems with the methods presently used to document nitrifier population numbers and they conclude that nitrification is not progressively inhibited in the course of ecological succession. Robertson and Vitousek (1981) conceded, however, that allelochemical inhibition could be the cause of low nitrification rates in certain sites examined and Vitousek et al. (1982), in pointing out a natural return to ammonium-based nitrification after disturbance, indicated that allelochemical inhibition could reinforce this process.

So where do we stand on this issue? There appears to be an abundance of information that supports both sides of the issue. In all fairness to the anti-Rice group, they have had little choice but to pursue their present line of thought after their rejection of some of the major ecosystem concepts presented by Odum (1969) (cf. Vitousek and Reiners, 1975). They have accumulated substantial information that refutes the inhibition of nitrification by climax vegetation hypothesis. One problem that exists may be the level of refinement that both schools are working at. The anti-allelopathy school has tended to look at the problem from an ecosystem scale; much of the information from the other school, it could be argued, is closer to the molecular level, especially with regard to studying the effects on plant growth of specific polyphenolic molecules. There are also a number of non-microbial nitrogen transformations in soil that are strictly chemical in nature. Manganese-dependent reactions, for example, involving nitrogen have been well documented (Bartlett, 1981). One has to wonder what the relative magnitude of these processes are in soil and what the effects of certain chemicals are upon these processes. Further, with nitrogen being mineralized from more than one organic pool and along several pathways, and the presence of both autotrophic and heterotrophic nitrifiers in certain soil systems, it would appear that the situation, with respect to nitrification, is not as simple as we would like it to be. There is

also the semantical question of climax. It should be expected that grasslands and forestlands, with their different life-forms, will behave at least somewhat differently with respect to nitrogen nutrition regardless of their successional status. This should be especially true at climax.

With respect to nitrate nutrition, this may be the largest obstacle to eventual agreement amongst researchers of the two schools. Haines (1977), for example, believes decreasing nitrate uptake velocities to be an evolutionary consequence of increased nitrification inhibition. Vitousek (1977) and followers, on the other hand, consider nitrate uptake to be an important process in mature forests. Wollum and Davey (1975) indeed indicated that plants will take up whatever nitrogen is available and Ho and Trappe (1980) found that many forest mycorrhizae can take up nitrate. Nadelhoffer et al. (1983), in refuting the Rice-Pancholy hypothesis, also invoked measurable nitrate uptake in forests throughout the growing season. Interestingly, Bormann and Likens (1979) rejected the arguments of Vitousek (1977) that elimination of nitrogen uptake by plants could wholly explain increased NO_3-N concentrations in streams draining harvested forest sites.

The questions become more complex, though, when one considers the senescing canopy of a mature, climax forest. Doley (1982), for example, has hinted that canopy development is closely related to nitrogen cycling in Australian

forests. It is a well known fact that photosynthetic rate declines with leaf age and that nutrient absorption capacity declines with root age (Chapin, 1980). Even in a species like white spruce, which tends to maintain a deep crown, the amount of new needles and fine roots produced annually must obviously decline as maturity is approached. Agren (1983) found nitrogen productivity (annual yield of foliage per unit of nitrogen in the foliage) to increase in some conifer species as needle biomass decreased. This would tend to indicate that nitrogen is very much in demand in older crowns, and that uptake is very important at this stage. Where, then, would the energy for extensive nitrate uptake come from? The question deserves more consideration. There is also the problem of short-term vs. long-term adaptations to NH_4-N or NO_3-N nutrition. No one has yet really worked out the preference in forest tree species.

Robertson (1982a) attributed lack of correlation between certain soil chemical indices and nitrification to present-day field methodology. Perhaps, as Caskey and Tiedje (1979) have urged, the use of N^{15} as a tracer in ecological studies in soil involving nitrogen might be one way in which the relationship between nitrate uptake by plants and nitrification could be evaluated; $N^{15}O_3$-N applications to a variety of successional stages with subsequent analysis for N^{15} in biomass components should be considered. There is also the question of the actual flow of N through both the

NH_4-N and NO_3-N pools. No present method has successfully been able to estimate the N turnover time in these pools due to internal recycling by microbes. Nitrogen may turn over many more times during incubations than is actually estimated. This is a methodological problem that might be solved through the use of N^{15}.

In partial summary, perhaps the best general explanation for nitrification-vegetation inter-relationships was given by Wheeler and Donaldson (1983) who combined hypotheses of earlier workers and Rice and Pancholy (1972). They stated that "nitrification is inhibited by some vegetation and inhibition has a tendency to increase with succession". I tend to agree with them, but would like to point out that many processes work at different rates and in different manners in aggrading and changing ecosystems the world over. Much of the argument to date has dealt with allelopathy. Many other factors in the soil physical and chemical environments and plant growth strategies need to be considered.

NUTRIENT AND NITROGEN CYCLING

The secondary nutrient cycle, as distinguished from the geologically-long global nutrient cycle, allows for the re-use of nitrogen, phosphorus, potassium and other elements by forest trees and associated vegetation on an annual basis and for this reason has been termed the "key to continuous forest production" (Jorgensen et al., 1975). It is not within the

scope of this work to go into a detailed account of nutrient cycling; it suffices to say that many excellent reviews of temperate forest nutrient cycling exist (Brown, 1972; Charley and Richards, 1983; Cole and Rapp, 1981; Krause, 1975; Krause et al., 1978; Ralston, 1978). Savinsky (1981) has provided a good historical perspective on the subject. Many new ideas (and old ones, in a new light) on nutrient cycling concepts have been recently put forth (DeAngelis, 1980; Melillo and Gosz, 1983; Vitousek, 1982). Rekindled interest in the genetic specificity of nutrient cycling by plants, for example, has sparked many recent publications on that topic (Clark, 1983; Popp, 1983; Saric, 1983).

As with most global nutrient cycles, the global nitrogen cycle is well-understood and many reviews exist (Rosswall, 1981, 1983; Soderlund and Rosswall, 1982; Soderlund and Svennson, 1976). At the more specific terrestrial level, Rosswall (1976) has summarized much information for what he calls the "world" ecosystem and Clark and Rosswall (1981) have edited a very comprehensive international workshop on terrestrial nitrogen cycles. Heal et al. (1982) give a very neat synthesis of nitrogen cycling in United Kingdom forests but much of the information contained therein may actually be applicable to many forests world-wide. For example, they point out the importance of the soluble organic nitrogen pool to saprophytic and ectomycorrhizal fungi and thus to trees through nitrogen uptake that does not involve the inorganic

pool. The variable effects on the nitrogen cycle in forests by wildfire have also been documented (cf. MacLean and Wein, 1980; Raison, 1979), but more research is needed on the effects of other natural and man-made disturbances on the nitrogen cycle.

FOREST MANAGEMENT EFFECTS ON NUTRIENT/NITROGEN CYCLING

The effects of forest clearcutting on nutrient cycling have been under investigation for some time now (see previous discussion-introduction). More general principles have emerged than have site-specific solutions (cf. Rapp, 1983). As the methodology for the harvesting of forest trees has swung towards the whole-tree (intensive) concept so has the research emphasis (cf. Boyle et al., 1973; Hornbeck and Kropelin, 1982; Kimmins, 1977; Raison et al., 1982) and several good summaries of the effects of whole-tree harvesting on nutrient cycling are available (Anonymous, 1979a; Lyman, 1982; Mann and West, 1981; West and Mann, 1982; West et al., 1981).

Information on whole-tree harvesting effects in the boreal forest of North America is not as widespread. Weetman and Webber (1972) suggested that shallow low-fertility soils under red spruce (Picea rubens Sarg.) - balsam fir and black spruce stands could support conventional (tops, branches left on site) logging but not full-tree harvesting. The same conclusions were reached by Weetman and Algar (1983) for low-

site class jack pine (Pinus banksiana Lamb.) sites in Quebec, by Timmer et al. (1983) for shallow black spruce sites in Ontario and by Weetman et al. (1979) for low-quality Jack pine sites in Ontario. Gordon (1981) noted that Ontario mixedwood (white spruce-trembling aspen) stands with their higher mineral soil nutrient capitals, could likely support whole-tree harvesting although phosphorus may become limiting after harvesting. Weetman et al. (1979) also predicted phosphorus limitations after harvesting in a spruce-fir stand on good sites. Further, Gordon (1979) showed that phosphorus and potassium could become limiting to seedling growth in even good-site red spruce stands. Freedman et al. (1981) investigated whole-tree harvesting in spruce-fir but failed to make any substantial recommendations. In general, it could be said that phosphorus, potassium and calcium could become limiting to subsequent growth in the succeeding rotation on shallow boreal soils. I should point out that the extent of damage to sites under whole-tree harvesting will depend upon the time of year that harvesting takes place; due to branch-breakage in colder winter temperatures, more slash will be left on the site during winter as compared to summer harvesting operations.

Despite the accumulation of such site-specific information, Morrison and Foster (1979) suggested that present-day knowledge is inadequate to make definitive statements about the effects of intensive harvesting under "medium-

rotation" (25 to 75 years) forestry over much of the boreal forest. It is interesting to note too that Freedman et al. (1982) have pointed out inherent errors in present calculations of nutrient removals due to intensive harvesting. These may be overestimating actual operational removals by large amounts.

The effects of several forest management practices on nitrogen cycling processes specifically have also been evaluated. For example, Sollins et al. (1981) found increased dissolved N concentrations on herbicide-treated plots. It was thought this was mainly due to reduced uptake by vegetation and increased mobilization of nitrogen due to foliage decay. This is supported by Nakos (1980), in Greece, who found that only one of nine forest-use herbicides had any effect on nitrification. (This effect was negative.) Goring and Laskowski (1982) present an excellent review of the effects of individual pesticides on process-level nitrogen transformations in agricultural soils. In addition, Rodenkirchen (1984) found increases in nitrogen mineralization of up to 625% through combinations of fertilization, tillage and underplanting (Lupinus polyphyllus: a perennial legume) in Scots pine. He also found nitrification to be enhanced by fertilization and underplanting. This is consistent with the results of Martikainen (1984) in Finland, who found several N-fertilization treatments to stimulate nitrification. Fumi-

gation also tends to increase mineralization (Shen *et al.*, 1984).

Vitousek (1981) has summarized the effects of clear-cutting on many of the nitrogen cycling processes. Initially, both mineralization and immobilization are enhanced by clearcutting. For example, Glavac and Koenies (1978a, 1978b) working in German spruce forests, found that mineralization was increased by a factor of three. In New Brunswick, Udit (1981) found mineralization of nitrogen to be closely linked to organic matter decomposition, which almost doubled after clear-cutting. Matson and Vitousek (1981) also found that increased mineralization occurred in clearcuts but only after 4 years. Further, using the controlled lab methods of Stanford and Smith (1972), Burger and Pritchett (1984) found that mineralization actually decreased with harvesting and site-preparation. These results were reversed when field conditions were simulated. Increases in mineralization were attributed to increased temperature and moisture regimes.

It would appear that disturbance of any type will generally enhance mineralization. Powlson (1980a), for example, found increased mineralization after normal field cultivation and Williams *et al.* (1979) found that afforestation of bog lands with lodgepole pine (*Pinus contorta* Dougl.) also increased mineralization. Matson and Boone (1984) found nitrogen mineralization rates to have doubled 18 years after a pathogen-induced natural disturbance in mountain hemlock in

Oregon, and Hobbs and Schimel (1984) reported that prescribed burning (in mountain grasslands) increased rates of nitrogen mineralization for up to two years. Most of the increase was attributed to increased soil temperatures.

Matson and Vitousek (1981) also found nitrification to be higher in laboratory incubations of soils from clearcut areas when compared with control soils. They noted that increased moisture and temperature increased rates of nitrification and also attributed increases in nitrification in the soils from clearcut areas to the initial size of the nitrifying population. Populations of nitrifying bacteria have been previously found to be larger in clearcut areas (Smith et al., 1968), possibly due to a better physical environment, an enhanced ammonium substrate, removal of allelochemicals or combinations of these factors.

In Sweden, forest harvesting also results in increased nitrate formation (Nommik, 1982; Popovic, 1974; Tamm, 1982). Losses in these forests will be largely offset by atmospheric deposition (up to 15 kg/ha/yr from new industrial sources!) except where whole-tree utilization is employed. Whole tree harvesting can be expected to decrease nitrogen immobilization (lack of woody residues) and increase the amount of nitrogen mineralized. Vitousek (1981) indicates that, with decreased plant uptake and increased mineralization, there is an excess of nitrogen in the system. Depending upon the nitrification rate, nitrogen will accumulate as ammonium

(slow rate) or will be leached from the system (fast rate). According to Dyck et al. (1983) and Vitousek et al. (1981), fertile sites will have large, rapid, and brief losses of nitrate. Poorer sites will have smaller losses partially due to increased immobilization (Vitousek, 1981) but these will be extended in time. On fertile sites, provision should be made for the rapid immobilization of leached nitrogen by (additions of) litter with a low nitrogen content (Berg and Staaf, 1981).

Nitrate has traditionally been the anion of most interest in watershed studies because it is a limiting mobile form of an element generally limiting to plant growth. It is also a nutrient that can carry important cations with it through the soil. This is a consequence of processes associated with the maintenance of electro-neutrality in soil. Nitrate appears to be very sensitive to disturbance (Vitousek et al., 1981), and many ecosystem studies have utilized it as an index of system stability (Dyck et al., 1983; Krause, 1982; Likens et al., 1969; Sollins and McCorison, 1981; Vitousek and Melillo, 1979; Vitousek et al., 1979, 1982; and many others). Generally speaking, nitrate concentrations in streamflow increase after harvesting in watersheds, presumably due to increased nitrification and reduced plant uptake. The latter is supported by the fact that insect defoliation can enhance nitrate export from forest ecosystems (Swank et al., 1981). Nitrate losses can be decreased through uptake

by regrowing vegetation, nitrification lags, immobilization and a lack of water for transport (Vitousek et al., 1979). The chemical composition of litter types will also tend to affect nitrate losses; those with the most variable composition will tend to reduce nitrogen losses (Berg and Staaf, 1981). Nitrate losses will also be minimal of lower quality sites with inherent low rates of net nitrogen mineralization (Vitousek et al., 1982). In systems where overland flow of water (drainages) is minimal, three major sinks to mineralized nitrogen following forest disturbance are recognized. These are denitrification, leaching losses below the rooting zone and immobilization into two root fractions (fine and woody) (Aber et al., 1983).

I should point out that the watershed concept is not as sensitive as it appears. Nitrate export may be more a function of riparian vegetation than anything else. Deep leaching to levels below the rooting zone may actually be more important. Nutrient cycling studies employing only tension lysimeters, for example, have been successfully conducted (cf. Gessel and Cole, 1965).

Finally, Vitousek (1981) has suggested that process-level studies on the effect of harvesting on the nitrogen cycle would be more beneficial than additional ecosystem-level studies. Nothing could be farther from the truth. As Botkin (1979) declares, "A forest is not characterized by a single deterministic pattern of recovery." What we need now

are site-specific compartment studies that will enable management of forest resources to proceed within the confines of expected nitrogen losses. It is quite evident that the results of ecosystem-level studies cannot be applied universally. What is so special about process-level studies that would make them so?

NITROGEN AND PLANT NUTRITION

In terms of plant growth and development, nitrogen is probably the one element in soils that is most critical and limiting. An excellent compendium of information on general soil nitrogen processes can be found in Stevenson (1982). The subject is too extensive to deal with thoroughly here, but there are several facets which should be discussed. The reader is referred to Kramer and Kozlowski (1979) for a good discussion on nitrogen metabolism and nutrition in forest trees and to Miflin and Lea (1976) for an extensive treatment of the biochemical pathways of nitrogen assimilation in plants.

Dealing first with the question of ammonium versus nitrate nutrition, it should be noted that this subject area has been studied extensively but much controversy remains. Lee and Stewart (1978) indicate that many higher plants exhibit high concentrations of nitrate in roots and shoots. Nitrate accumulates here against the so-called "electrochemical gradient", which tends to indicate active inward

nitrate transport. They also point out that net nitrate and net potassium uptake are highly correlated (presumably because of KNO_3) and that for certain species, the presence of ammonium will inhibit nitrate uptake. This has also been noted by Haynes and Goh (1978) who provide a good general review of ammonium and nitrate nutrition in plants. For a specific example, McFee and Stone (1968) found growth and nitrogen uptake in Picea glauca seedlings to be enhanced by ammonium over nitrate nutrition, regardless of several levels of acidity, root zone temperature or growth media.

Adams and Attiwill (1982b) also studied the growth response of forest species in Australia to ammonium and nitrate sources of nitrogen. They indicated that the preference for particular nitrogen sources by seedlings was supported by related soil properties of mature forests. They concluded that the level of nitrate reductase in root tissues could indicate N-preference but not the ability of the seedling to utilize specific nitrogen sources. Nitrate uptake and nitrate reductase activity (NRA) are almost always universally correlated but Adams and Attiwill (1982b) caution that induced levels of NRA in roots may be more a result of preference for a particular form of nitrogen rather than the cause of a certain form of nitrogen uptake.

Ammonium and nitrate have different energy demands for assimilation into plant constituents (Kirkby, 1981). Middleton and Smith (1979) indicate that, for ryegrass, only

8% more energy is required for nitrate nutrition over ammoniacal nutrition. However, the latter required more oxygen and produced more water. Of the carbohydrate used to convert inorganic nitrogen into an amino acid, a large portion is returned as free energy regardless of which form is utilized.

Based on a study of soil mineralization and nitrification rates in some temperate forest ecosystems, Nadelhoffer et al. (1984) have recently suggested that nitrate uptake by forest trees is more widespread than previously thought. For some species, e.g. sugar maple, they even suggest that nitrate is preferentially taken up even when both nitrate and ammonium are readily available.

From an evolutionary point of view, vegetation at an ecological climax should favour ammoniacal nutrition because of lower energy costs and the better moisture budget associated with the incorporation of nitrogen as ammonium. Reiners (1981) also indicated that nitrification inhibition might be adaptive due to the higher energetic costs associated with nitrate uptake. The question of ammonium versus nitrate uptake is a complex one, though, and more work needs to be done. Plant life-form is definitely a major factor. Many agricultural crops, for example, grow better when supplied with nitrate as opposed to ammonium (Kirkby, 1981); yet many other organisms, such as mycorrhizae on coniferous trees, prefer the latter (Bowen and Smith, 1981).

Another form of nitrogen that is receiving considerable attention is the soluble organic phase, which consists of low molecular weight amino acids and perhaps protein fragments. Reddy (1982) and Sollins and McCorison (1981) showed dissolved organic nitrogen to be an important form of nitrogen movement within ecosystems. Reddy indicated that certain organic soils in Florida can release almost 400 kg/ha/yr of soluble organic nitrogen. Similarly, Van Cleve and White (1980) in an Alaskan white birch ecosystem found the soluble organic pool to be much larger than the inorganic pools, although laboratory incubations for N-mineralization at 20°C tend to show less soluble organic N in the forest floor (Van Cleve (1981; personal communication). Interestingly, across a wide range of C/N ratios in the forest floors from a variety of forest cover types soluble organic nitrogen made up a significant portion of "available" nitrogen at high C/N ratios only (Van Cleve, pers. comm., 1981).

Mori and Nishizawa (1979) and Mori et al. (1979) found that barley (Hordeum vulgare L.) took up certain amino acids preferentially to nitrate and that this resulted in better growth rate. The latter authors cite references dating to 1917 that support organic nitrogen assimilation by higher plants. In addition, Durzan (1983) provides evidence for the utilization of "simple pivotal compounds containing both carbon and nitrogen such as urea" by white spruce seedlings. Bowen and Smith (1981) also indicate that mycorrhizal fungi

can effectively utilize relatively simple organic nitrogen compounds.

TERRESTRIAL NITROGEN CYCLING MODELS

Simulation models of terrestial nitrogen cycling (and components therein) have been proposed for many ecosystems. Van Veen *et al.* (1981) evaluated the major components of some nitrogen cycling models in grassland and agricultural systems. These appear to be the simplest terrestrial systems to model (cf. Risser and Parton, 1982 (ELM grassland model); Tanji and Gupta, 1978). In forest ecosystems, Bosatta (1980) has proposed a model of nitrogen behaviour in soils and Ingestad *et al.* (1981) utilized a simple model to analyze growth and nutrition in a Scots pine ecosystem, based on the nutrient (nitrogen) flux density, or the amount of nutrients available per unit of time and area. MacLean and Wein (1980) used simulation models to look at the effects of wildfire on nitrogen cycling in a jack pine ecosystem; deJong and Klinkhamer (1983) also used simulation to model the effects of burning on nitrogen cycling in heathlands.

At least three extensive models of nitrogen (nutrient) cycling in forest ecosystems exist. FORCYTE (Kimmins and Scoullar, 1979) examines, site-specifically, the effects of intensive forest management practices on nutrient budgets and productivity. Yarie (1983) has modified FORCYTE to model growth and yield in interior Alaskan white spruce forests

with special reference to nitrogen. FORTNITE (Aber and Melillo, 1982a) models organic matter and nitrogen dynamics in the northern hardwood forest and can be used to predict changes in basal area, forest floor biomass, etc. after harvesting. NITCOMP (Rauscher et al., 1983) simulates nitrogen cycling in upland Appalachian hardwood forests and allows the user to predict the harvesting intensity that a given site can support.

THE ALASKA EXPERIENCE

Information is currently available on various silvicultural aspects of harvesting in interior Alaska (Zasada et al., 1977; Zasada and Grigal, 1978; Fox et al., 1984) and new research is currently underway to improve our understanding of forest biology-management interactions. As well, the relationships between site quality, productivity and nutrient cycling have been documented. Estimates for major pool sizes, fluxes, biomass and associated parameters are available for many covertypes (cf. Van Cleve, 1971a; Van Cleve and Alexander, 1981; Van Cleve and Noonan, 1971, 1975; Van Cleve and Sprague, 1971; Van Cleve and Viereck, 1972, 1981; Van Cleve and White, 1980; Van Cleve et al., 1980, 1981, 1983; Yarie and Van Cleve, 1983a).

There is also some information available on soil respiration (Brunberg, 1983; Cowling, 1980; Cowling and MacLean, 1981; Schlentner and Van Cleve, 1985) and decomposition pro-

cesses (Flanagan and Van Cleve, 1983; Fox and Van Cleve, 1983). In terms of specific nitrogen fluxes, Billington (1981) studied nitrogen fixation by moss-epiphyte communities in interior black spruce forests, Weber (1982) and Weber and Van Cleve (1984) have examined the nitrogen dynamics of the forest floor in interior black spruce stands, and Benson (1983) has looked at nitrogen mineralization in soil in white spruce floodplain forests.

However, very little research has been conducted on the effects of commercial timber harvesting and other silvicultural activities upon nutrient cycling in Alaskan forests. Due to the prevalence of the generally colder soil temperatures in interior Alaska, information from temperate latitude forests (cf. Bormann and Likens, 1979) is often not directly applicable. Studies in interior Alaska on silvicultural effects upon nutrient cycling have concentrated on white spruce, birch and aspen cover types. Combinations of fertilization and thinning treatments have been assessed by Van Cleve (1971b, 1973), Van Cleve and Moore (1978) and Van Cleve and Zasada (1976). Recently, Yarie and Van Cleve (1983b) summarized some of the potential effects of short rotation forestry at high latitudes on soil processes. They suggested that the calibration of existing productivity models for interior Alaskan forests would be a good way to assemble the data required to evaluate potential site degradation as a result of short-term rotation forestry.

In terms of modelling efforts, Moorehead (1982) has proposed a model of upland boreal forest succession which will provide an invaluable basis for future management decisions. This model is not yet fully operational. Two forest management-nitrogen cycling models for interior Alaskan white spruce stands have been developed. The more comprehensive one is that of Yarie (1983), although its usefulness over a wide spectrum of operationally harvested sites has not yet been fully demonstrated. The present study developed nitrogen-cycling models for uncut and harvested white spruce sites in the interior. The strength of these models lies in their development around field estimates of N-mineralization and nitrification from bagged-soil experiments. However, due to the linear nature of these models, their predictive power is rather limited.

INCUBATION METHODOLOGY - POLYETHYLENE BAGS

Many methods have been proposed for studying ammonification and nitrification rates in the field *in situ*. The majority of these have attempted to "contain" a small amount of soil, aerobically, without interference by root uptake and leaching (cf. Howard and McNeilly, 1973). Many problems have been encountered using this approach.

Keeney (1980) has discussed the advantages and shortcomings of the aerobic and anaerobic techniques commonly employed in the laboratory and field and indicated the need

for more *in situ* tests. Other researchers have shown that net nitrogen mineralization in the lab is correlated with aerobic production of mineral nitrogen in bagged soil in the field (Campbell and Biederbeck, 1972; Campbell *et al.*, 1974; Eno 1960; Van Praag and Weissen, 1973). It has also been demonstrated that field incubations for mineral nitrogen can be highly correlated to plant uptake of available nitrogen (Bremner, 1965; Gerlach, 1978; Harmsen and Van Schreven, 1955; Runge, 1970; Westermann and Crothers, 1980). However, there has been much concern among researchers over the maintenance of aerobic conditions during incubation of soils enclosed in plastic bags (Bartlett, 1965; Bremner and Douglas, 1971; Eno, 1960; Runge, 1971; Van Schreven, 1968).

Polyethylene bags were first proposed by Eno (1960) as a means of incubating soil sampled *in situ* wherever loss of moisture is undesirable and an aerobic atmosphere must be maintained. The method prevents leaching and plant uptake of available nitrogen that would, under normal conditions, be continually removed or transported. Since the work of Eno, direct research upon the use of polyethylene bags for *in situ* experimentation has been exemplified by the studies of Bartlett (1965) on aeration status of soils and of Runge (1970), Van Schreven (1968) and Westermann and Crothers (1980) on nitrogen mineralization. In addition, Bremner and Douglas (1971) have evaluated the gas and water permeabilities of a variety of thicknesses and types of plastic films.

The results of these studies indicated that there is a strong potential for the use of polyethylene bags in monitoring soil nutrient transformations, aerobically, *in situ*. Accordingly, there has recently been an increase in the use of polyethylene bags for a variety of soils research; at least twenty-five studies on nitrogen mineralization alone have utilized the "bag technique" (Table 2). However, many of those utilizing polyethylene bags (in Table 2) did not report the bag thickness used. Where bag thickness was reported, the range varied from 0.006 mm (Westermann and Crothers, 1980) to 0.1 mm (Federer, 1983). All studies that utilized thin plastic film and reported the thickness of film used, however, lay within the range of films tested by Bremner and Douglas (1971): 0.013 mm to 0.102 mm. While most researchers have opted for bag thicknesses of close to 0.25 mm, or slightly greater, Bremner and Douglas (1971) concluded that polyethylene film having a thickness of 0.13 mm was considerably more permeable to gas exchange than film of 0.25 mm, although the latter had a lower permeability to water vapor. Most importantly, Bremner and Douglas (1971) indicated significant decreases in gas permeability in polyethylene as temperature was lowered.

Table 2. Summary of some studies utilizing polyethylene bags or thin films for soil incubations.

Polyethylene bags		
Purpose	Thickness (mm)	Source
Nitrogen mineralization	d.n.r.[a]	Aber et al., 1983
Nitrification inhibition	0.025	Boswell and Anderson, 1974
Liming studies	d.n.r.	Curtin and Smillie, 1983
Temperature effects on soil-N	0.025	Campbell and Biederbeck, 1972
Temperature effects on soil-N	0.025	Campbell et al., 1973
Temperature effects on soil-N	0.012[b]	Campbell et al., 1974
Nitrogen mineralization	d.n.r.	Ellenberg, 1971
Technique evaluation	0.025[c]	Eno, 1960
Nitrogen mineralization	0.100	Federer, 1983
Nitrogen mineralization	d.n.r.	Gerlach, 1978
Nitrogen mineralization	0.015-0.032	Gordon and Van Cleve, 1983; This study
Nitrification	0.030	Gorlitz and Hecht, 1980
Nitrogen mineralization	d.n.r.	Hobbs and Schimel, 1984
Nitrogen mineralization	d.n.r.	Lamb, 1980
Nitrogen mineralization	0.030	Mahendrappa, 1980
Nitrogen mineralization	d.n.r.	Matson and Boone, 1984
Nitrogen mineralization	0.051	Matson and Vitousek, 1981
Nitrogen mineralization-nitrification	d.n.r.	McClaugherty et al., 1985
Nitrogen mineralization	0.051	Melillo, 1977
Nitrogen mineralization	0.040	Nadelhoffer et al., 1983
Nitrogen mineralization	d.n.r.	Nadelhoffer et al., 1984
Nitrogen mineralization	d.n.r.	Pastor et al., 1984
Nitrogen mineralization	d.n.r.[d]	Popovic, 1971
Nitrogen mineralization	d.n.r.	Popovic, 1980
Nitrogen mineralization	0.030[e]	Rehder, 1982
Nitrification	d.n.r.	Rice and Smith, 1983
Nitrogen mineralization	d.n.r.	Rodenkirchen, 1984
Nitrogen mineralization	0.050	Rosswall and Granhall, 1980
Technique evaluation	0.050	Runge, 1970
Nitrogen mineralization	0.050	Runge, 1971
Nitrogen mineralization	d.n.r.	Runge, 1974a
Nitrification	d.n.r.	Runge, 1974b
Nitrogen mineralization	0.018	Smith et al., 1977
Temperature effects on soil-N	d.n.r.	Thiagalingam and Kanehiro, 1973
Humus-nitrogen interactions	0.030-0.050	Van Praag and Weissen, 1973
Technique evaluation	0.030	Van Schreven, 1968
Nitrogen mineralization	d.n.r.	Virzo de Santo et al., 1982
Nutrient mineralization	d.n.r.	Vitousek, 1977
Nitrogen mineralization	0.006	Westermann and Crothers, 1980
Nitrogen mineralization	d.n.r.	Williams, 1983a

Table 2. Continued.

Polyethylene Films		
Technique evaluation	0.025[c]	Bartlett, 1965
Technique evaluation	0.013-0.102[f]	Bremner and Douglas, 1971
Nitrogen-carbon mineralization	d.n.r.	Ellis, 1974
Nitrogen-sulphur mineralization	d.n.r.[g]	Haque and Walmsley, 1972
Nitrogen-sulphur mineralization	0.038	Lowe and Hinds, 1983
Nitrogen-carbon mineralization	d.n.r.	Popovic, 1984
Technique evaluation	d.n.r.[h]	Rogers et al., 1956
Nitrogen mineralization	d.n.r.	Vallis and Jones, 1973

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[a] d.n.r.: did not report thickness used
[b] Garmil plastic
[c] Kordite, approximate thickness given
[d] incubations in flasks with an attached aeration bag
[e] bags were incubated within another bag
[f] polyethylene, polyamide, polypropylene and others
[g] polyethylene film was singly-holed for aeration
[h] many thin films were tested

STUDY AREA

Most portions of this study were conducted in white spruce habitat. Three intensive sites and one semi-intensive site were selected adjacent to the south-west corner of the Bonanza Creek Experimental Forest (64° 45'N, 148° 15'N), 32.2 km west of Fairbanks, Alaska (Figure 2). The control area is a mature, 133-year-old stand of white spruce, with some white birch and aspen present in the stand as near-dead, over-mature individuals. A minor shrub component of alder (Alnus crispa (Ait.) Pursh.) is present but other tall and low shrub species are non-existent or represent a very small component of the stand. Herbaceous cover is also generally very low, with indigenous mosses comprising virtually all of the ground cover. This moss layer is continuous, consisting principally of the feather-mosses Hylocomium splendens (Hedw.) B.S.G.[a] and Pleurozium schreberi (B.S.G.) Mitt. Hypnum crista-castrensis Hedw. is also present in scattered small patches. Viereck et al. (1983) describe a similar but slightly older white spruce stand in the Experimental Forest, pointing out that it is typical of a commercial (white spruce) stand in interior Alaska.

A harvested area resulting from commercial logging in the winter of 1977 is located immediately adjacent to the

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[a] non-vascular flora follows Cunningham (1972)

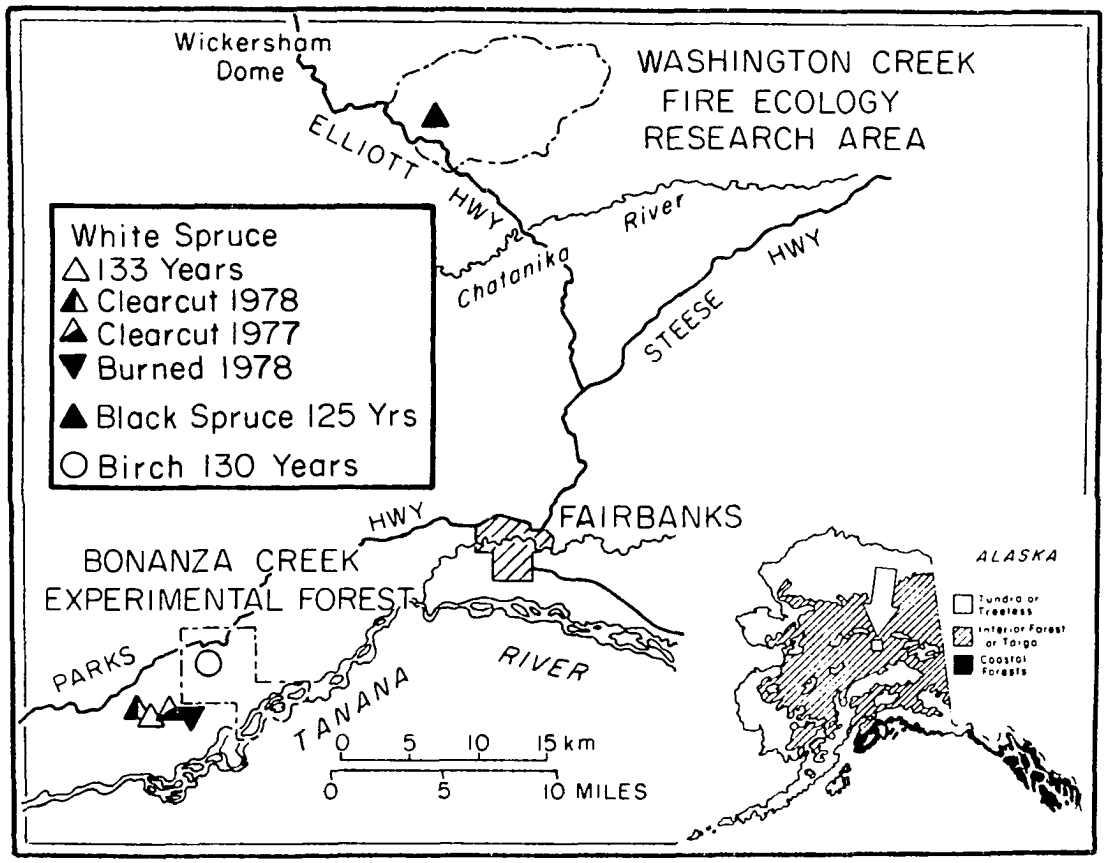
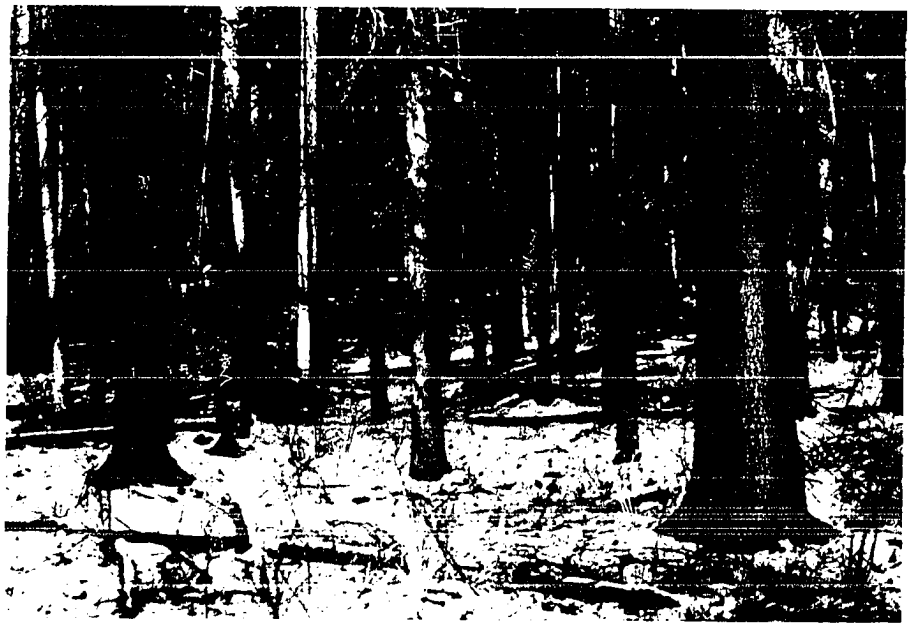


Figure 2. Location of study areas in interior Alaska.

control on the east; a 1978 fall cut lies immediately to the west (Figure 3). The logging method was "conventional" in the sense that chainsaw and skidder were employed. The term, "whole-tree harvesting", where referred to in this report is used to define that type of logging where entire trees, with the exception of stumps, are individually removed from the site by shears and skidders. Part of the decision in choosing clear-cuts was in order that a sequence of "months after clearcutting" could be portrayed; this was done despite the fact that fall and winter harvesting can have different effects on the site in terms of forest floor disturbance, due to excessive branch-breakage in the winter.

Regardless of when logged, the integrity of the forest floor within the clearcut areas was, for the most part, destroyed. This resulted in a layer of mixed organic material, logging slash, fine roots and twigs to a depth of approximately 10 cm (Table 3, Figure 4). Scattered patches of feather moss remain but these are declining in size as the mosses die back from exposure. Some bare patches of mineral soil have been colonized by a fourth moss, Polytrichum juniperum Hedw.

The 1977 cut, due to branch breakage from winter harvesting, had a higher proportion of semi-decomposed, medium-thickness (2-3 cm diameter) branches than did the 1978 cut. At the start of the study, aspen suckers were present in both cuts, but were larger in the 1977 cut. A few aspen seedlings



(a)

(b)

Figure 3. (a) 133-year-old control stand of mature white spruce on upland micaceous loess. Standing crop biomass is about 17,000 g/m^2. (b) adjacent clearcut to the west, cut in 1978. The clearcut depicted is six ha in area, from which about 1700 m^3 of mature white spruce was removed.

Table 3. Selected soil characteristics for the forest floor and mineral soil horizons of the intensive sites.[a]

	133-yr Old White Spruce Control	Clearcut 1977	Clearcut 1978
	Forest Floor		
C/N ratio	27.1[b]	39.2	27.8
pH	5.1	5.4	5.8
organic matter (%)	62.2	63.3	48.7
bulk density (g/cm^3)	0.07	0.17	0.24
depth (cm)	13.9	11.4	8.3
lignin (%)	20.8	24.5	19.6
cellulose (%)	24.2	26.8	21.4
ash (%)	39.3	37.0	46.7
A.D.F.[c] (%)	74.7	79.4	77.7
	Mineral Horizon (<2mm fraction)		
C/N ratio	10.0	11.8	13.0
pH	5.1	5.3	5.2
organic matter (%)	3.3	3.1	3.2
bulk density (g/cm^3)	1.03	1.01	0.91
lignin (%)	1.5	1.3	1.6
cellulose (%)	1.3	1.1	1.5
ash (%)	96.7	97.0	97.0
A.D.F.[c] (%)	85.8	86.4	85.4

[a] See Table 13 for results of chemical analyses.
[b] $S_{\bar{x}}$ < 5% of mean in all cases.
[c] A.D.F. - acid detergent fibre.

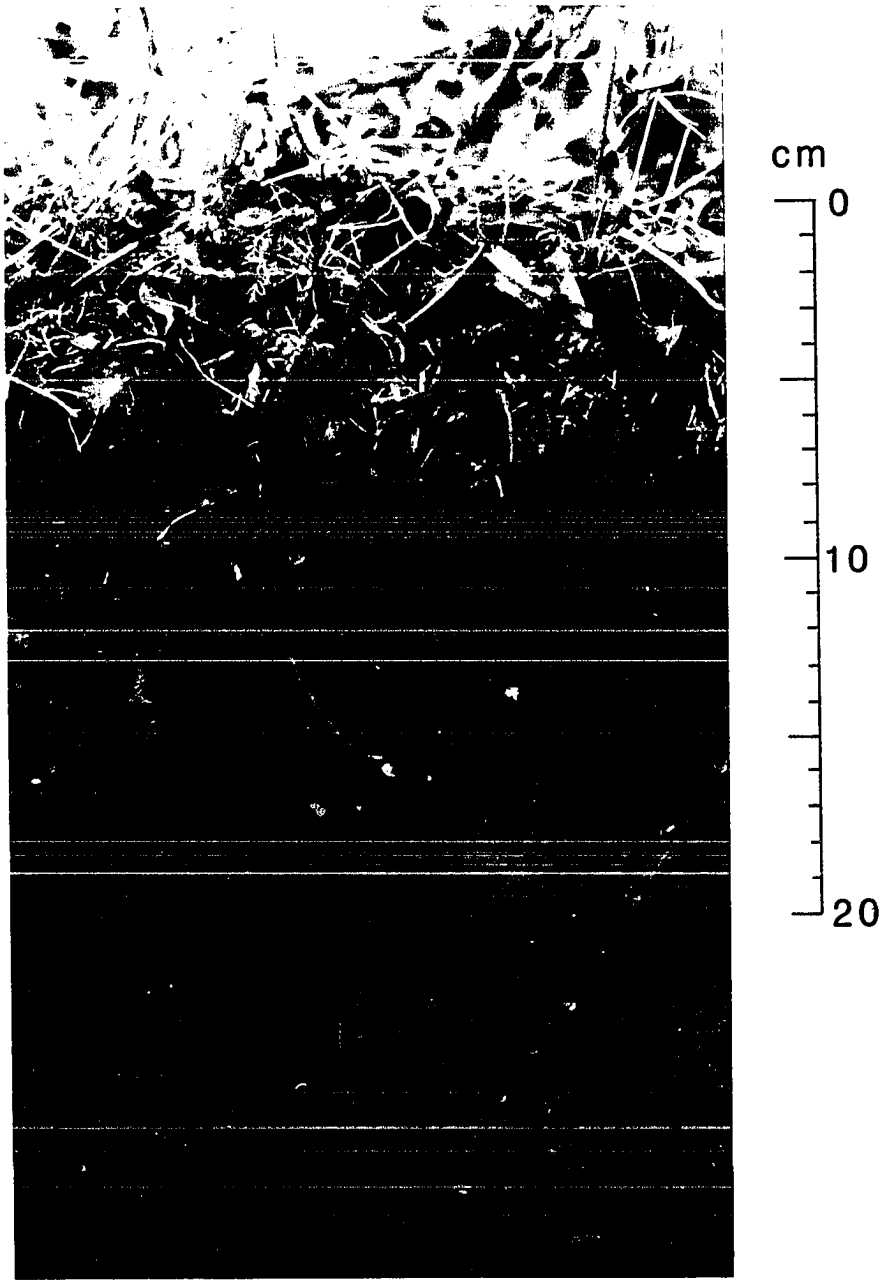


Figure 4. Profile of clearcut area cut in 1977. Note quality and depth of organic matter (∿15 cm). Recent accumulations of herbaceous litterfall give the appearance that the forest floor remains undisturbed.

were present in the 1978 cut. Growth of the suckers over the past 5 years has resulted in several dense clumps of aspen in the older cut to a height of approximately 5 m. Pioneer ground vegetation within both cleared areas was comprised principally of Mertensia paniculata (Ait.) G. Don, Rosa acicularis Lindl., Epilobium angustifolium L., Galium boreale L., Equisetum arvense L., Delphinium glaucum S. Wats., and Calamagrostis canadensis (Michx.) Beauv.

The semi-intensive white spruce site was accidentally burned in the spring of 1978. A small stand (<0.5 ha) of blackened snags was intentionally left for research purposes after a salvage operation to recover burnt timber. Prior to burning, this site was similar in many aspects to the (intensive) control stand. At the time of investigation, burning had left patches of charred forest floor (23%) and thoroughly ashed (to mineral soil) areas (8%). Pioneer vegetation similar to that found in the clearcut areas had rapidly covered almost 70% of the area.

This area of Alaska was unglaciated and lies in the zone of discontinuous permafrost at about 200 m elevation, with gently-sloping southern aspects. The mineral soil (Alfic Chyrochrept) underlying all four sites is a micaceous loess silt (Pewe, 1955) over precambrian schist and gneiss bedrock (Johnson and Hartman, 1971). The loess deposits in the general vicinity of the study sites vary in depth to a maximum of approximately 60 m (Pewe, 1982); on hilltops and

steep slopes depth of loess may be less than 1 m.

Some climatic data for the Bonanza Creek Experimental Forest are given by Barney and Berglund (1973). Generally, the climate of the region is continental, with a growing season limited to about 100 days by late-spring and early-fall frosts. Mean annual air temperature is -3.5°C, and average annual precipitation is 28 cm, the bulk of which falls as rain. Day length fluctuates dramatically from about 3 hours in the dead of winter to over 21 hours in mid-summer.

Two other semi-intensive sites were chosen. A white birch stand about 130 years old is situated at about 350 m elevation within the Bonanza Creek Experimental Forest and a 125-year-old black spruce stand (400 m elev.) is located in the Washington Creek Fire Ecology area (65° 45'N, 147° 55'W) about 50 km northwest of Fairbanks (Figure 2). Productivity and nutrient cycling data for typical stands of white birch, black spruce and white spruce are given by Van Cleve *et al.* (1983). Viereck *et al.* (1983) summarize vegetation and soil characteristics for these same covertypes (Table 4).

It was hoped that sampling of these other covertypes would aid in understanding variation in mineralization rates in natural forests as affected by different temperature and moisture regimes.

Table 4. Selected soils and vegetation characteristics of upland interior forest stands included in this study (modified from Viereck et al., 1983).

	Intensive Site	Semi-Intensive Sites	
	White Spruce	White Birch	Black Spruce
Soil Series	Fairbanks	Gilmore	Saulich
Soil Type[a]	Alfic Cryochrept	Alfic Cryochrept	Histic Pergelic Cryaquept
Drainage	well-drained	well-drained	poorly-drained
Forest Floor Thickness (cm)	14	5	20
Subsoil Texture[b]	silty clay loam	(stony) clayloam	silt loam
Depth to Permafrost (cm)	none	none	40
Maximum Rooting Depth (cm)	100+	45	40
Soil Degree Days	876	1019	700
Principal Species			
Density (no.$\cdot$ha^{-1})	700	500	4700
Basal Area ($m^2 \cdot ha^{-1}$)	55	25	20
Height (m)[c]	25	18	10
Diameter (cm)[c]	30	25	6.5
Age (years)[c]	133	130	125
Site index (m)	28.3[d]	20.7[e]	-

[a] parent material under all is wind-deposited loess
[b] surface texture under all is silt loam
[c] average for stand
[d] 100-year basis
[e] estimated from Gregory and Haack (1965)

MATERIALS AND METHODS

FIELD PROCEDURES

Nitrogen Mineralization

In Situ field incubations utilizing buried polyethylene bags (Eno, 1960; Ellenberg, 1977; Melillo, 1977; and many others) were used to estimate nitrogen mineralization and nitrification. Net fluxes were calculated by before-and-after incubation differences in instantaneous pool sizes for NH_4-N and NO_3-N. In theory, the method prevents leaching and plant uptake of mineral nitrogen but allows for the effects of natural diurnal temperature patterns. At the same time, due to the permeability of polyethylene to CO_2 and O_2, but not to H_2O, aerobic conditions are maintained and moisture is held constant. Some moisture typically builds up on the inside of the plastic as condensation; this was reincorporated into the sample in the lab. Pastor *et al.* (1984) briefly discuss some of the implications of using polyethylene bags, citing Van Schreven (1968; 1968 in text and 1967 in their review; actual citation is 1967) who found that the amount of nitrogen mineralized after one month of incubation under fluctuating moisture conditions (such as those that may occur outside the bag) was equivalent to the amount mineralized under constant moisture conditions (e.g., within bag). It is not evident how Pastor *et al.* (1984) derived this information from Van Schreven (1967), who found

that the mineralization of nitrogen was in fact stimulated by drying. It is also interesting to observe that Van Schreven (1968) actually indicated the amount of nitrogen mineralized in the bags was greater than the amount mineralized outside, due to less favourable moisture conditions outside the bags. Despite this, the method seems to be a good comparative one when different ecological associations physically separated in space are compared.

Within each of the disturbed sites, a preliminary vegetation survey by line-point (150 points in the burned area; 300+ in each of the two clearcuts) revealed the basic ground cover pattern (Table 5). This allowed for the stratification of soil-sampling points within the burned area, and the vegetatively heterogeneous clear-cut areas. In retrospect, a sampling of organic matter depth would also have been useful. For all white spruce sites (3 intensive and 1 semi-intensive) 30 permanent sample points were established. For the 133-year-old control, because of the uniformity of the moss layer and upper horizons, these points were established randomly; for the disturbed sites, these points were stratified by micro-site as described above. For the three intensive sites, sampling was on a monthly basis for August and September, 1979 and from June to September, 1980. The monthly sampling was less than the 6-week incubation of Ellenberg (1971), during which he found no adverse effects of using polyethylene bags on nitrogen mineralization pro-

Table 5. Degree of disturbance and vegetative cover for disturbed study sites at the time of study initiation (% cover).[a]

	Clearcut 1977	Clearcut 1978	Burned 1978
burned	-	-	23
severely burned	-	-	8
disturbed[b]	25	79	-
bare mineral soil	-	8	-
Equisetum arvense	27	-	-
Calamagrostis canadensis	33	-	-
Populus tremuloides	5	-	13
other vegetation[c]	10	13	56
total	100	100	100

[a] see text (Study area) for principal moss species in the uncut stand

[b] intermixed layer of former forest floor, and small to medium logging slash

[c] *Delphinium glaucum*, *Epilobium angustifolium*, *Galium boreale*, *Mertensia paniculata*, *Rosa acicularis*, decomposing or dried *Pleurozium*-*Hylocomium*-*Polytrichum*

cesses. The overwinter periods 1979 to 1980 (approximately 240 days) and 1980 to 1981 (230 days) were also monitored (giving a total of 8 incubation periods). These periods were substantially longer than the monthly incubations but were felt necessary to account for the seasonal flush of nitrogen usually released just after the annual spring thaw. As the overwintering bags were placed in the ground in early October and removed in early May, it should also be noted that they were frozen for a substantial part of the incubation.

The semi-intensive burned white spruce site was monitored into the second (1980) field season but many samples were lost due to a freezer malfunction in the laboratory. The other two semi-intensive sites (black spruce, white birch) were monitored from August 1979 to May 1980. Twenty soil-sampling points were randomly established in each stand. In the black spruce site, 12 sampling points (six in each) were also established in a pair of heated-control plots, previously established by the IBP Taiga Project at the University of Alaska (Anon., 1979b). In that project, heat tapes were run under portions of the black spruce forest, creating "heated" plots where the effects of temperature on productivity and nutrient cycling could be studied.

At the start of each sampling period in the intensive sites, a standard soil core (15 cm diameter) was removed from the vicinity of each sampling point. The mineral horizon was loosely mixed; major root portions and woody debris were

removed. For the forest floor, the 01 horizon was removed (to be later used as a cap for the hole) and the remaining 021 and 022 horizons were mixed in such a way so as to destroy the integrity of each horizon. This procedure has also been used by Gerlach (1973). This resulted in a "relatively homogeneous" mass of organic matter. It is well-known that one of the major effects of sieving or grinding soil samples is to cause an increase in nitrogen mineralization (cf. Gerlach, 1973; Powlson, 1980b; Ross et al., 1979b; Van Praag and Weissen, 1973; Waring and Bremner, 1964b). However, as previously discussed with reference to moisture, the method is a good comparative one when all treatments to the sample are equivalent across areas. In the case of the clearcuts, much disturbance upon logging resulted in mixing of the upper organic horizons to such an extent that identification of individual horizons was impossible. In these cases, mixing of samples upon incubation probably had little effect. In the control area, with its structured horizons, the effect would be more likely to cause parity with the clearcuts rather than divergency, at least in terms of nitrogen mineralization. Differences between the control area and clearcuts could thus theoretically be minimized. This might be accompanied, however, by a corresponding decrease in within-site variability due to mixing.

A subsample of each horizon was taken (from the mixed mass) for initial mineral nitrogen content. The remaining

mixed material was molded into a thin, 1 cm disk, enclosed in either a 0.020 mm or 0.032 mm polyethylene bag (Presto Products, Appleton, WI or Transparent Bag Co., Kirkland, WA respectively) and reinserted into the core hole at the appropriate depth (8-10 cm for forest floor; 20 cm for mineral soils). The thicker bags were used only in the early portions of the 1979 field season: see Discussion.

The core-holes were re-covered and the samples left to incubate under natural temperature fluctuations for the period of interest. Subsamples and, at the end of the incubation period, field samples, were transported to the lab and kept frozen until analyzed. Extraction of soil with KCl in the field and subsequent transport of KCl extracts was not employed because of the recommendations of Ross et al. (1979b). Due to the large number of samples, the storage time in the freezer for some samples was over a year. Arp et al. (1980) and Selmer-Olsen et al. (1971) both indicate that freezing of undried soil samples for variable periods had little effect on ammonium or nitrate content. The storage time of Arp et al. (1980) was 200 days.

The following field procedures were used for the semi-intensive sites. In the burned area, the charred remains of the organic horizons were mixed. Mineral soils were treated as in the intensive sites. In the white birch area, the Ol and 021 (mixed), 022 and mineral horizons were the sample units and in the black spruce the Ol, 021, and 022 horizons

of the organic layer were sampled. Mineral soil at this site was frozen throughout much of the summer and was not sampled. Singular and combined horizons were incubated for the semi-intensive sites in the same manner as the intensive sites. In the black spruce area, the forest floor horizons were well-defined and, instead of mixing each one, a thin strip was cut from the centre of each 1-cm-thick disk for the subsample. the remaining portions were put together as a small, somewhat concentric disk and used for the incubation.

In an attempt to gauge the amount of variability introduced into the study by the sampling technique, several separate experiments were conducted during the 1980 and 1981 field seasons. The area picked for study in 1980 was the oldest clearcut (1977). Preliminary analysis had indicated this site to be the most heterogeneous. In 1981, this experiment was extended to all of the intensive sites. From a variety of sites within each area, 10 soil cores (15 cm diameter) were taken. The organic and mineral horizons were separated, pooled together, and extensively mixed. Fine roots were removed. Ten subsamples were taken and soils were incubated for one month in polyethylene bags as described above. Incubation holes were located within 2 m of each other; this was done to minimize the added effect of micro-site temperature, which may have been a factor had the samples been incubated in their original holes.

Soil Respiration

Soil respiration was measured utilizing the soda-lime (lime (CaO) with 5-20% sodium hydroxide (NaOH)) absorption method of Edwards (1982). In this method, CO_2 released from the forest floor is captured in darkened chambers (to prevent plant or moss photosynthesis) inverted upon the ground. The CO_2 is subsequently absorbed by open pans of soda-lime under the chambers over a measured period of time. The carbon dioxide evolved is calculated as weight-gain of the soda-lime. Schlentner and Van Cleve (1985), working in Alaskan white spruce, and Edwards (1982) have both used the method successfully. Soil respiration estimates in this study follow very closely the methods of Schlentner and Van Cleve (1985).

During the field seasons of 1980 and 1981, the three intensive sites were all monitored for soil respiration on a weekly basis. Ten of the 30 previously established sample points were randomly chosen in each area. At each point, plastic chambers (29 cm X 18 cm X 12 cm high) covered with aluminum foil were inverted over small tin cans (open) containing 30 to 40 g of previously dried (100°C, 24 hours) and weighed soda lime. The chambers were weighted to ensure a tight seal around the bottom edge. The chambers covered a surface area of 522 cm^2 and the cans containing the soda-lime covered approximately 82 cm^2. Thus, 16% of the chamber area was covered with soda lime, meeting the 5% minimum

requirement suggested by Edwards (1982). In the control area, in order to avoid respiration by mosses, the Pleurozium layer was carefully removed and the chambers set down upon the upper 021 horizon. In the clearcut areas, all green plant parts were removed from underneath the chambers. Unlike Schlentner and Van Cleve (1985), soil temperature and moisture content under the chambers were not monitored. Estimates for these parameters were obtained from spot sampling nearby.

After 24 hours, the soda-lime cans were capped, removed to the laboratory, dried at 100°C for 24 hours) and re-weighed. Two blanks per area were employed by using capped cans of soda-lime under two separate chambers. This was to account for minute gains in CO_2 that occurred during oven-drying. This was the only time that the blanks were left uncapped.

Carbon Dioxide Content in Incubating Bags

Several spot-checks of the CO_2 concentrations in field incubating bags were conducted during the summer of 1980. Tekmar No. 625-2 gastight syringes were used to remove 3 ml gas samples from randomly selected bags incubating in both the forest floor and mineral horizons. Sampling was concentrated in the 1977 clearcut area. A portable incubator (Millipore Corporation No. XX63) was used to keep syringes warm in order to eliminate or minimize leakage of syringes while they were in transport to the laboratory for immediate

analysis.

Precipitation

During the 1980 field season, precipitation was measured in all intensive areas and in the semi-intensive burned site. Ten No. 10 cans were placed close to 10 of the previously established soil sampling points in each area. The tops of the cans were covered with heavy-duty aluminum foil (Reynolds Corp.), which was depressed and holed in the centre to allow water to fall into the can. The foil covers helped to prevent evaporation of water collected in the cans. The cans had a surface area of 188 cm^2. Collectors were checked weekly and the volume of rain recorded. Aluminum foil was replaced when required (usually after small animal attack); that week's sample was recorded as missing due to the evaporation that may have occurred. In the control area, collectors were placed randomly around the chosen sampling points so that an even distribution of open-to-sky and close-canopied areas were sampled. In the clearcuts, collectors were randomly located with the exception that low-growing vegetation was not allowed to over-top the cans.

Moisture Content

The calculation of mineral nitrogen content in soil samples on an oven-dry-weight basis requires the determination of moisture content in the sample before analysis. Thus, monthly forest floor and mineral horizon moisture contents for all intensive areas (n=30) and semi-intensive areas

(burn: n=30; black spruce, white birch: n=20) were available. In the 1980 field season, these were supplemented in the intensive areas and the burned area by weekly samplings (n=10) of both horizons. An Oakfield horizon sampler (2 cm diameter) was used.

Air Temperature

Three intensive sites were monitored in 1980 and 1981 for ambient air temperature. The burned site was monitored in 1980 but not 1981. Belfort and Casella recording thermographs (one per area) were used to obtain continuous temperature readings on a weekly basis. The thermographs were placed 1.3 m above the ground inside either U.S. Weather Bureau weather shelters or shelters modified for use by the Forest Soils Laboratory. Maximum and minimum temperatures were recorded each week (Weksler, Science Associates) within the shelter. All thermographs were calibrated in laboratory incubators before placement in the field.

Soil Temperature

Soil temperature was monitored in the intensive sites and the burned area during the 1980 field seaso. Thermistor probes were used in the burned area (cf. Viereck et al., 1983) and soil thermometers (Soiltest, Weston-Schlumberger) were employed in the three intensive sites. Sampling was at the same ten points employed for respiration and moisture content measurement. Only spot weekly values were obtained, but the time of sampling in each area was the same each week.

In support of this method, Van Cleve (pers. comm., 1980) has found good correlations between weekly spot samples of soil temperature and ambient air temperature. Thermistor probes in the burned area were inserted into the charred forest floor, and about 7 cm below the mineral forest floor horizon interface. They were read once weekly using a YSI model 42SL Tele-Thermometer. In the intensive sites, the probe of each thermometer was placed into the forest floor, the temperature was allowed to equilibrate and the value recorded. The thermometer tip was then pushed to the 7 cm mark of the mineral horizon and the procedure repeated. Soil thermometers were calibrated prior to use.

Soil Solution

The export of nutrients in soil solution was monitored in 1981 in the three intensive sites using soil solution samplers constructed by laboratory personnel. PVC pipe (5 cm diameter by 45 cm long) was attached onto ceramic cups (Soil Moisture Equipment Co.; 1-bar (1 bar=100 kpa), high flow, No. 1910, 5 cm X 6 cm). Six samplers were randomly placed in each area so that the center of the ceramic cup lay about 7 cm below the forest floor-mineral soil interface. The chambers were evacuated with a small hand pump equipped with a suction gauge (Soil Moisture Equipment Co.) to a suction of 80 centibars and left for one week. Soil solution was removed, transported to the laboratory and frozen until analyzed.

Miscellaneous

Soils from both forest floor and mineral horizons were sampled from the intensive sites from 1979 through 1982 for total nitrogen and carbon, other major elements, pH, bulk density, dry ashing (for organic matter) and cation exchange capacity.

Vegetation was sampled in 1981 (late summer) for major elemental analysis. Mosses (Pleurozium, Polytrichum, Hylocomium, Hypnum), aspen foliage and twigs and white spruce seedlings (all components) were collected from all of the intensive sites (n=~25). Calamagrostis was absent from this particular stand of white spruce (the control area) and was collected from the clearcuts only. In the control area, current and older foliage and twigs from mature white spruce (n=10) were sampled. Trees were also cored for age and elemental analysis of bole-wood. The number per hectare (by diameter class) of overstory and shrub species in the control area was established by measurement on several 0.04 hectare plots. Basal area was calculated by prism estimate.

LABORATORY PROCEDURES

All samples were replicated at least twice for laboratory analyses. Results are presented on a dry weight basis for all samples excluding soil solution aliquots.

Available Nitrogen - Soils

Ten g of all samples were thawed and immediately extracted for NH_4-N and NO_3-N using 2 N KCl (Bremner, 1965), in

a 7.5:1 ratio (soil:KCl). Extracts were shaken for 1 hour, suction-filtered and analyzed colorimetrically using a modified dual channel Technicon II Autoanalyzer system (Whitledge et al., 1981) with a sensitivity of 0.01 ppm. Ammonium-N was measured on one channel by a variation of Technicon industrial method No. 98-70W. On the second channel, the extracts were passed over a copperized cadmium column, reducing the nitrate to nitrite. Total nitrite was analyzed using a variation of the Griess reaction and Technicon industrial method No. 100-70W. A test for the presence of nitrite in samples proved negative, thus (NO_3-N + NO_2-N) is reported as NO_3-N. Subsamples were taken for percent moisture content and ppm N as NO_3 or NH_4 was converted to a dry weight basis (ug N/100 g dry weight).

During the initial phases of the project, a sample of known nitrogen content (286 mg N as urea per 100 g dry organic matter) from an affiliated experiment (laboratory incubations in polyethylene bags) was run on the auto-analyzer with every set of forest floor samples. Results were consistent and this procedure was discontinued.

The autoanalyzer procedures, especially for nitrate, were modified for efficiency several times during the study. Thus, other methods were employed for mineral nitrogen analysis when auto-analytical procedures were not available. Orion and HNU specific-ion electrodes were occasionally used to analyze 2N KCl extracts for NO_3-N and NH_4-N respectively.

Results from ion-electrode analysis compared favourably with results obtained from the auto-analyzer system, although the nitrate-sensitivity was lower for the electrode than the auto-analyzer. Replicability of analysis by electrode was poorer when water or aluminum sulphate was used as the extractant in place of KCl.

Nitrate was also estimated by difference. Extracts (2N KCl) were analyzed on the auto-analyzer for NH_4-N. Magnesium oxide and Devarda's Alloy were then added to a 50-ml aliquot of these extracts and distilled into boric acid (Bremner, 1965). The distillate (representing NH_4-N + (NO_3-N + NO_2-N) as NH_4-N) was then analyzed for NH_4-N on the auto-analyzer. Nitrate-N was calculated as the difference between preliminary auto-analyzer NH_4-N and distillate NH_4N.

All three methods compared favourably, within expected error. However, the auto-analytical method was preferred for consistency, ease-of-use and speed of analysis.

Available Nitrogen and Phosphorus - Soil Solution

Soil solution was analyzed directly on the autoanalyzer system for available N and P (NH_4^+, NO_3^-, PO_4^{3-}). Results are reported in parts per million. Orthophosphate was determined by its combination with molybdate in acid solution to form molybdophosphoric acid complex which, on reduction, forms a blue colour with an absorption maximum in the 650-700 um region.

Total Nitrogen and Phosphorus - Soils

Air-dried, ground (40-mesh) forest floor samples (100 - 200 mg) were digested in 5 mls of digestion mixture (sulphuric plus selenous acid) for 1.75 hours on a Technicon BD-40 block digester. All samples were digested in the presence of porcelain boiling chips. Two blanks and 1 standard (50 mg, orchard leaves; National Bureau of Standards reference material No. 1571) were employed per set of 40 samples. Samples from separate areas were replicated three times.

The digestions were allowed to cool, diluted to known volume with distilled, de-ionized water, and analyzed for total nitrogen (organic-N + NH_4) and phosphorus on the auto-analyzer system described above. Nitrate-N is not reduced in this process and was not determined here.

Air-dried, sieved (<2 mm fraction) mineral horizon samples (500 mg - 2 g) were analyzed for total nitrogen and phosphorus using macroKjeldahl procedures. Samples were digested for 1.25 hours in large flasks in the presence of boiling chips, 10 g of K_2SO_4, and 20 mls of digestion mix. Boiled, diluted digestions were then analyzed for N and P on the autoanalyzer system. Results are reported on %, dry weight basis.

Total Nitrogen and Phosphorus - Soil Solution

The procedure for soil solution followed that described for forest floor samples above with the following modifica-

tion. Twenty mls of soil solution (or less in cases where solution was in low quantities) was first boiled for an hour in the presence of digestion mix and boiling chips to reduce the volume of water. The remaining solute (now in solution with the digestion mix) was then digested for 1.75 hours and analyzed for total N and P (ppm).

Soluble Organic Nitrogen and Phosphorus - Soil Solution

Soluable organic nitrogen and phosphorus (ppm) were determined indirectly by subtracting the total available concentration in solution from the total element concentration obtained on digestion.

Total Nitrogen and Phosphorus - Plant Materials

The procedure for plant materials follows the total N and P procedure for soils described above with the exception that the sample weight was 50 mg. Plant materials were air-dried and ground (40-mesh). Where a 50-mg sample was impossible to obtain (some seedling root components, for example), the entire sample was digested without grinding. Results are reported on %, dry weight basis.

Cation Exchange Capacity and Exchangeable Bases - Soils

Cation exchange capacity and exchangeable bases (potassium, calcium, magnesium, manganese and iron) were determined on forest floor and mineral soil samples using sequential ammonium acetate (1N) and sodium chloride (10%) extractions as described by Van Cleve and Viereck (1972). Results are reported as meq per 100 g dry weight.

Miscellaneous

Concentrations of potassium, calcium and magnesium were determined by atomic absorption spectrophotometry (Perkin-Elmer 5000) on soil solution samples (ppm), digests of all organic matter samples (%), and exchange capacity extracts of forest floor and mineral soil. The total concentration of these primary cations was not determined for mineral soil. Total carbon (%) was determined on dried soil and plant samples by use of an induction furnace (Leco TC-12) as described by Allison et al. (1965). Organic matter content (%) was determined by dry ashing at 400°C for seven hours (Jackson, 1958) and soil acidity was determined by the saturated paste method using a glass pH electrode (Broadley-James Corporation) coupled to a Radiometer PHM64 pH meter. Carbon dioxide and O_2 concentrations (%) were determined on an A.I.D. No. 512 gas chromatograph as described by Van Cleve et al. (1979). Moisture content was determined on an oven-dry weight basis. Forest floor material was dried at 65°C and mineral soil at 105°C for 48 hours. Bulk density (g/cm^3) was determined by dividing the oven-dry weight of soil cores (forest floor and mineral horizon) by the volume of the core. Finally, % acid detergent fibre, lignin, cellulose and ash were determined at the Agricultural Experiment Station, Palmer, Alaska, using standard methods (U.S. Department of Agriculture, 1970).

Laboratory Incubations in Polyethylene Bags

Forest floor organic matter from the older (1977) harvested site was used in the incubations. The forest floor was chosen as the incubating medium as opposed to the mineral horizon in order to ensure a moderately high level of microbial activity. In late September 1980, a bulk sample of the 021 and 022 horizons was mixed in the field and allowed to air-dry at room temperature in the laboratory. A major portion of both living and dead roots, stems and twigs from vegetation invading the clearcut and *in situ* debris was removed. The remainder was ground in a Wiley mill and passed through a 2 mm mesh screen in order to increase the homogeneity of the material. This was then moistened with distilled, deionized water to 150% moisture content (oven-dry-weight basis; 48 hours at 65°C) which approximated average summer field conditions and ensured that microbial respiration would proceed. The material was allowed to equilibrate for six days in large, loosely-closed plastic bags in an effort to minimize the initial buildup of CO_2. The pH of the material was 5.8, determined by the saturation paste method described above. Fifty g samples of the moistened material were placed in polyethylene bags made from three thicknesses (0.015 mm (Colgate-Palmolive Co., N.Y.), 0.020 mm (Presto Products, Inc., Wi), 0.032 mm (Transparent Bag Co., Wa): 0.6, 0.8, and 1.25 mils respectively) of plastic. After filling the bags, excess air was pressed out and all bags were sealed

to a final size of 12 by 17.5 cm, using a Hamilton Beach Scovill Seal-o-Bag device. Each of the three groups of bag thicknesses were randomly divided into three sub-groups, which were incubated at 5, 15 and 25°C, respectively, in constant temperature incubators (Percival Lab 400). At time zero (3 hours), 1, 2, 3, 7, 14, 21 and 28 days, four replicates of each bag thickness were removed from each incubator and analyzed for % CO_2 and available nitrogen (NH_4-N and NO_3-N + NO_2-N).

Open-air controls consisting of 50 g of the pre-moistened material were spread onto 48 plastic trays, 14 by 14 cm. The original moisture content of the material was maintained by placing the controls on a balance and remoistening with a fine mist sprayer to their original weight on days 1, 2, 3 and every other day of the experiment therafter. Two open-air controls were removed for analysis on each of the eight sampling dates.

Temperature and humidity in each incubator were constantly monitored using Belfort Instrument recording hydrothermographs. The air was humidified to 85% relative humidity by placing a full pan of water directly under the fan inside the top of each unit, which circulated the air freely throughout the incubator. The incubators were calibrated and maintained at 5, 15 or 25°C plus or minus 1.5°C for the duration of the experiment. Aerobic conditions within the incubators were maintained by opening the chamber

doors at least every other day after day three of the experiment. The CO_2 level in each incubator was measured on each sampling date.

Tekmar No. 625-5 gas-tight syringes were used to remove gas samples (3 mls) from within the bagged soil, and CO_2 concentration was determined as described above. To prevent moisture loss, needle holes left in the bags were quickly covered with tape before freezing at -10°C for subsequent nitrogen analyses.

The influence of temperature on the permeability of these bags to water was examined using a variation of the method described by Bremner and Douglas (1971). Twenty-five mls of H_2O were added to each of four replicate petri dishes and covered with 0.015, 0.020, or 0.032 mm plastic bag material. The plastic film was sealed onto the perimeter of each dish using two taut rubber bands. To detect water losses, the 12 dishes were weighed and placed in each incubator. On the eight sampling dates, the dishes were reweighed and water loss calculated by difference.

In order to provide a highly metabolizable source of carbon to stimulate CO_2 production, a separate experiment involving urea additions was conducted on the same material. Nitrogen was added as urea (Baker Chemical Co.) at the rate of 286 mg N per 100 g dry organic matter and the moisture content of the forest floor material was adjusted to approximately 150%. Four replicate 50 g samples of the material

were placed in each thickness of polyethylene bag. The bags were flattened to removed excess air and tied securely with a rubber band. Sets of the bags were then incubated for periods of 1, 2, 3, 5, 8, and 11 days at 25°C on refrigerator racks which ensured adequate circulation of air around the bags. On these sampling days, four bags of each thickness were analyzed for available nitrogen (NH_4-N and NO_3-N). Potassium chloride extracts (2N) were analyzed on HNU and Orion specific-ion electrodes for NH_4-N and NO_3-N, respectively. CO_2 (%) was analyzed on days 1, 3, 5, 8 and 11, and O_2 (%) was measured on days 1, 2 and 3.

NUMERICAL AND STATISTICAL ANALYSES

All data were statistically analyzed using one-and multiple-way analyses of variance, Student's t-test, repeated measures and multiple linear and stepwise regressions. The SPSS (Nie, et al., 1975) and BMDP (Engelman et al., 1977) statistical packages were employed for most statistical analyses. Zar (1974) was used as a technical reference. Soil chemical data were not en-transformed for statistical analyses as some authors have done (cf. Robertson, 1982b). Where non-normally distributed data sets were encountered (eg. some nitrate estimates) or where homogeneity of variances between data sets was not achieved, (eg., soil solution estimates) non-parametric statistics were employed. Superscripts (*,**) indicate eiher statistical significance

at probability level of 0.05 or 0.01 respectively. Lack of significance is indicated by n.s.

Environmental Factors

Volume of rain recorded in gauges in 1980 was converted to cm of precipitation falling per week. Despite my personal experience with intense localized rain shower activities near the study sites, strong linear relationships (r^2=.83** to .87**) were found between precipitation falling on the intensive study sites and precipitation falling at the Fairbanks International Airport, 30 km to the east. These relationships were used to estimate precipitation falling on the intensive study sites during the 1979 and 1981 field seasons. Where it was necessary to estimate soil moisture content, precipitation falling on-site served as a relatively good predictor in some cases (eg., forest floor horizon, clearcut areas). It is interesting to note that, due to variable throughfall in the control area, the moisture content of the forest floor shows little relationship to precipitation (r^2=n.s.). However, once the water is in place, the moisture content of the mineral soil, due to uniform suction and filtering by the contiguous moss cover, can be predicted from the forest floor moisture content (r^2=.69**).

Thermograph charts were read at hourly intervals on a digitizer (Hewlett-Packard Model No. 9864A) supplied by the U.S. Forest Service, and daily means of air temperature were

calculated. Chart recordings were corrected, where necessary, to the maximum and minimum weekly temperatures inside the recording station. Missing data for 1979 was estimated from linear relationships with the average daily temperature at Fairbanks Airport (r^2=.89** to .92**). The spot soil temperatures from both the forest floor and mineral horizon were then compared with the thermograph readings at the exact time the soil temperature was read and for each of the previous three hours. The best regressions were picked and soil temperature data for 1979 and 1981 estimated. For the forest floor, the r^2 values ranged from .85** to .92**, depending upon the study site. The relationship between mineral soil temperature and ambient air temperature was not as good; however, mineral soil and forest floor temperature were significantly related, although the correlations were lower (.48** to .60**). An estimate of mineral soil temperatures for 1979 and 1981 was obtained from this relationship. Degree-days were calculated from temperature data using a base temperature of 0°C.

Soil respiration (g CO_2 evolved/hr/m^2) was calculated by multiplying field estimates by 1.41 to allow for loss upon drying of water produced by the adsorption of CO_2 by soda lime (cf. Schlentner and Van Cleve, 1985). Polynomial regressions were used to relate soil respiration to forest floor or mineral horizon moisture content or temperature. Although the correlations were significant, they were also

relatively weak (Table 6). Recognizing this, some estimates of soil respiration were thus available for parts of the 1979 field season. The GRESP (Bunnel et al., 1977) and BRESP (Schlentner and Van Cleve, 1985) soil respiration models were also used to predict soil respiration from soil temperature and moisture content.

Discriminant analysis on many measured environmental and chemical parameters was used to characterize the study site by the most important environmental factor and by the nutritional status of white spruce seedlings.

Nitrogen Mineralization and Nitrification

Ammonium and nitrate sub-sample and incubated data sets were screened and extreme outliers (usually one or two) that could only be attributable to procedural error or on-site anomalies (inadvertent inclusion of rabbit pellets in samples, for example) were excluded. Analysis for normality before and after this exercise indicated that this procedure normalized many of the data sets.

Concentration (ug/100 g) values were corrected to a unit-area basis (g/m^2) using bulk density estimates from all three intensive study sites. For the forest floor, depth to mineral soil was taken as total depth. For the mineral soil, a 5-cm profile was employed. This is substantially less than the normal depth profiles used by many researchers (eg., depth to bedrock, depth of rooting-zone or a standard 1-m depth). Thus, mineral soil horizon pool sizes of ammonium

Table 6. Multiple regressions of soil respiration on forest floor or mineral horizon temperature and moisture content.

		r^2
	Forest Floor	
133 yr-old White Spruce Control	Respiration = $-1.35 + .30\ (MC/10) - .01(T) - .01(MC/10)^2 + .001(MC/10)\ X\ (T)) + .0002\ (T)^2$	.32**
Clearcut 1977	Respiration = $-.20 + .04(MC/10) + .02(T)$	.48**
Clearcut 1978[a]	Respiration = $-3.19 + 1.09(MC/10) - .57(T) - .10(MC/10)^2 + .08((MC/10)\ X\ (T)) + .01(T)^2 + .003(MC/10)^3 - .002((MC/10)^2\ X\ (T) - .001((MC/10)\ X\ (T)^2) + .00004(T)^3$	.74**
	Mineral Horizon	
133 Yr-old White Spruce Control	Respiration = $-.08 + .02(MC) + .02(T)$	.31**
Clearcut 1977	Respiration = $-.78 + .03(MC) + .05(T)$	.48**
Clearcut 1978	Respiration = $-.22 + .01(MC) + .04(T)$	.55**

[a] High-order polynomials tend to give high r^2 values, but there is generally no biological or ecological basis for the equation's parameters

** significant at $p<.01$

MC soil moisture content (%)

T soil temperature (^oC)

and nitrate may be under-estimated. However, the bags in the mineral horizon were incubated at 5 to 7 cm below the forest floor interface and moreover, included material only from the 0-5 cm depth of mineral soil. Therefore it was not felt justified to extend mineralization or nitrification rates to the entire profile. Although many larger roots extend into the top metre of mineral soil, much absorption of nutrients is by fine roots and root hairs that are concentrated near the top of the mineral profile (cf. Youngberg, 1978).

For both horizons in all three intensive study sites, the nitrification and mineralization rate (on both a concentration and unit-area basis), were step-wise regressed upon a variety of environmental parameters. These include soil respiration, soil moisture content (both inside and outside the bags) soil and air temperature, air degree days and precipitation. The absolute difference in either ammonium or nitrate before and after incubation, and the final amount of ammonium or nitrate accumulated after incubation (cf. Robertson, 1982a), were also used as dependent variables. The best regressions were used to predict nitrogen mineralization rates for the model described in Appendix V. In addition, substrate NH_4-N control on nitrification was tested by regressing incubated NO_3-N values on subsample NH_4-N values for data sets grouped by horizon within the intensive study sites.

I would like to point out the recommendations of Gove et al. (1982). They indicated that regressions should have a minimum of n=16. This study employed only 8 incubation periods and thus these regressions may be suspect and should be used with caution. However, the sampling intensity over time employed in this study allowed for the best opportunity to measure changes in nitrogen production in a generally cold-dominated environment.

Calculations specific to the nitrogen cycling model will be discussed in that section.

RESULTS AND DISCUSSION

LABORATORY INCUBATIONS IN POLYETHYLENE BAGS

Polyethylene bags 0.032 mm thick were used for the first portions of the 1979 field season. Shortly thereafter, the supplier of these bags became unreliable and the decision was made to switch to locally-available bags 0.020 mm thick. This prompted an experiment to ascertain that no effect on nitrogen mineralization or nitrification was being introduced into the study through the use of bags of different thickness. The results and discussion in this section pertain to that experiment.

Regardless of treatment NH_4-N was the predominant form of available nitrogen in the forest floor material sampled. Up to 100 times more N was present in that form compared to NO_3-N. One-way analysis of variance ($p<.05$) indicated that no difference in NH_4 levels existed across treatments at 15°C. At 5°C, differences were noted on days 3 and 28, and at 25°C differences existed on days 2, 21 and 28 (Figure 5). However, no one thickness showed consistently higher or lower levels of NH_4-N. This was also found to be true when levels of nitrate were examined. Although significant differences among bag thicknesses and temperatures were noted for NO_3-N, no consistent pattern across bag thickness was evident in the results.

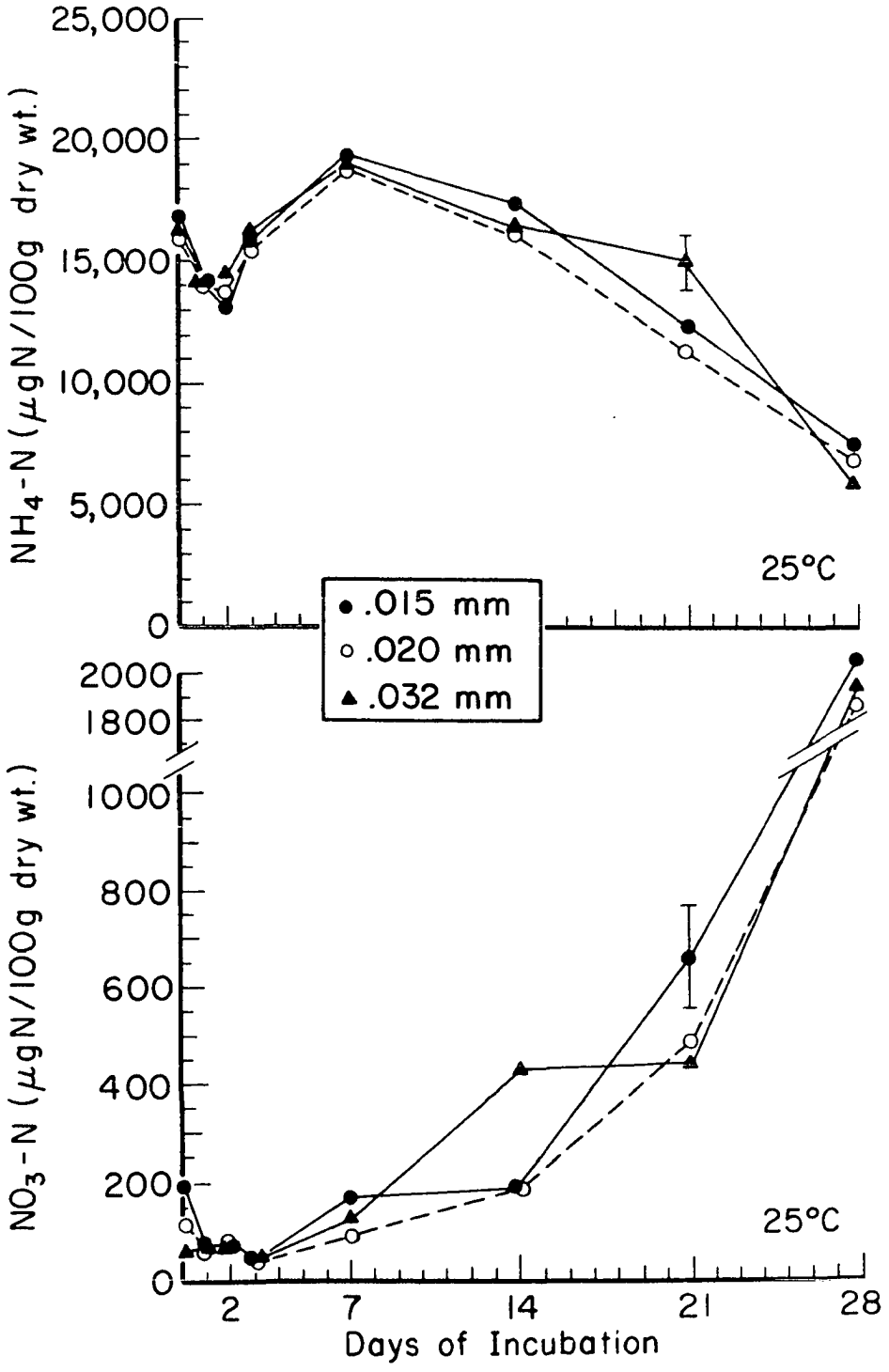


Figure 5. Patterns of nitrogen mineralization and nitrification for three thicknesses of polyethylene bags incubated at 25°C for 28 days. Some typical standard errors are indicated.

The patterns of mineral nitrogen production presented in Table 7 are varied. For all temperatures, net changes in NH_4-N and NO_3-N have been calculated by subtracting time=0 values from time=28 values. In general, the bags behaved identically. Differences in NH_4-N and NO_3-N between day 0 and day 28 were encountered for all bag thicknesses and the open-air controls. At 5°C differences were small but significant, with the 0.020 and 0.032 mm bags showing slight increases in NH_4-N and the 0.015 mm bags showing net immobilization. At 15°C, only the 0.02 mm bag showed a significant increase, but at 25°C, all bags showed a major decline in NH_4-N, a pattern also noted by Kubat *et al.* (1981). This corresponded to a significant rise in NO_3-N presumably due to nitrification for all bags at that temperature (Figure 5). However, the increase in NO_3-N was not large enough to offset the corresponding decrease in NH_4-N. As a result, a net decrease in total available nitrogen occurred. At 5°C, significant increases in NO_3-N were noted for the 0.015 and 0.020 mm bags; at 15°C, the increases in NO_3-N were associated with the 0.020 and 0.032 mm bags. With the exception of the decrease in NH_4-N at 25°C for all bags, no specific temperature effects could be determined. As well the maximum significant production of NH_4-N occurred at 5°C in the 0.020 mm bags (Table 7) and it was thus impossible to calculate a Q_{10} coefficient for ammonium production between 5° and 25°C.

Table 7. Ammonium and NO_3-N at the start and end of incubation for three bag thicknesses, and open-air controls at three temperatures.

Temp (°C)	Thickness (mm)	NH_4-N (ug/100g) Day 0	NH_4-N (ug/100g) Day 28	NH_4-N (ug/100g) Net Change	NO_3-N(ug/100g) Day 0	NO_3-N(ug/100g) Day 28	NO_3-N(ug/100g) Net Change
5°	0.015	16201.72 (64.87)[a]	11883.35 (317.69)	-4318.37**	197.79 (28.22)	1162.81 (133.84)	965.02**
	0.020	16006.91 (265.11)	18632.67 (170.89)	2625.76**	114.56 (0.31)	145.60 (1.09)	31.04**
	0.032	16162.18 (103.95)	17824.21 (137.49)	1662.03**	56.80 (32.79)	142.83 (0.58)	86.03
	none[b]	16123.60 (91.64)	8849.54 (202.95)	-7274.06**	123.05 (21.79)	877.30 (135.41)	754.25
15°	0.015	16201.72 (64.87)	20229.24 (2147.84)	4027.52)	197.79 (28.22)	181.20 (34.98)	-16.59
	0.020	16006.91 (265.11)	18375.94 (285.37)	2369.03**	114.56 (0.31)	144.64 (0.31)	30.08**
	0.032	16162.18 (103.95)	25264.30 (2014.86)	9102.12	56.80 (32.79)	288.99 (2.16)	232.19**
	none	16123.60 (91.64)	8306.76 (81.84)	-7816.84**	123.05 (21.79)	659.92 (34.21)	536.87**
25°	0.015	16201.72 (64.87)	7471.39 (345.13)	-8730.33**	197.95 (28.22)	2064.95 (217.58)	1867.16**
	0.020	16006.91 (265.11)	6891.56 (596.10)	-9115.35**	114.56 (0.31)	1873.85 (137.41)	1759.29**
	0.032	16162.18 (103.95)	5971.72 (159.34)	-10190.46**	56.80 (32.79)	1952.48 (151.78)	1895.68**
	none	16123.60 (91.64)	8303.20 (226.01)	-7820.40**	123.05 (21.79)	1045.80 (155.67)	922.75**

** significant at $p<.01$, Student's t-test

a $S_{\bar{x}}$

b open-air controls

For those bags incubated at 25°C net immobilization of NH_4-N probably occurred during the last 14 days of incubation due to the decomposition of roots and organic remains. Popovic (1980) suggested that the decomposition of fine root hairs during plastic bag incubations contributed to the increase in C/N ratios, and thus immobilization, particularly at higher temperatures. Smaller roots and root hairs low in nitrogen (Keeney, 1980) were not removed during sample preparation, and decomposition of these and other organic materials was probably enhanced by the initial grinding of the organic material (Van Praag and Weissen, 1973). Since the open-air controls also showed a net decrease in NH_4-N (Table 7) it is unlikely that the decrease in the bags incubated at 25°C reflects an effect of the bag itself. Further, since NO_3-N was initially low and CO_2 levels were within the normal range for soils in general (Brady, 1974; Stolzy et al., 1981) denitrification was probably not a significant process contributing to the net loss of mineral nitrogen seen at 25°C. This immobilization phenomenon might represent, however, a shift in microbial populations or species that could result from an extended incubation at a constant 25°C. This is even more likely when one considers that repeated wetting and drying tends to stimulate mineralization (Agarwal et al., 1971a and many others); if anything, the open-air controls should have seen an increase in NH_4-N due to stimulated ammonium production.

As previously mentioned, concurrent with a drop in NH_4-N at 25°C was a marked but much smaller rise in NO_3-N. Similar trends have been previously observed during other incubation studies (Bartlett, 1965; Mitchell, 1981; Ohta and Kumada, 1978). One possible explanation lies in the fact that nitrification can be inhibited by metabolic substances toxic to nitrifiers (Ellis, 1974; Harmsen and Van Schreven, 1955; Van Praag and Weissen, 1973; Rice and Pancholy, 1972). With increasing incubation time, some of these compounds may have been detoxified and decomposed, especially in the absence of living roots and throughfall(Robertson, 1982a), allowing the nitrifiers to flourish late in the incubation.

The incubated open-air controls, regardless of temperature, showed an average 43% drop in NH_4-N between days 1 and 28 of incubation (Table 7). Notably, this severe drop was not seen until after day 21 and corresponded to an average four-fold increase in NO_3-N levels during the same time. Increased rates of nitrification after day 21 did not make up for the losses due to immobilization and resulted in a net loss of mineral nitrogen at all three temperatures. With little exception, patterns of nitrogen mineralization in the open-air controls were similar to the bagged samples regardless of temperature. When one-way analysis of variance was used to test all three bag thicknesses against the open-air controls, no differences were noted for either NH_4-N or NO_3-N on many of the sampling dates, regardless of temperature.

Where differences did exist, these appeared to be random and no pattern was apparent.

Carbon dioxide levels in the 0.020 and 0.032 mm bags over the duration of the experiment are shown in Figure 6. Regardless of bag thickness, the highest apparent levels of CO_2 always occurred in the early days of the experiment, but as explained later, these were not always significantly higher than CO_2 levels at the end of incubation. (High initial CO_2 releases are common during the initial phases of incubation cf. Hendrickson and Robinson, 1984; Heng and Goh, 1984.) After 28 days of incubation, CO_2 levels were in the same range as those normally found in the forest floor horizon in the field where the material was collected (Table 8). At day 28 the 0.015, 0.020 and 0.032 mm bags, respectively,averaged 0.63%, 0.75% and 0.77% CO_2. Although significant differences among bag thicknesses were encountered during the incubation period, no pattern of CO_2 concentration in relation to bag thickness or temperature could be established. In addition, few significant differences in CO_2 (%) existed between day 0 and day 28 (Table 9).

Carbon dioxide accumulation in soil increases when respiration of micro-organisms is stimulated upon rewetting (Agarwal *et al.*, 1971a; Ross and Bridger, 1978a; and others), which is a common practice in incubation experiments where an adjusted soil moisture content is required. Despite an

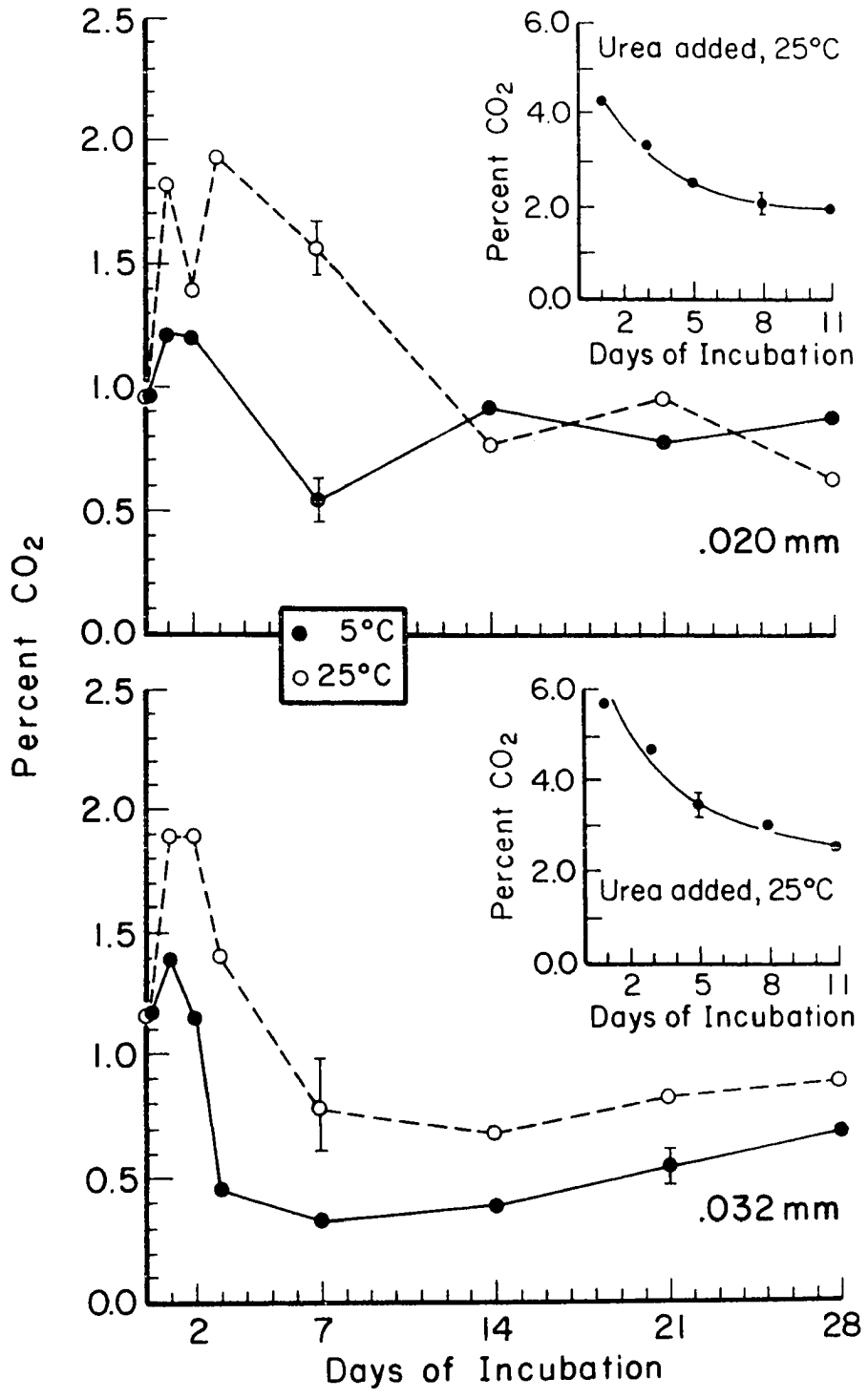


Figure 6. Carbon dioxide (%) levels in 0.020 and 0.032 mm bags incubated at 5°C or 25°C for 28 days. The insets illustrate % CO_2 inside bags (containing urea-amended soil) that were incubated for 11 days at 25°C. Some typical standard errors are indicated.

Table 8. Carbon dioxide (%) from field-incubating bags. Gas samples were taken from the 1977 clearcut in the summer and fall of 1980.

Sample	Horizon	CO_2(%)	n
1	forest floor	0.59	3
2	forest floor	0.20	1
3	forest floor	0.73	1
4	forest floor	0.48	1
5	forest floor	0.23	2
6	forest floor	0.11	1
7	forest floor	0.16	1
8	forest floor	0.09	1
9	mineral	0.24	1
10	mineral	0.15	1
11	ground[a]	0.10	2

[a] needle injected into mineral-forest floor interface

Table 9. Carbon dioxide (%) in polyethylene bags at the start and end of incubation at three temperatures for three bag thicknesses.

Temp (°C)	Thickness (mm)	CO_2 (%) Day 0	Day 28
5	0.015	2.05 (0.24)[a]	0.57** (0.05)
	0.020	0.97 (0.01)	0.86 (0.05)
	0.032	1.16 (0.10)	0.42 (0.16)
15	0.015	2.05 (0.24)	0.68 (0.03)
	0.020	0.97 (0.01)	0.75 (0.13)
	0.032	1.16 (0.10)	0.67 (0.15)
25	0.015	2.05 (0.24)	0.65** (0.04)
	0.020	0.97 (0.01)	0.63** (0.05)
	0.032	1.16 (0.10)	0.89 (0.28)

** significant difference at $p < .05$, Student's t-test

[a] $S_{\bar{x}}$

Table 9. Carbon dioxide (%) in polyethylene bags at the start and end of incubation at three temperatures for three bag thicknesses.

Temp (°C)	Thickness (mm)	CO_2 (%) Day 0	Day 28
5	0.015	2.05 (0.24)[a]	0.57** (0.05)
	0.020	0.97 (0.01)	0.86 (0.05)
	0.032	1.16 (0.10)	0.42 (0.16)
15	0.015	2.05 (0.24)	0.68 (0.03)
	0.020	0.97 (0.01)	0.75 (0.13)
	0.032	1.16 (0.10)	0.67 (0.15)
25	0.015	2.05 (0.24)	0.65** (0.04)
	0.020	0.97 (0.01)	0.63** (0.05)
	0.032	1.16 (0.10)	0.89 (0.28)

** significant difference at $p < .05$, Student's t-test

[a] $S_{\bar{x}}$

attempt to allow the remoistened material to equilibrate before being enclosed in the plastic bags, the results indicated that CO_2 accumulated rapidly in the bags. However, even in the urea-amended system in the present study, diffusion of CO_2 across the plastic resulted in normal levels of CO_2 within the bags by the end of incubation. No relationship appeared to exist between CO_2 level and mineral nitrogen production or immobilization processes.

A three-way analysis of variance, using bag thickness, temperature and time of incubation as the independent variables, was used to examine NH_4-N, NO_3-N and CO_2 patterns over the course of the incubation. When only the main effects model was considered, thickness of bag never made a significant contribution to the % variation in the distribution of NH_4-N, NO_3-N or CO_2. However, significant interactions between independent variables were noted, making thickness significant in four out of five designs. For NH_4-N and NO_3-N the largest two-way interaction was between temperature and incubation time. Multiple linear regressions with NH_4-N, NO_3-N, and CO_2 as the dependent variables regressed upon bag thickness, temperature and incubation time (day), produced statistically significant but not exceptionally strong relationships. Stepwise regressions on the strongest regressions for NH_4-N, NO_3-N and CO_2 indicated that bag thickness was added only as the third independent variable for NH_4-N, was never added for NO_3-N, and was added as the fourth variable

for CO_2. A thickness interaction was added at step 5 for NH_4-N and CO_2, and step 2 for NO_3-N. The increase in r^2 due to the inclusion of thickness or a thickness interaction never exceeded .022, regardless of the dependent variable being regressed.

Water losses through the three plastic films over the 28 days were minimal (Table 10). No significant differences among film thicknesses or sampling period existed. Furthermore, temperature did not appear to affect the permeability of the plastic to H_2O. The moisture content of the soil within the bags also remained constant over the course of the incubation (Table 11).

The results of the incubation with urea are given in Figure 7. The effects of urea additions on nitrogen levels (Figure 8) and CO_2 levels (Figure 6, inset) can be readily seen. Urea is an easily decomposed compound and, as expected, within one day of incubation, levels of NH_4-N noted were higher than those normally found in the forest floor of mature white spruce stands in interior Alaska. The urea was added at the rate of 286 mg N per 100 g dry weight, and by the end of the first day, levels of NH_4-N were approximately 150 mg N per 100 g dry weight (Figure 7). After another day of incubation these levels, regardless of bag thickness, doubled and thereafter declined gradually until the end of the experiment. Conversely, NO_3-N levels rapidly declined during the first two days of incubation from normal levels

Table 10. Weight changes in petri dishes due to water loss through 3 thicknesses of plastic bags at three temperatures.

Temp (°C)	Thickness (mm)	Total Weight (g) Day 0	Day 28	Change[b] (g)
5	0.015	66.61[a]	65.81	.80
	0.020	64.72	63.92	.80
	0.032	63.46	62.48	.98
15	0.015	61.75	60.90	.85
	0.020	63.70	62.97	.73
	0.032	62.50	61.47	1.03
25	0.015	59.77	58.95	.82
	0.020	63.31	61.38	1.93
	0.032	63.52	62.09	1.43

[a] n = 4, $S_{\bar{x}}$ < 5% in all cases.
[b] no significant differences ($p<.05$) between bags or sampling period.

Table 11. Moisture content (%) in bags of three thicknesses incubated at three temperatures for a maximum of 28 days.[a]

Temp (°C)	Thickness (mm)	Days of Incubation 0	1	2	3	7	14	21	28	
5	0.015	138.88[b]	141.23	139.58	136.65	141.50	140.80	138.03	143.98	140.08
	0.020	142.10	141.73	143.50	139.15	142.90	142.68	141.35	144.63	142.26
	0.032	141.85	141.33	141.05	136.60	140.63	141.13	138.68	142.05	140.42
15	0.015	138.88	142.25	145.45	139.03	139.03	142.93	139.18	142.93	141.21
	0.020	142.10	141.53	143.25	141.25	145.15	143.90	142.03	143.73	142.87
	0.032	141.85	140.95	144.80	141.75	141.13	144.65	139.35	143.75	142.28
25	0.015	138.88	142.83	135.68	140.13	141.95	—	144.60	142.03	140.87
	0.020	142.10	142.18	137.43	141.80	144.75	—	145.38	144.48	142.59
	0.032	141.85	143.25	137.95	141.25	145.28	—	145.95	143.65	142.74

[a] $n = 4$, $S_{\bar{x}} < 5\%$ in all cases.
[b] no significant differences ($p<.05$) between bags, at any time, at any temperature.

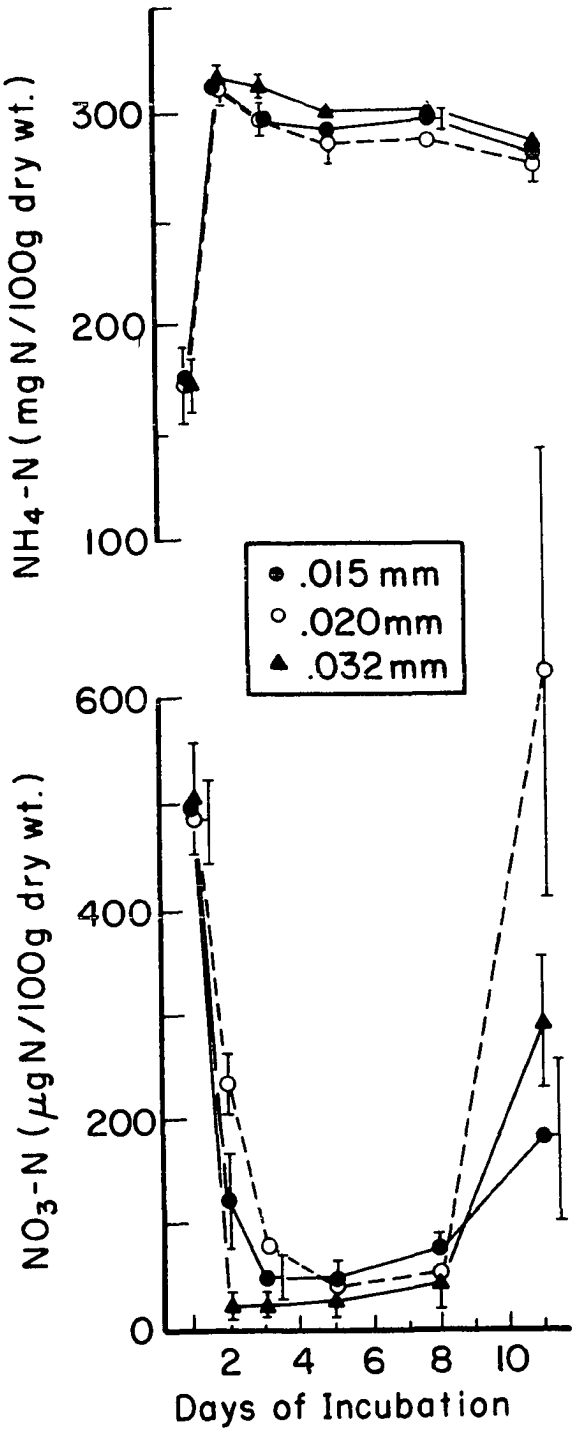


Figure 7. Patterns of nitrogen mineralization and nitrification for three thicknesses of polyethylene bags incubated at 25°C for 11 days. Soil amended with urea. Some typical standard errors are indicated.

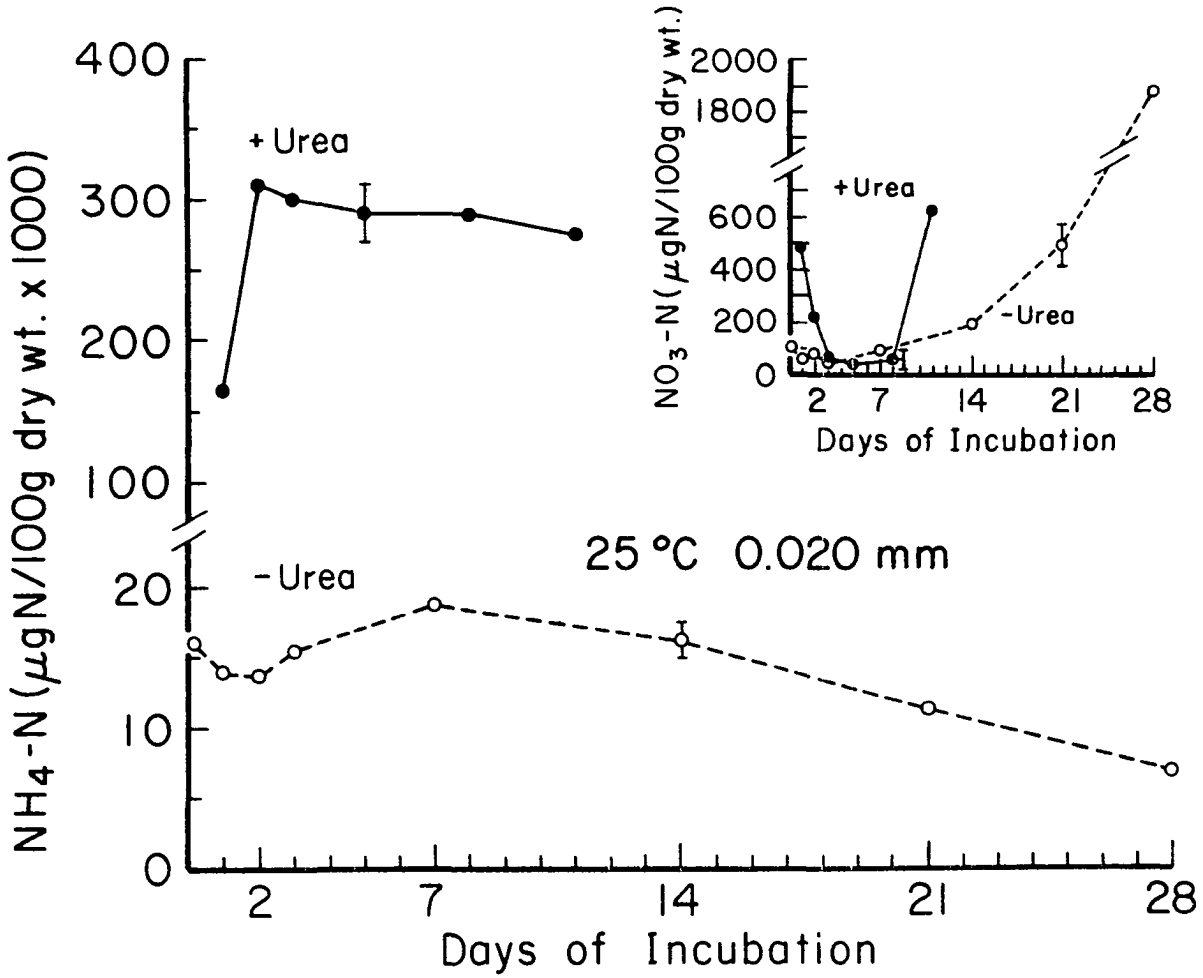


Figure 8. Comparison of nitrogen mineralization and nitrification between non-amended and urea-amended soils incubated in 0.8 mil bags. Some typical standard errors are indicated.

(400-600 ug N per 100 g dry weight) to very low concentrations. These low levels persisted over most of the incubation but had increased again by the 11th day of incubation. However, they were not as great as those encountered in non-amended soil. No significant differences among bags were noted for NH_4-N or NO_3-N on any sampling day.

Initial levels of CO_2 for 0.020 and 0.032 mm bags were 4.41% and 5.88% respectively (Figure 6, inset). For these bags, CO_2 levels were much greater than those reported for field or non-urea amended soils. Despite the indicated decline in CO_2 (%) there was no significant difference between day 1 and day 11 levels, regardless of bag thickness. No statistical difference existed among bags on any one sampling date. Initial levels of O_2 on day 1 were 18% for all bag thicknesses. Thereafter, O_2 levels declined by day 3 to 10.0%, 15.68% and 7.23% for the 0.015, 0.020 and 0.032 mm bags, respectively.

When urea is applied to a forest soil, rapid gains in ammonium and a corresponding rise in pH are evident (Marshall and Debell, 1980). For example, Broadbent et al. (1958) reported gains of up to 400 ppm NH_4-N within one week at 10°C. In the case of the data presented in Figure 7, almost 150 mg NH_4-N per 100 g dry weight became available during the second day of incubation. Levels thereafter were approximately 300 mg N per 100 g dry weight, indicating a full recovery of added urea. Initial levels of NH_4-N were 14 to

15 mg N per 100 g dry weight (Figure 8). This allows for the possibility that levels of NH_4-N reached by day 2 were due solely to urea hydrolysis and not to stimulation of protein mineralization.

The rapid decrease of NO_3-N in the untreated soil within the first days of incubation (Figure 7) might appear to be a result of denitrification given the initial high levels of CO_2 (Figure 6, inset). Despite this, as previously discussed, denitrification or even conversion of NO_3-N to NH_4-N (Buresh and Patrick, 1978) is unlikely. The drop is probably the result of NO_3-N utilization (Fewson and Nicholas, 1961) indicating a high level of heterotrophic microbial activity. These results may be compared to those of Mitchell (1981) also working in Alaska, who incubated soil amended with a lower level of urea and reported short-term increases in NH_4-N followed by a severe decline. Corresponding rises in NO_3-N due to nitrification were also reported.

The main purpose in adding urea was to provide a readily metabolized source of nitrogen and carbon in order to evaluate the impact of increased CO_2 levels in the bag on nitrogen mineralization and oxidation under optimum conditions of temperature and moisture. Of concern also was the effect of bag thickness on nitrogen mineralization patterns that might result under a strong fertilization regime characteristic of an intensive forest management or agricultural situation. Any differences existing between bags might be

accentuated at high levels of fertilization. However, as in the non-amended experiment, bag thickness was not important in determining the pattern of mineral nitrogen production. It is important to note that in the urea-amended situation, with high CO_2 production, O_2 levels remained greater than 7% even when CO_2 levels were highest. Stolzy et al. (1981) and Amoore (1961) indicated that mere traces of O_2 (.001%) were adequate to allow certain soil processes to continue. It is unlikely then that in non-urea amended situations O_2 will be depleted to inhibitory levels through the use of polyethylene bags, although the interior of soil aggregates may remain anaerobic. However, Stolzy et al. (1981) also cautioned that O_2 diffusion rather than concentration may become a limiting factor. They also pointed out that O_2 concentrations are indirect measurements of soil aeration (as opposed to redox techniques) that require a large number of samples over time in order to quantify soil aeration status in the range where denitrification may occur.

Denitrification can occur during certain conditions of warm temperature, neutral pH and lower O_2 availability in soils (Keeney, 1980), but may be limited by lack of substrate, i.e., NO_3-N (Dommergues et al., 1978). However, even in the urea-amended soils, where initial NO_3 levels rapidly dropped, and the highest CO_2 levels were found, it is unlikely that conditions for denitrification were present. Stolzy et al. (1981) have indicated that levels of CO_2 in excess of

4% in soil air are actually fairly typical. Further, after three days, the O_2 levels in the urea-amended soils in the 0.020 mm bag were still at 16%, indicating at least a partially oxygenated environment. Finally, the moisture content of the soil was low enough that anaerobiosis due to waterlogging was highly unlikely.

The hypothesis tested here was that thickness of polyethylene bags, within the range employed in this study (0.020 to 0.032 mm) is relatively unimportant as a factor affecting nitrogen mineralization, when compared to other factors such as temperature and length of incubation. The specific objectives were to evaluate the effect of bag thickness on CO_2 permeability, nitrogen mineralization and nitrification, and to evaluate the effect of temperature on bag permeability to H_2O and CO_2.

The results indicate that thickness of plastic bags over the tested range of 0.015 to 0.032 mm is not an important factor in determining mineral nitrogen production or nitrification, when compared to other factors such as temperature and length of incubation. These latter factors were more important, but in this study it was not possible to show conclusively how these factors affected nitrogen mineralization or nitrification. Regardless of thickness, the bags were permeable to CO_2 and O_2 but not to H_2O. The range of temperatures employed did not affect the permeability of bags to either H_2O or CO_2. The urea-amendment treatment

provided an easily metabolized source of carbon to stimulate CO_2 production and indicated that, even under circumstances of high CO_2 evolution, the bags remained well oxygenated. It would appear then that the use of plastic bags of 0.015 to 0.032 mm thickness is adequate for certain laboratory and *in situ* measurements of mineral nitrogen production and nitrification.

INTENSIVE SITE CHARACTERISTICS

Environmental Factors

Environmental factors thought to be the primary controls on nitrogen mineralization processes are summarized in Table 12. A number of these factors were regressed upon field nitrogen mineralization and nitrification estimates; these relationships will be discussed later. When these 10 variables, in addition to 4 estimates of nitrogen mineralization (daily rate on a concentration and area basis, absolute periodic difference, final accumulated amount) were simultaneously subjected to discriminant analysis, the study areas separated nicely on the basis of mineral soil moisture content (Figure 9). The classification was 75% correct, but all of the error was between the two clearcut areas; the separation of the control area from the clearcut areas was very distinct and significant. The canonical variables in this case are linear functions of mineral horizon moisture content

Table 12. Measured environmental characteristics of the three intensive study sites for the duration of the field-sampling period.[a]

		Temperature (°C) Soil Mineral	Soil Organic	Ambient	Moisture Content (%) within bags Mineral	within bags Organic	outside bags Mineral	outside bags Organic	Respiration ($g/m^2/hr$)	Degree Days[b]	Precipitation (cm)
	Cut 1978	11.4	19.5	16.2	29.2	100.9	29.2	155.1	.5675	503.5	2.6
August 1979	Cut 1977	9.1	20.8	14.6	29.3	106.6	31.0	157.2	.6053	452.0	2.5
	Control	9.1	15.4	15.1	15.6	98.8	17.1	121.4	.5378	468.8	1.6
	Cut 1978	8.2	10.3	7.6	32.1	105.1	32.1	105.5	.4176	236.9	0.4
September 1979	Cut 1977	6.4	12.3	7.4	31.0	139.6	29.3	123.9	.4202	220.9	0.4
	Control	6.8	7.9	7.2	20.8	90.1	12.7	88.4	.3767	214.8	0.3
	Cut 1978	0.5	-12.4	-13.6	30.9	132.7	30.9	118.2	.0891	205.2	1.0
Overwinter 79-80	Cut 1977	-0.6	-9.5	-11.2	30.4	154.2	29.8	132.4	.0831	194.2	0.9
	Control	0.9	-11.9	-13.4	16.7	94.3	13.9	96.9	.1564	184.4	0.6
	Cut 1978	8.1	16.8	13.6	37.2	82.5	37.2	193.7	.6712	408.6	4.3
June 1980	Cut 1977	6.2	15.0	11.4	41.5	103.8	33.0	197.1	.5203	340.6	5.0
	Control	6.1	14.2	13.0	19.8	46.2	21.7	161.0	.6081	391.0	3.0
	Cut 1978	12.5	21.5	17.5	33.4	112.2	33.4	260.7	.8602	542.2	7.2
July 1980	Cut 1977	10.0	21.4	14.0	34.1	93.4	34.6	229.2	.7583	434.2	6.9
	Control	9.1	16.8	15.7	21.8	72.4	25.4	192.7	.7073	486.7	4.1
	Cut 1978	12.0	16.3	13.2	32.2	112.3	26.2	138.4	.6342	409.2	4.3
August 1980	Cut 1977	11.1	14.3	11.3	32.6	124.7	28.7	145.8	.6635	349.4	3.8
	Control	9.2	11.8	12.2	25.1	107.1	14.0	104.6	.5094	377.0	1.6
	Cut 1978	5.9	7.2	4.4	29.5	106.2	30.6	148.8	.4362	131.2	3.5
September 1980	Cut 1977	4.7	8.0	5.3	31.7	179.1	33.0	161.5	.4619	160.1	3.3
	Control	4.8	5.5	5.2	17.2	91.2	13.1	142.5	.4247	154.6	1.3
	Cut 1978	0.5	-12.4	-13.6	32.6	129.6	32.6	150.8	.1457	205.2	2.4
Overwinter 80-81	Cut 1977	-0.6	-9.5	-11.2	83.0	162.0	30.9	154.3	.1158	194.4	2.3
	Control	0.9	-11.9	-13.4	19.0	102.9	16.7	118.6	.2029	184.4	1.4

[a] $S_{\bar{x}} < 5\%$ in almost all cases.
[b] base 0°C

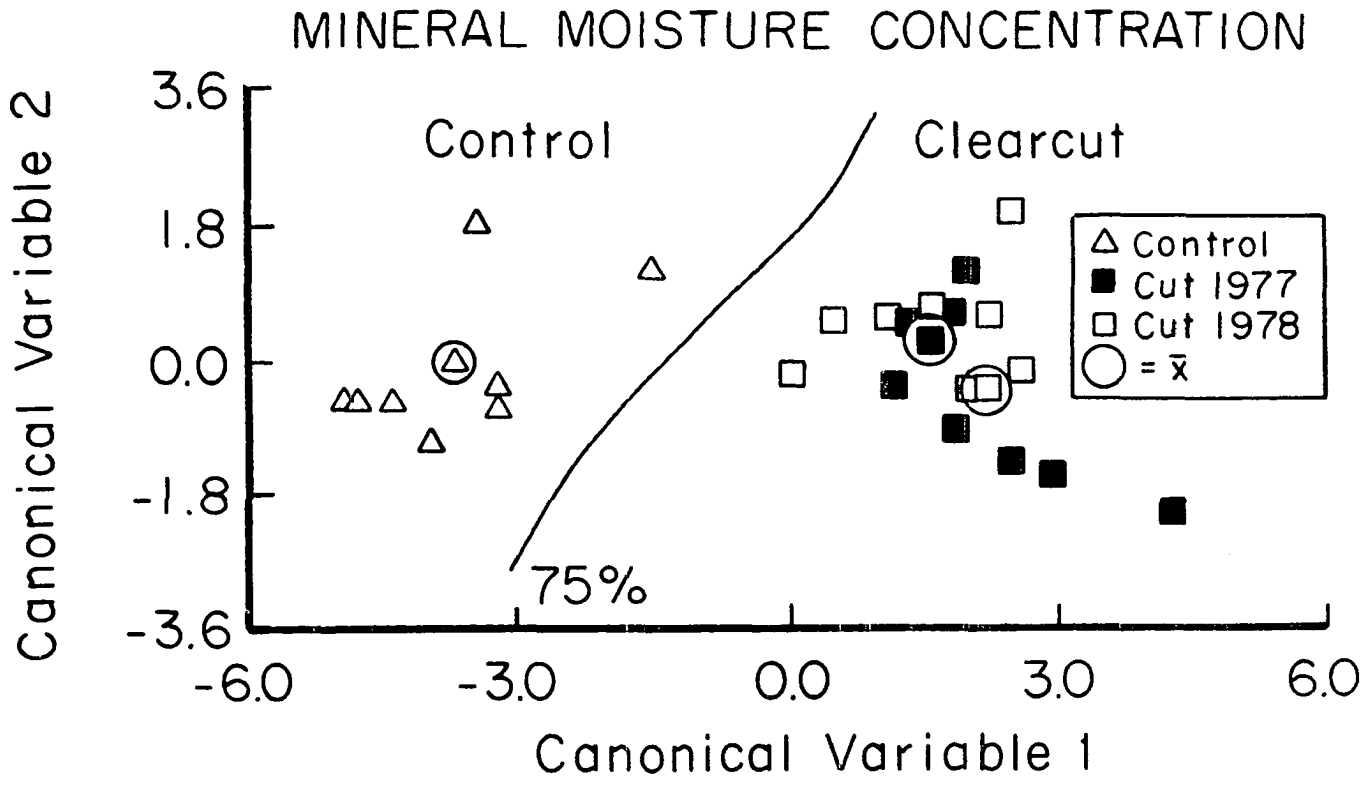


Figure 9. Discriminant analysis of intensive study sites based on mineral soil moisture content.

both within and outside the bags. Both variables were significant at $p<.01$.

The fact that moisture content proved to be a better discriminating value than any of the nitrogen mineralization estimates simply indicates that some physical characteristics were more dissimilar between sites than nitrogen mineralization estimates. This preliminary evidence tends to indicate that nitrogen mineralization does not vary greatly (or as much as other factors) between the sites.

When the analysis was performed on just the environmental variables, the same pattern of separation appeared (79% correct) based on differences in mineral and forest floor moisture content and precipitation reaching the ground. Error in classification was again between the clearcut areas, which grouped as a distinct entity apart from the control area. Generally, timber harvesting resulted in higher soil moisture contents in both the forest floor and mineral soil, presumably due to a lack of transpiration in the clearcuts, although, as expected, precipitation reaching the forest floor was higher in the cleared areas due to lack of canopy interception. Harvesting also caused an increase in forest floor temperatures, but the effects on ambient air and mineral soil temperatures were variable and dependent upon time within season.

Soil Chemical Factors

Selected chemical properties of the forest floor and mineral soil horizon are presented in Table 13. Generally, only minute differences existed between areas; many of these were non-significant. This implies that either the laboratory analysis was not sensitive enough or that the mobility of many elements in interior Alaska forest ecosystems (soils) is not strongly affected by clearcutting processes, at least under the less than moderate precipitation regime found in interior Alaska.

Some anomalies can be noted. As will be discussed later, potassium exports from the control area in soil solution were much higher than potassium losses in the clearcut areas. Under this pattern, we might expect either a very large pool of potassium in the forest floor of the control to "feed" the export, or a very small K pool, reflecting large losses. Neither scenario presents itself; neither total nor exchangeable potassium in the forest floor exhibit any real trends when compared across areas. This is also the case when potassium concentration of white spruce seedling current foliage is considered: seedlings from the control area were intermediate in potassium levels when compared to seedlings from the two clearcut areas.

On the other hand, the cation exchange capacity in the forest floor is slightly higher in the control area than in the clearcut areas ($p<.05$). This may reflect the

Table 13. Selected chemical characteristics of the forest floor and mineral soil horizons of the intensive sites.[a,b]

	133-yr Old White Spruce Control	Clearcut 1977	Clearcut 1978
	Forest Floor		
C.E.C.[c] (meq/100g)	50.4	46.5	41.4
Exchangeable bases (meq/100g)			
K	1.2	1.5	1.0
Ca	25.6	31.6	35.7
Mg	5.7	6.7	7.2
Fe	0.08	0.08	0.05
Mn	0.5	0.4	0.3
Total (%)			
C	24.0	28.5	25.4
N[d]	0.99	0.83	0.88
P	0.10	0.10	0.10
K	0.35	0.32	0.36
Ca	1.08	1.14	1.19
Mg	0.28	0.25	0.33
	Mineral Horizon		
C.E.C. (meq/100g)	8.1	7.7	8.1
Exchangeable bases (meq/100g)			
K	0.14	0.12	0.15
Ca	5.87	6.87	5.90
Mg	3.60	3.51	3.95
Fe	0.10	0.09	0.08
Mn	0.04	0.03	0.08
Total (%)			
C	0.70	0.59	0.63
N[d]	0.05	0.05	0.05
P	0.05	0.04	0.04

[a] see Table 3 for other chemical and physical characteristics
[b] All values are the average of samples taken yearly from 1979 to 1982. $S_{\bar{x}} < 5\%$ in all cases.
[c] C.E.C. - cation exchange capacity
[d] (Organic + NH_4-N)

undisturbed nature of the forest floor with its lower bulk density (Table 3) under the mature white spruce stand. The cation exchange capacity in the mineral horizon appears unaffected by harvesting, as would be expected. Mineral horizon carbon also follows an expected trend, with lower % carbon in the warmer clearcut areas ($p<.05$). A more in-depth discussion of this will follow in a later section.

Seedling Nutrient Analysis

The results of analyses for nitrogen, phosphorus, potassium, calcium and magnesium on the major vegetative components of the intensive sites are given in Appendix I. Nitrogen estimates were used for various compartments in the model concurrently developed within this study. The other elements are provided as auxillary information only.

White spruce seedlings growing in all three areas were used as a bioassay to evaluate the nutritional capacity of the site. Armson (1959a, 1959b) working with white spruce seedlings in Ontario nurseries found that an increase in soil available nitrogen through fertilization with ammonium nitrate resulted in a 0.27% increase in foliar nitrogen levels. (Nitrogen concentrations showed no relationship to growth or treatment under other fertilization treatments such as ammonium sulphate.) Nitrogen concentrations in white spruce seedling foliage may thus be a good bioassay of enhanced soil nitrogen levels. The assay is strengthened by the fact that, with the exception of early (cotyledonous)

growth where nitrogen uptake rates are high (Armson, 1960c), white spruce seedlings show little evidence for seasonal periodicity of absorption of nitrogen (Armson, 1960b). White spruce seedlings are also capable of above and below-ground growth well into the seasonal period when air and soil temperatures are below freezing (Armson, 1960c). It should be recalled here that Armson was working in Ontario nurseries, however, and not in clearcuts in interior Alaska.

The seedlings from the control were older than those from the clearcuts by seven to eight years. In addition, those from the control were primarily found growing on rotting wood as compared to those in the clearcuts, which were often found established on mineral soil. Despite this, the same age of needles and twigs were sampled on the seedlings. Thus, the bioassay may reflect the true nutrient-supplying power of those sites capable of supporting seedling establishment and growth in either situation.

Analysis of the seedlings collected indicated that current needles of seedlings from the clearcut areas had different concentrations of nitrogen (Figure 10) and other elements than seedlings from the control area. Nitrogen and phosphorus were significantly higher in the clearcut seedlings; magnesium was slightly less. Nitrogen and phosphorus were also higher in the roots of clearcut seedlings. A discriminant analysis on nutrient concentration in current foliage of seedlings showed a good separation between the

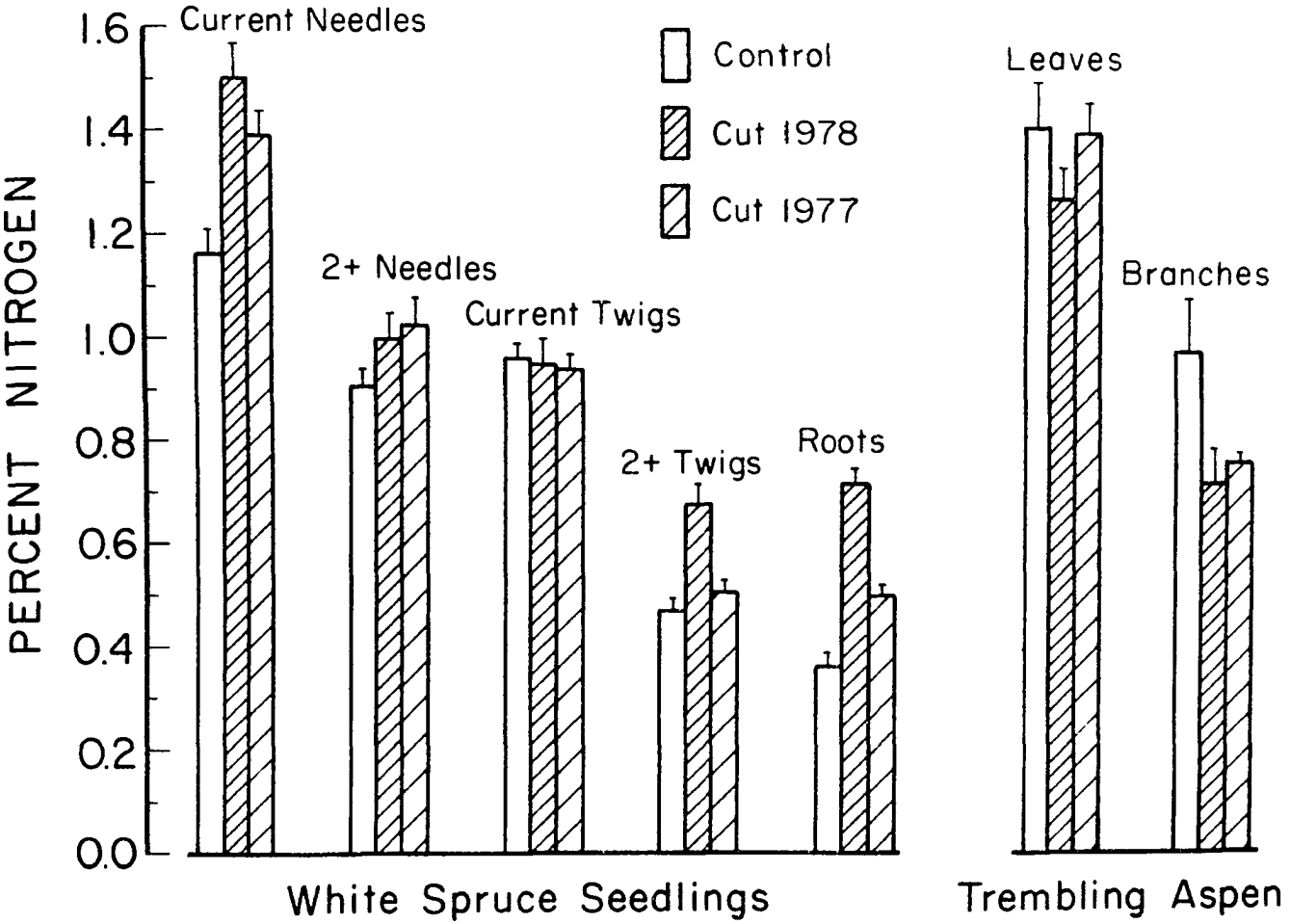


Figure 10. Nitrogen concentrations (%) for biomass components of white spruce seedlings and trembling aspen growing in the three intensive study sites. "2+" refers to samples comprised mainly of 2-year-old components; a small portion of older components may have been included in analysis. Standard errors (upper range) are given.

control and clearcut areas (Figure 11). The classification was 70% correct with some "error" being introduced between the clearcuts themselves. The canonical variables were linear functions of phosphorus, magnesium, potassium and nitrogen with the discriminating power of each element occurring in that order. This simply means that, although nitrogen exhibited a more understandable pattern, it was not as statistically strong as potassium in separating the areas in any direction (not necessarily the clearcuts from the control).

Zasada and Grigal (1978) examined the characteristics of white spruce seedlings on scalped and debris surfaces after logging in white spruce in interior Alaska. Their estimates of needle nutrient content and those of Armson's (1960a), working with unfertilized white spruce seedlings in Ontario nurseries, are in relatively close agreement with those determined in this study. Zasada and Grigal (1978) found only calcium to be higher in shoots and roots on debris sites when compared to scalped sites. In addition, they found root phosphorus and magnesium levels to be actually lower on debris as opposed to scalped surfaces. This indicates that the upper portions of the mineral horizon, moreso than forest floor layers, are important not only in seedling establishment (moisture-supplying ability) but also in the nutrition of recently-established seedlings.

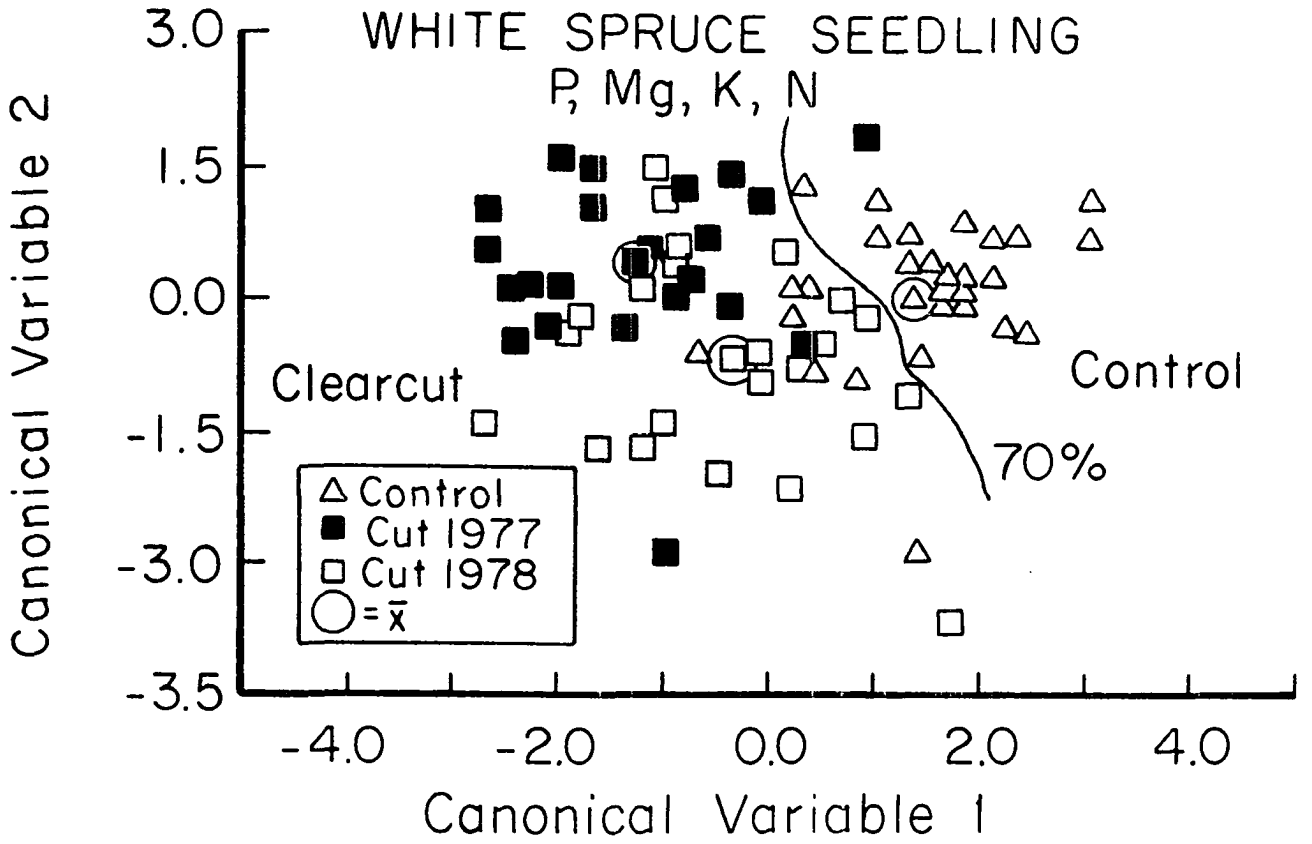


Figure 11. Discriminant analysis of intensive study sites based on major nutrient concentrations in current foliage of white spruce seedlings.

The higher levels of nitrogen in current needles of clearcut seedlings suggests either that uptake rates are higher in the clearcut area as opposed to the control or that more nitrogen is available for uptake in the clearcuts. For mature conifers, Cole and Rapp (1981) have stated that very little translocation from old to new tissue occurs, uptake almost entirely supplying demand. This infers that levels of available nitrogen may be higher in the clearcut areas. However, it is not possible to say which of NH_4-N or NO_3-N is preferentially utilized, although McFee and Stone (1968) found that Picea glauca seedlings responded more, in terms of growth and N-uptake, to ammonium than to nitrate nutrition. On the other hand, Clark (1961) found that after July, the photosynthetic rate in new white spruce needles was substantially greater than in any needles from older age classes. This suggests that the photosynthetic capacity of seedlings growing in the clearcut areas is much greater than that of those in the control as one would expect. With increased photosynthetic capacity may come the inherent ability to take up and reduce nitrate effectively.

Component biomass ratios for seedlings are presented in Table 14. It can be seen that the ratio of current to older needles is much greater in seedlings from the clearcut areas, although the ratios of current needles to current twigs are roughly the same across areas. Interestingly, it is the root/shoot ratios of seedlings from the control area, not the

Table 14. Total biomass and component biomass ratios for white spruce seedlings from the 3 intensive sites (mean($S_{\bar{x}}$)).

biomass (g) or ratio (g/g)	133-yr-Old White Spruce Control	Clearcut 1977	Clearcut 1978
total biomass	1.70 (0.22)	1.44 (0.39)	0.88 (0.22)
root/shoot	0.33 (0.04)	0.20 (0.03)	0.19 (0.10)*
current needles/ 2-yr+ needles	0.42 (0.06)	3.31 (0.43)	2.17 (0.36)*
current twigs/ 2-yr+ twigs	0.18 (0.03)	0.83 (0.15)	0.58 (0.05)*
current needles/ current twigs	2.71 (0.28)	2.20 (0.16)	2.88 (0.23)

* indicates clearcuts significantly different from the control ($p<.05$) but not from each other.

clearcut areas, that compare favourably to the root/shoot ratios of the clearcut seedlings from Zasada and Grigal (1978). The root/shoot ratios of the seedlings from the control area also compare favourably to those fertilized (not control) white spruce seedlings of Armson (1959a). Armson (1966) noted that fertilization of white spruce seedlings resulted in increased production of secondary needles and that height growth in the same seedlings was subject to control by soil fertility. In this case, the physical differences (Table 14) in seedlings from the clearcut and control areas are the result of many factors, including increased light levels and soil fertility. The root/shoot and other component biomass ratios in Table 14 are generally in the direction expected for limited (control) vs. more adequate (clearcut) resources in terms of nutrients, water, and light. Krasny et al. (1984), studying root/shoot ratios of white spruce seedlings in floodplain forest communities similarly found the highest root/shoot ratios in sites with the lowest amount of available nitrogen.

Soil Respiration

Seasonal patterns of soil respiration for the three intensive sites are illustrated in Figure 12. Generally, mid-summer estimates ranged to about 0.7 g CO_2 evolved per hour per m^2 and tapered off to 0.2 to 0.3 g $CO_2/hr/m^2$ in late season. Early season estimates were comparable to late season estimates. A two-way analysis of variance indicated that

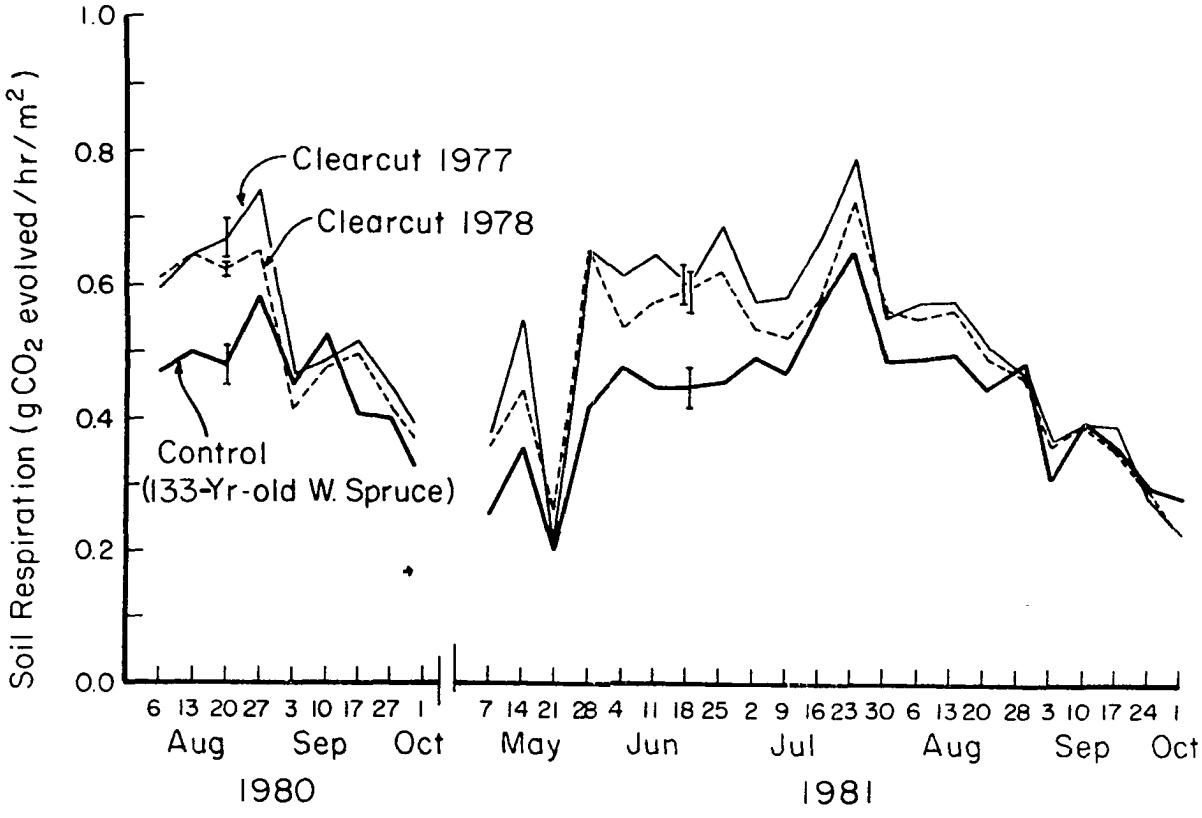


Figure 12. Soil respiration (g CO_2 evolved/hr/m^2) estimates (soda-lime absorption) for the three intensive study sites for portions of the 1980 and 1981 growing seasons. Some typical standard errors are indicated.

both area and sampling date within season had a significant effect ($p<0.01$) on soil respiration in both 1980 and 1981. A very slightly significant interaction between area and sampling date was noted in each case. Multiple classification analysis revealed that only 7% and 6% of the variation in respiration could be attributed to area in 1980 and 1981 respectively. Conversely, 46% and 62% of the variation was due to sampling date in those years.

When sampling times were pooled, one-way analysis of variance and multiple-range testing showed the two clearcut areas to have significantly higher respiration rates than the control in 1980. Respiration in the clearcuts did not differ. In 1981, all three areas had different respiration rates with the 1978 cut being higher than the 1977 cut. The control area had the lowest soil respiration rate at about 0.4 g $CO_2/hr/m^2$.

One-way analysis of variance and multiple-range testing across areas by sampling date showed variable results. Generally, in mid-season or at high levels of respiration, the clearcuts did not differ significantly from one another, although both showed higher respiration than the control. During other parts of the growing season in both 1980 and 1981, none of the areas differed significantly in their respiration rates from one another. Similarly, Hendrickson and Robinson (1984), in looking at forest floor and mineral soil respiration in the lab found that clear-cutting enhanced

CO_2 evolution but that whole-tree harvesting did not.

The values of soil respiration obtained in this study are comparable to those reported by Schlentner and Van Cleve (1985), also working in interior Alaskan white spruce ecosystems. They are also within the acceptable range of respiration rates from other coniferous forests world-wide (Singh and Gupta, 1977), although comparability is hampered by the lack of standard methodology.

de Jong et al. (1974) found cultivation of native grasslands to result in increased soil respiration. In general, disturbance of natural ecosystems by management practices will tend to result in increased soil respiration. This appears to be the case after forest harvesting in interior Alaska. Soil respiration appears to be enhanced under the altered temperature and moisture regimes found in cleared areas (Table 12).

It is unlikely that mechanical site preparation would also enhance respiration through increased aeration. At the time of the study, carbon reserves had not increased in either the forest floor or mineral horizon of the clearcut areas (Table 13: the trend was to an actual decrease in the mineral soil but this can't be stated statistically). However, with enhanced decomposition under these higher temperature and moisture regimes it is likely that carbon levels will shortly increase, possibly stimulating heterotrophic respiration. It should be noted, however, that normal levels

of CO_2 evolution due to plant growth or decomposition (Buyanovsky and Wagner, 1983) could effectively hide disturbance effects depending upon the time of sampling.

One of the problems in obtaining soil respiration estimates is the separation of microbial from root respiration. Although Singh and Gupta (1977) state that partitioning of soil respiration into root, faunal and microbial components is extremely difficult, some information has recently become available. Bāāth et al. (1981) used estimates of 40%, 40% and 20% of the total soil respiration for fungi, bacteria and root respiration (plus soil animals) respectively in soil biomass studies in Sweden and Tesařová (1979) and Tesařová et al. (1979), working in Czechoslovakian grassland soils, estimated root respiration to account for 40% of the total CO_2 output. Hendrickson and Robinson (1984) estimated that between 43% and 58% of total soil respiration was attributable to roots in the forest system they were studying. These authors also give a good summary of two methods useful in assessing root respiration in the lab and list studies that employed a variety of "compartmental" techniques to calculate soil respiration.

The major reason for estimating that portion of soil respiration attributable to microbial activity stems from the desire to examine the possible correlation between nitrogen mineralization and soil microbiological activity. If root biomass and root respiration could be assumed to be equal

across all three intensive study sites, then partitioning would not be necessary. However, because of the impact of clearcutting on the vegetation and its distribution among study sites, it is likely that this is not the case. In this study soil cores were initially gathered from all sites in order to determine root biomass (roots, rhizomes, underground shoots) on a volume basis. It was thought that perhaps soil respiration estimates could be standardized to root biomass across areas, thus partially accounting for the large root respiration component that must exist in the clearcut areas with extensive Calamagrostis cover. This was assuming that all species respire at the same rate per unit surface area of root. Alternatively, Gilson respirometry could have been used to examine respiration of freshly exised fine roots or soils including fine roots from the three areas. In the latter case, if the same patterns of field respiration had been repeated in the lab then root respiration could have been assumed to be a similar component in all three areas.

However, both Van Cleve and Sprague (1971), working in interior Alaskan birch and aspen stands, and Schlentner and Van Cleve (1985) working in Alaskan white spruce stands found good relationships between soil respiration, uncorrected for respiration of roots, soil moisture and soil temperature. When one considers that soil respiration includes a gaseous component directly related to root growth, and hence, to root exudates, soil moisture uptake, availability and flow, and

soil structure it is not unreasonable to expect that nitrogen mineralization might correlate well with total soil respiration as derived by soda-lime absorption. In addition, root respiration is a controlling factor on the soil CO_2 atmosphere, perhaps even more so than microbial respiration. Since anaerobiosis is an important factor in determining the extent of nitrogen mineralization it would seen reasonable that soil respiration, in controlling soil CO_2 content, should correlate well with nitrogen mineralization. In this study I desired to look at the important factors, including soil respiration, that might affect nitrogen mineralization. For this reason and those listed above it was decided that soil respiration estimates should not be partitioned.

Soil moisture content and temperature are the two important factors governing soil respiration, although depth, time of day, aeration, and nutrient (both energy-supplying and inorganic) status of the soil are also important (Singh and Gupta, 1977). The effects of temperature on soilrespiration appear easier to understand than those of soil moisture (cf. Howard and Howard, 1979). It is known with some certainty, however, that fluctuations in moisture content (deJong et al., 1974) and temperature (Novák and Kubát, 1981) definitely stimulate soil respiration and CO_2 production. The combination of soil moisture and temperature, for example, has been found to account for greater than 50% of the annual fluctuations in CO_2 levels in

certain agricultural soils (Buyanovsky and Wagner, 1983).

As shown previously in Table 6, significant regressions of soil respiration (CO_2 evolved through top horizon) on soil temperature and moisture content were obtained. In an attempt to more fully examine these relationships, the data were evaluated using the GRESP soil respiration model of Bunnell et al. (1977) and the BRESP model of Schlentner and Van Cleve (1985). Since this exercise is peripheral to the primary reason for obtaining soil respiration estimates (to estimate general soil microbial activity), only a brief discussion is presented here.

The GRESP model is as follows:

$$GRESP=(M/(a_1 + M)) \text{ X } (a_2/(a_2 + M)) \text{ X } a_3 \text{ X } a_4^{(T-10)/T} \quad (2)$$

where GRESP=respiration rate at temperature T(^{o}C) and moisture level M(g H_2O/g dry weight X 100%)

a_1=% H_2O at half "field capacity"

a_2=% H_2O at "maximum retentive capacity"

a_3=theoreticallyoptimal respiration rate at 10^{o}C

a_4=temperature Q_{10} value

This was modified by Schlentner and Van Cleve (1985) to form the BRESP model:

$$BRESP=(M/(a_1 + M)) \times (a_2/(a_2 + M)) \times a_3 \times ((1/(a_6 + (a_4^{-((T-10)/10)}))) + a_5 \quad (3)$$

where BRESP=soil respiration as g $CO_2/m^2/hr$

M=% soil moisture (dry weight basis)

a_3=scaling factor

a_4=Q_{10} related parameter

a_5=lower limit of CO_2 evolution

a_6=1/((upper limit of respiration)-a_5)

The coefficients for the GRESP and BRESP respiration models for the three intensive sites are given in Table 15. Significant relationships were found in all cases. The highest r^2 found was 0.89^{**} for GRESP soil respiration in the 1978 clearcut as predicted from mineral horizon moisture content and temperature. In general, the coefficients are roughly equivalent to those found by Schlentner and Van Cleve (1985) for interior white spruce forests with the exception of a_2 in the BRESP forest floor model. This coefficient appears to be in error, being too large across all study areas. A more reasonable value (109.9) is given by Schlentner and Van Cleve (1985) although this is based on 15 cm depth and not forest floor temperatures.

Three-dimensional graphical representations of actual field data and the BRESP model of soil respiration predicted from forest floor temperature and moisture content are shown

Table 15. Parameter and correlation coefficients for two soil respiration models (GRESP, BRESP)[a]. Respiration is predicted from forest floor or mineral horizon temperature and moisture content.

Coefficient	133-yr-Old White Spruce Control	Clearcut 1977	Clearcut 1978
		Forest Floor	
GRESP			
a_1	150.0	150.0	150.0
a_2	252.0	252.0	252.0
a_3	1.53	1.54	1.51
a_4	1.24	1.27	1.32
r^2	0.32**	0.33**	0.44**
BRESP			
a_1	169.0	169.0	169.0
a_2	2708.01	986.6	555.54
a_3	2.1	2.14	2.34
a_4	5.1	7.51	8.72
a_5	0.1	0.1	0.1
a_6	2.0	2.0	2.0
r^2	0.40**	0.41**	0.51**
		Mineral Horizon	
GRESP			
a_1	150.0	150.0	150.0
a_2	252.0	252.0	252.0
a_3	6.59	4.19	4.02
a_4	1.73	2.01	2.15
r^2	0.30**	0.42**	0.89**
BRESP			
a_1	135.0	150.0	150.0
a_2	63.95	252.0	252.0
a_3	11.71	6.89	6.83
a_4	9.98	8.00	8.00
a_5	0.1	0.1	0.1
a_6	2.0	2.0	2.0
r^2	0.32**	0.38**	0.59**

[a] GRESP model developed by Bunnell et al. (1977)
BRESP model developed by Schlentner and Van Cleve (1985)
For explanation of coefficients, see text.

** significant at $p<.01$ (estimated using Zar (1974) - models are non-linear)

in Figure 13. The variability of the data can be seen in Figure 13(a), but this is effectively smoothed when the BRESP model ($r^2=0.51^{**}$) is applied (Figure 13(b)). An almost linear response in respiration to moisture content can be seen although no relationship between soil respiration and moisture appears to exist below 100%. Maximum respiration occurred when forest floor moisture was between 140% and 200% and temperature was between 12 and 20°C. The effect of increasing temperature in general is to increase soil respiration with the greatest rate of increase in respiration in the range between 5°C and 10°C.

Soil Solution

Seasonal patterns of potassium, calcium and magnesium solution are shown in Figure 14. A two-way analysis of variance was performed on potassium data and indicated an overall effect of area but not of sampling time. There were no significant interactions. When data were analyzed by sampling time, however, homogeneity of variance requirements were not often met. Subsequent Kruskal-Wallis testing on those data where this was the case revealed few times where significant differences existed between areas. Where the homogeneity of variance assumption was met, multiple-range testing revealed only several times during the season where potassium levels were highest in soil solution from the uncut area.

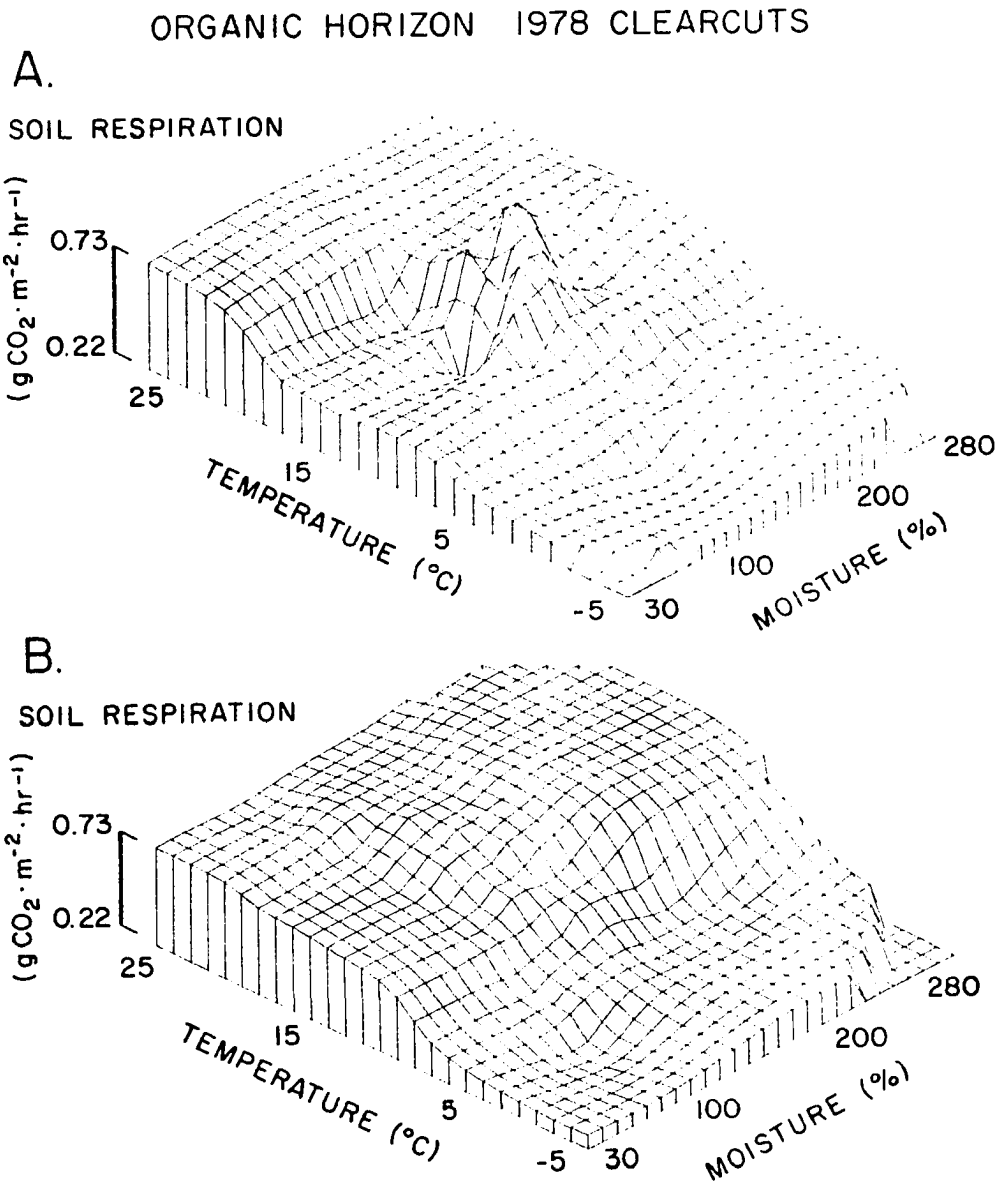


Figure 13. Three-dimensional graphical representation of the soil respiration-moisture-temperature matrix found for the forest floor (organic horizon) of the 1978 clearcut. (a) actual variability in the original data (b) data smoothed by the BRESP model (see text). The r^2 for this particular modelling effort was 0.51^{**}.

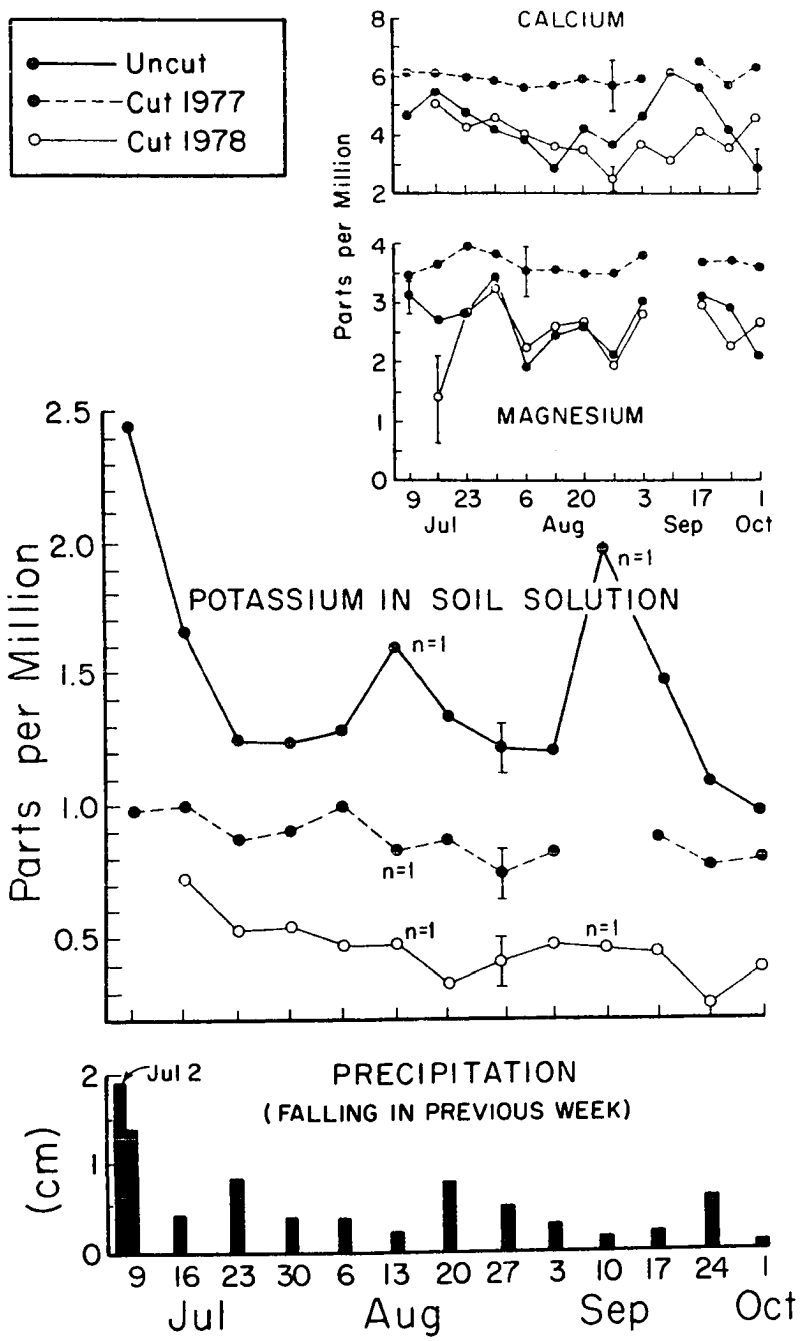


Figure 14. Potassium, calcium and magnesium concentrations (ppm) from soil solution collected from the three intensive study sites during the 1981 growing season. Some typical standard errors are indicated. Precipitation falling on the control area (cm) during the previous week is also shown.

Nonetheless, the patterns shown in Figure 14 for potassium are of interest. Much of the potassium introduced into forest ecosystems is done so as canopy wash. Although no throughfall data for interior Alaskan white spruce ecosystems are available, Van Cleve et al. (1983) reported throughfall potassium levels of 1.3 and 2.2 kg/ha/yr for two interior black spruce stands. Gordon (1983) working in mixed-wood white spruce in Ontario found potassium inputs to range to 5.7 kg/ha/yr in throughfall and Foster and Morrison (1976) determined potassium in throughfall in Ontario jack pine stands to be 10 kg/ha/yr. Further, Krause (1975) summarized data from selected ecosystem studies and noted potassium levels in throughfall to exceed 10 kg/ha/yr in several coniferous forest ecosystems.

It might be expected then, as shown in Figure 14, that the 1978 clearcut, being the most denuded, might show the lowest levels of potassium in solution. As vegetation reinvades the site, potassium levels in soil solution might be expected to rise (e.g., clearcut 1977). In addition, the soil solution in the uncut area could actually have relatively high concentrations of potassium due to extensive canopy wash. When precipitation falling in the control area (predicted from the Fairbanks Airport - Figure 14) is compared to soil solution potassium levels, some interesting patterns are revealed. However, this data set is not strong enough to say

conclusively that potassium inputs are a function of precipitation events in interior Alaska although many other forest ecosystem studies have found this to be the case. Buldgen (1982), for example, states that the influence of rainfall on potassium and sodium mobility is more pronounced than on calcium and magnesium mobility. However, he also indicated that potassium mobility may be limited by microbial uptake due to decomposition since K leaching increased with increasing temperature (see also Cronan, 1980). Note that Buldgen and Remacle (1981) did not always find this to be the case. The other scenario to consider concerning potassium movement then is this: decreased concentrations of K in the clearcuts may indicate either a high decomposer demand for potassium compared to the control or simply increased uptake of K by the profusion of associated vegetation in the clearcuts.

In general, potassium is usually not re-translocated within tissues, but tends in other ways to be a very mobile cation. Thus precipitation events may be important in terms of potassium inputs to the soil system, especially in interior Alaska where precipitation is minimal.

Calcium and magnesium (Figure 14) concentrations in soil solution were more variable than potassium and no signficant patterns among areas were apparent. Both of these bivalent cations are integral parts of plant structures; studies have indicated that they are slowly released and have low leaching rates (Buldgen, 1982). However, it is interest-

ing to note that in this study the overall levels of losses are higher for both calcium and magnesium (Figure 14, inset) than for potassium; this reflects relative exchangeable pool sizes of these elements (Table 13).

Component nitrogen and phosphorus concentrations in soil solution are given in Figure 15. No significant difference between areas was noted for movement in solution of NH_4-N, NO_3-N, soluble organic P, and available P. However, soluble organic nitrogen concentrations were always highest in solution from under the uncut stand, lower under the oldest clearcut and least under the youngest clearcut. Total phosphorus concentration in the control area was higher than in both clearcuts, which did not significantly differ from one another.

The soluble organic nitrogen pool may play a more important part in forest nutrition than previously recognized. As discussed previously, Van Cleve and White (1980) for example, noted the soluble organic pool to be much larger than the other pools of available nitrogen. The soluble organic nitrogen pool also appears to be a pathway for mass movement of nitrogen through soil horizons (cf. Reddy, 1982; Sollins and McCorison, 1981). By virtue of residence in the pool, nitrogen is moved into deeper mineral horizons in the profile where it becomes available for uptake by large roots.

There is also some evidence to indicate that in interior Alaskan forest ecosystems soluble organic nitrogen is

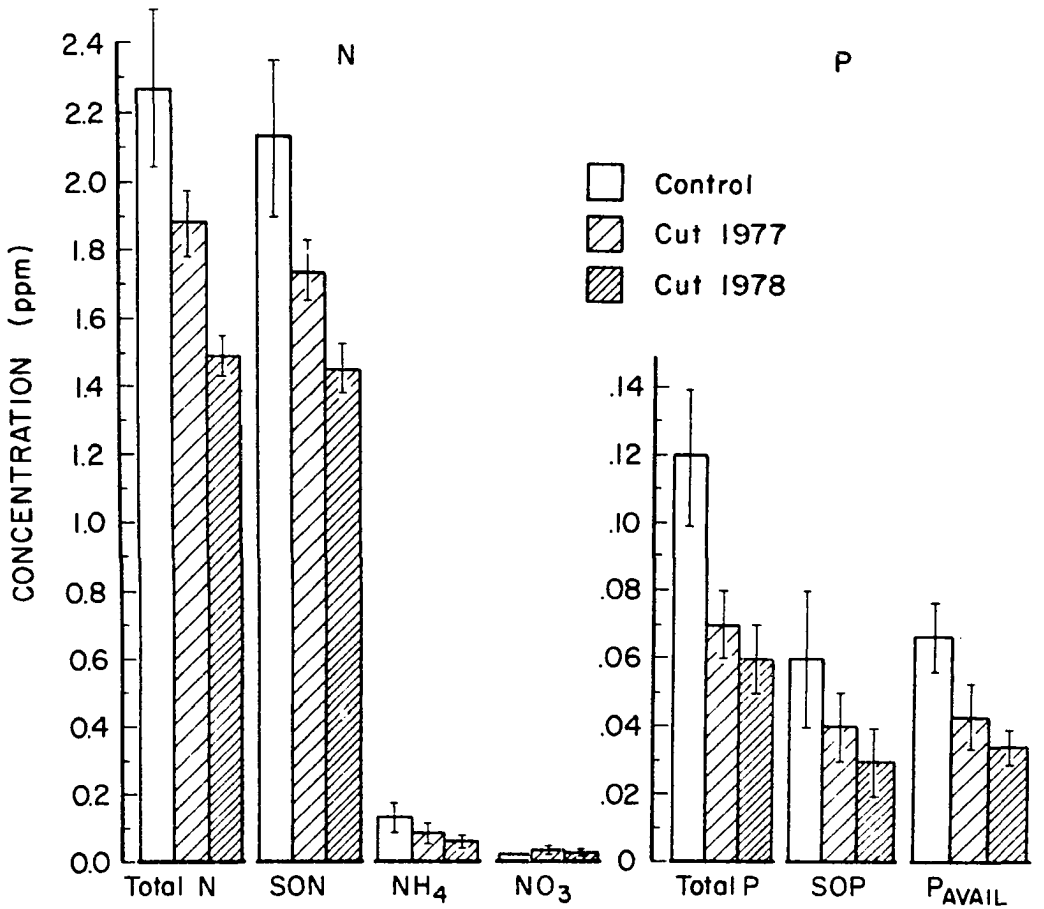


Figure 15. Concentrations of total nitrogen, soluble organic nitrogen (SON), NH_4-N, and NO_3-N, total phosphorus, soluble organic phosphorus (SOP) and available phosphorus (ppm) collected from the three intensive study sites during the 1981 growing season. Standard errors are given.

involved in certain chelation complexes with a variety of metals such as copper, iron and magnesium. This relationship is seasonal for certain elements and also appears to be largely controlled by secondary succession, at least in clearcut areas. This information is from a portion of this study not reported on here (data on file, Forest Soils Laboratory), and follows the initial investigation of chelate mobility by Candler and Van Cleve (1982).

The larger soluble organic-N losses from the uncut area are likely a result of a higher degree of root exudation or perhaps canopy wash of low molecular weight organic compounds in the control area. Plant cover in general tends to control the fate of nutrients supplied to the forest floor through throughfall and temperature regulation (Buldgen and Remacle, 1981). Increases in temperature generally increase the mobility of most nutrients including available nitrogen and organic anions (Buldgen, 1982; Cronan, 1980; Hart et al., 1981). This was not the case here; increased soil temperatures in the clearcut areas (Table 12) did not increase leaching of soluble organic nitrogen or other elements such as potassium. This indicates that, in interior Alaska, the physical presence of the canopy and its throughfall characteristics are more important than temperature in governing leaching processes. Additionally, the degree of microbial activity in the clearcuts along with

rapidly-growing vegetation that is recolonizing the sites must be exerting at least as much influence as canopy wash.

Potassium exports usually correlate well with nitrate losses (cf. Buldgen et al., 1983; Vitousek, 1984) but in this study, nitrate losses in solution were too low to show any correlation with potassium. Nitrate leachings also did not correlate to precipitation events as has been noted in other studies (Buldgen et al., 1983).

Analysis of variance by area across time on all nutrients analyzed revealed no seasonal patterns for any nutrient. Thus, seasonal averages were calculated for each area. These are presented in Table 16.

Carbon-Nitrogen Ratios

One of the primary controls on nitrogen mineralization is the quality of the organic matter substrate as indicated by the C/N ratio, initial lignin or cellulose content, acidity and other indices. As discussed previously, the C/N ratio in particular appears to be an important factor, reflecting the potential energy supply (carbon) for microbial activity and the potential supply of an inorganic nutrient (nitrogen). The 4-year trends in C/N ratios for the three intensive sites are given in Figure 16. The older clearcut (1977) had the highest C/N ratio in the forest floor, even in 1979, only two years after logging. This indicates potentially rapid decomposition of the excess logging slash left

Table 16. Selected chemical characteristics of soil solution from the 3 intensive sites (seasonal mean, ppm).[a]

	133-yr-Old White Spruce Control	Clearcut 1977	Clearcut 1978
Soluble organic N	2.13	1.74	1.45
NH_4-N	.13	.09	.06
NO_3-N	.03	.04	.04
Total N	2.27	1.88	1.49
Soluble organic P	.06	.04	.03
PO_4	.07	.04	.03
Total P	.12	.07	.06
K	1.45	.87	.49
Ca	4.03	5.51	4.06
Mg	2.69	3.66	2.61

[a] $S_{\bar{x}} < 5\%$ in all cases

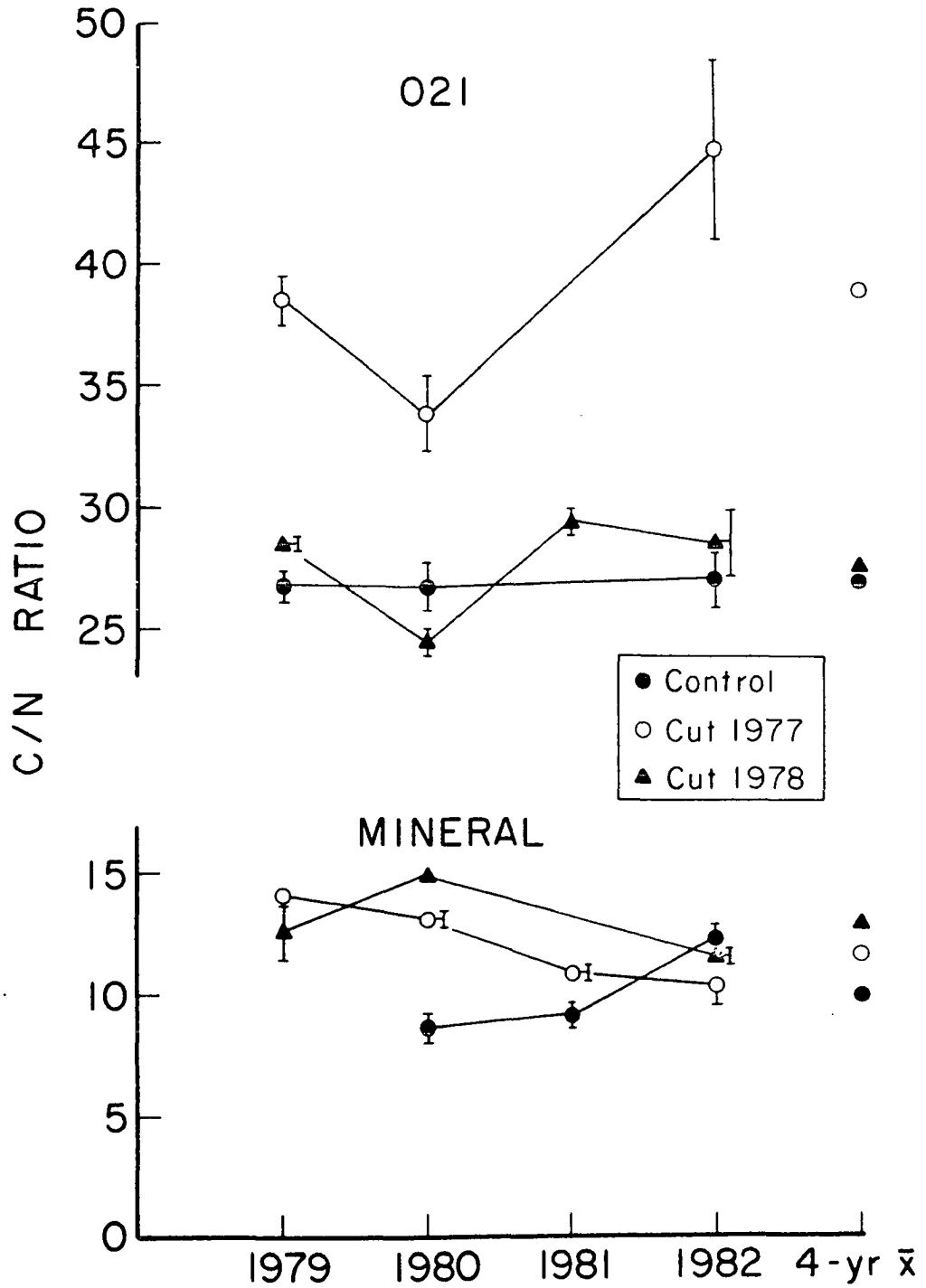


Figure 16. Carbon-nitrogen ratios for the forest floor (021) and mineral horizon of the three study sites for the four-year period from 1979 to 1982. Standard errors given show the variation in five laboratory reps taken from a composite of 25 samples.

on that site due to branch breakage in winter-logging. Normally, had the clearcuts been logged similarly, we would expect the youngest clearcut to have the widest C/N ratio and the older clearcut to have a narrower C/N ratio due to decomposition.

The year-to-year variation in C/N ratio for this area and for the younger clearcut (1978), which did not fluctuate as widely, is likely due to sampling error in these very heterogeneous sites. The C/N ratio in the 1978 clearcut appears to drop below the level of the C/N ratio in the control in 1980, but again this may be just sampling error. It would be normal to expect some increase in C/N ratio after harvesting with the large mortality of fine roots in the forest floor that must occur. Wide C/N ratios in general indicate the potential for higher microbial activity, nutrient conservation by microbes and thus reduced loss of nutrients from systems. With time, C/N ratios should narrow.

One of the major differences between the two clearcuts, the amount of debris left on-site after harvesting, is dramatically illustrated by this graph. If the 1978 cut was identical to the 1977 cut, we should expect a dramatic rise in C/N for the 1978 cut in 1980, just as the ratio in the 1977 cut shows in 1979. This is not the case, however, and the C/N ratio of the forest floor in the 1978 cut approximates the C/N ratio in the control area which shows little variation year-to-year.

The mineral horizons of all three areas show little variation in C/N ratio over time. One could hypothesize that with increased leaching in the clearcut areas, organic residues may percolate down from the forest floor, thus increasing the C/N ratio in the mixed horizon as shown in 1980. However, the rising trend for the control area again suggests that sampling even many microsites over a large area may not have been adequate. (Note that the standard error bars indicated in Figure 16 represent variation in 5 laboratory reps taken from a composite of 25 field samples.)

Mineral soil carbon content, as it relates to soil degree days and forest cover types in the interior is illustrated in Figure 17. The trend shows warmer sites to possess less mineral soil carbon, presumably because of increased conversion of organic matter to CO_2 under higher temperature regimes. Schlentner and Van Cleve (1985) actually found the highest CO_2 evolution (2-year mean) under white spruce, followed in order by the birch, aspen and black spruce stands. Generally, their trend holds true for this diagram: it is likely that the soda-lime method for CO_2 absorption measures a larger proportion of CO_2 evolved from the forest floor than from the mineral soil. In any event, warmer sites would appear to have less mineral soil carbon.

Carbon determinations for the white spruce control mineral horizon and the average of the clearcuts used in this study are also shown in Figure 17. It can be seen that the

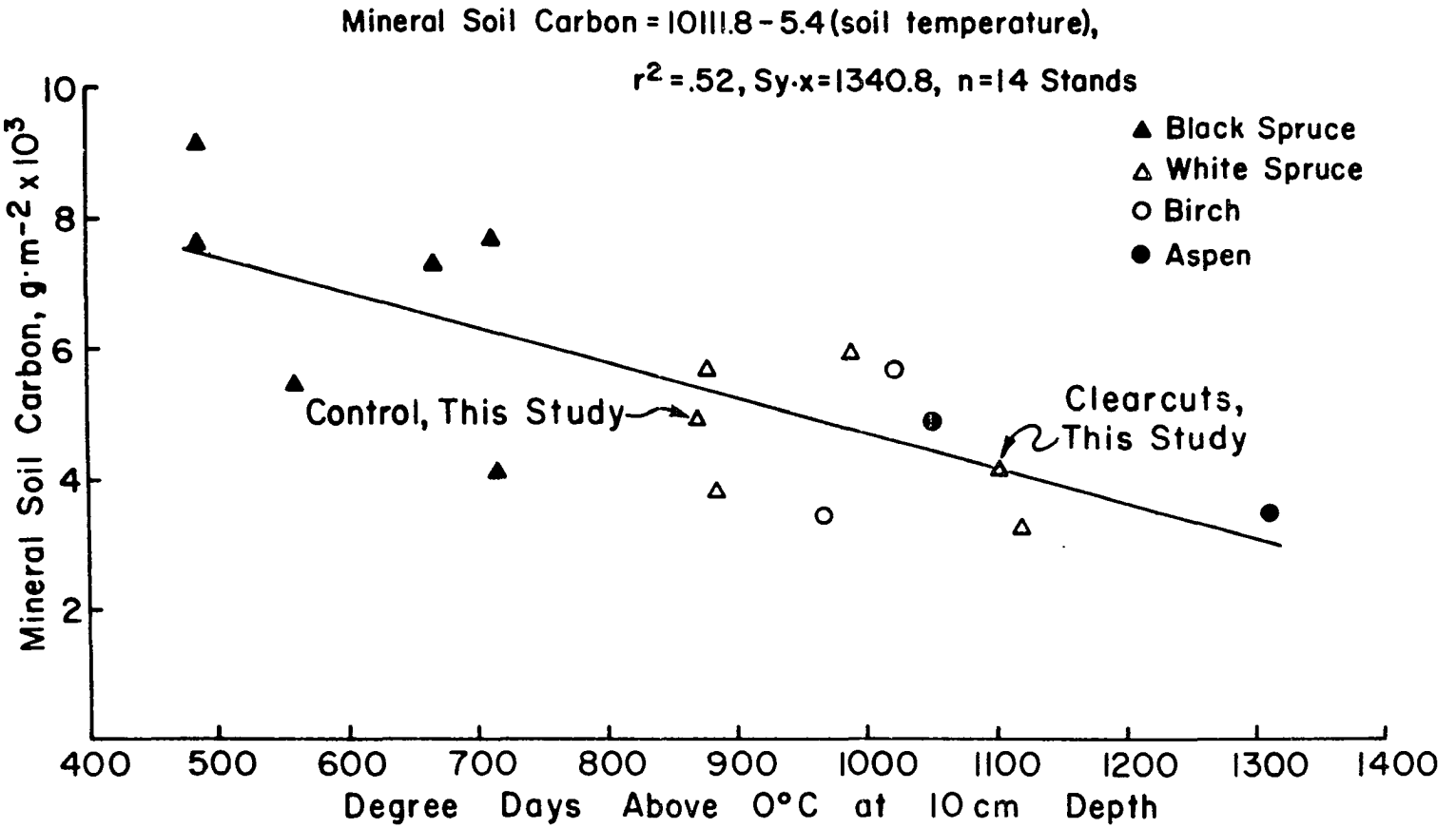


Figure 17. Relationships of mineral soil carbon to soil degree days at ten cm depth. This study was not included in the original regression (Van Cleve, pers. comm., 1984). Soil degree days from this study were estimated from above-ground ambient degree days.

intensive study sites span the breadth of the white spruce stands sampled in the original study in terms of soil degree days (data on file, Forest Soils Laboratory). Contrary to the earlier idea that increased leaching in the clearcut areas would lead to an enhanced carbon regime in the top portion of the mineral horizon, carbon in the clearcut mineral horizons actually decreased. This indicates that, for interior Alaska, temperature-related constraints on respiration are a more important control on carbon conversion and movement than leaching events. With low precipitation and water movement through the profile, substantial time may be required to affect carbon regimes in this manner. This may not be the case under higher precipitation regimes.

If it is assumed that the C/N ratio in the mineral horizon is not changed by forest harvesting (Figure 16) and that mineral soil carbon decreases with clearcutting (Figure 17) then a very interesting scenario arises. The only way to keep the ratio constant under decreasing carbon levels is to have corresponding decreases in total nitrogen (such as might occur with decreased soluble organic nitrogen inputs - see previous discussion). Such nitrogen losses could conceivably result from increased leaching losses of the soluble organic pool (unlikely in interior Alaska), or from increased N-immobilization in plant tissue. Total nitrogen loss could also result from enhanced mineralization rates and rapid plant uptake. This could occur even in the presence of

lowered nitrogen inputs in soil solution. Such decreased inputs of organic nitrogen would result from loss of fresh plant litter inputs, as illustrated in Figure 15, or from increased immobilization by microbes and plant uptake in the cleared areas.

NITROGEN MINERALIZATION AND NITRIFICATION

Variation in Data

The results of the pooled mineralization field experiment (see Field Procedures - nitrogen mineralization) are given in Table 17. Subsample and incubated levels of NH_4-N are comparable with actual field data obtained from these areas and will be discussed later. Of greatest interest are the coefficients presented. The average coefficient of variation for NH_4-N subsamples is 0.13 (13% of the mean) and for NH_4-N incubated samples, 0.16. These are averages across soil horizon and area. The average coefficient of variation is 0.34 for both sub- and incubated samples of NO_3-N. All of these are compared to coefficients of variation from the main project, also averaged across horizon and area, in Table 18. It would appear that the variation in data sets from the pooled experiment appears to be much less than that in sets from the main experiment (not statistically tested). This is in spite of the fact that the n from the main study was 3 times that from the pooled experiment!

Table 17. Results from the pooled mineralization field experiment, 1980, 1981[a].

Study	Area	Horizon	Mineralization (NH_4-N) Subsample	C.V.[b]	Incubated	C.V.
1980	Clearcut 1977	Forest Floor	4203.67(255.06)	.19	5303.94(204.46)	.11
		Mineral Soil	181.62 (4.48)	.08	211.06 (14.59)	.22
1981	Clearcut 1977	Forest Floor	5955.70(161.75)	.09	4618.97(139.18)	.10
		Mineral Soil	334.01 (6.07)	.06	216.35 (11.62)	.16
	Clearcut 1978	Forest Floor	9551.26(402.14)	.29	5429.09(314.75)	.18
		Mineral Soil	316.81 (9.80)	.10	341.30 (13.40)	.12
	Control	Forest Floor	22397.97(674.00)	.10	19961.43(976.82)	.15
		Mineral Soil	261.36 (10.46)	.13	296.30 (12.63)	.22
			Mean	.13		.16
			Nitrification (NO_3-N)			
1980	Clearcut 1977	Forest Floor	0 (0)	-	0 (0)	-
		Mineral Soil	0 (0)	-	66.40 (6.27)	.28
1981	Clearcut 1977	Forest Floor	24.40 (3.83)	.47	42.05 (11.97)	.49
		Mineral Soil	0 (0)	-	105.54 (9.13)	.26
	Clearcut 1978	Forest Floor	0 (0)	-	0 (0)	-
		Mineral Soil	0 (0)	-	0 (0)	-
	Control	Forest Floor	200.46 (14.46)	.20	3800.71(448.51)	.33
		Mineral Soil	0 (0)	-	0 (0)	-
			Mean	.34		.34

[a] ug/100g dry weight
[b] coefficient of variation

Table 18. Coefficients of variation from the main study compared to those from the pooled mineralization experiment.

Group	Coefficient of Variation	
	Pooled	Main Study
NH_4-N, subsample	0.13[a]	0.50[b]
NH_4-N, incubated	0.16[a]	0.49[b]
NO_3-N, subsample	0.34[c]	1.09[b]
NO_3-N, incubated	0.34[c]	0.96[b]

[a] average of 8
[b] average of 48
[c] NO_3-N subsample, average of 2
NO_3-N incubated, average of 4
Some of these data sets were arrays of 0, hence it was not possible to calculate a coefficient of variation.

This indicates that the sampling procedure used in the main trials was more susceptible to inherent spatial variation in available nitrogen pool-sizes than the one employed in the pooled trials. Variation between neighbouring samples in the main experiment may even have been enhanced when mixing individual horizons to reduce variability within a sample itself. The pooling of samples collected over a large area, subsequent mixing, and incubation in a microclimatically similar area will reduce natural variation and should reflect only variation introduced through the use of the polyethylene bag technique and the pooling process itself.

The usefulness of this experiment was several-fold. First, it provided a rough estimate of the variation introduced into the study through utilization of polyethylene bags. For NH_4-N this value is about 15% of the mean; for NO_3-N the value is closer to 35%. Actually, variation introduced into the study by the technique would be somewhat less than these estimates since even the pooled, mixed bulk soil in the pooled experiment would have had some natural variation in available nitrogen pools. Theoretically, the coefficients of variation found in the pooled experiment could be used in conjunction with the standard deviations from the main experiment to correct the means for this variation. These corrected means could be used to portray trends but statistical analyses would be impossible since individual

data points could not be adjusted in this manner. Second, by subtracting the coefficient of variation (pooled) from the corresponding coefficient of variation (main) a rough estimate of natural variability in available nitrogen pool sizes, corrected for technique, was obtained. These were 35%-40% of the mean for NH_4-N, and even higher (70%) for NO_3-N. I acknowledge the unequal sample sizes between the two studies; it is nonetheless of interest and important to have an idea of variability in the measured variable. Finally, the study showed that mineralization and nitrification estimates (Table 17, calculation not shown) from a pooled design were comparable to estimates from a point design with a much larger sample size. This has implications for future estimations of nitrogen availability especially in ecosystems under management where simple and quick experimental designs may be desireable.

It is interesting to note that the pooled design gave this study its only significant nitrification value in the forest floor of the uncut stand (Table 17). This rate was 120.01 ug/100g/day which corresponds to roughly 2.1 $g/m^2/yr$. I would hypothesize, on the basis of other data that show little nitrification in the same area, that this value is elevated on the basis of the severe mixing that was inherent in the pooled experiment. On the other hand, the forest floors in the cut areas were also subject to severe mixing

and yet showed little nitrification. Thus, this value must stand as an anomoly.

No seasonal patterns of variation in the data from the main experiment could be detected when coefficients of variation for both sub- and incubated samples were plotted against time. However, when coefficients of variation for incubated samples were regressed upon coefficients of variation for sub-samples, some significant relationships appeared, depending upon how the data were grouped. Due to the low n, regressions on singular horizons from one area for a specific form of available nitrogen (e.g. control, forest floor, NH_4-N) were often not significant. However, other groupings were very significant (Table 19). Although the regression equations were not that strong, the intercepts (b) were all positive and fairly large in relation to the data itself. This indicates that the variation found in incubated samples was a function not only of initial variability in the soil but also of the technique itself. Researchers utilizing polyethylene bags in soil incubations should be aware of the variability introduced into the study by such techniques and be prepared to either increase sample size appropriately or to utilize a pooled sampling design.

Comparison with other Studies

Comparison of the nitrogen mineralization values obtained in this study with those from other ecosystems is given in Table 1. As mentioned in footnote "a" of that

Table 19. Variation in incubated samples as a function of variation in sub-samples.[a]

Grouping of Data	a	b	r^2
all	0.31	0.46	0.49**
forest floor	0.27	0.51	0.51**
mineral soil	0.42	0.35	0.50**
NH_4-N	0.33	0.31	0.32**
NO_3-N	0.15	0.90	0.23**
clearcut 1978	0.56	0.31	0.55**
clearcut 1979	0.25	0.49	0.65**
control	0.38	0.34	0.40**

[a] regression equation is of the form y=ax+b, where y, x are the coefficients of variation of incubated and sub-samples, respectively
a, b are regression coefficients

table, comparison between studies is hampered by differences in field and lab procedures employed, descriptions of soil horizons and most importantly, terminology dealing with mineralization processes. This study has defined nitrogen mineralization as biochemical ammonification. Under the incubation procedure employed, changes in the NH_4-N pool alone, then, reflect the net amount of N converted from the organically-bound pool to NH_4-N. The rationale for this is simple. The NH_4-N pool, measured after incubation, is that NH_4-N available for plant growth (or mycorrhizal uptake) after all major losses, including volatilization (if any), leaching and microbial uptake have been "satisfied". Under this definition, nitrification represents a loss to the NH_4-N pool but a gain to the NO_3-N pool. "Nitrogen mineralization" then reflects the net pool of NH_4-N formed rather than the total amount actually transferred from the organically-bound pool and, after all, that is really what is of most interest.

Many ecosystem studies, however, employ the concept of (ironically) "net nitrogen mineralization" (cf. Table 1: Aber et al., 1983; Federer, 1983; Melillo, 1977; Nadelhoffer et al., 1983 and Pastor et al., 1984). By subtracting initial NH_4-N + NO_3-N values from final NH_4-N + NO_3-N values an estimate of the total nitrogen "moved" from the organic pool into available form is obtained. However, this method says nothing about how that nitrogen is proportioned into NH_4-N and NO_3-N. As well, nitrification is not mineralization;

nitrification estimates still must be obtained by subtracting initial NO_3-N from final NO_3-N values. One advantage of using "net nitrogen mineralization", however, occurs when large positive changes (over incubation) in the ammonium pool are accompanied by large negative changes in the nitrate pool. This results in negative "net nitrogen mineralization" (see Appendix II), or, according to the definition, an increase in the organic nitrogen pool. When using the polyethylene bag incubation technique, this could only indicate uptake by microbial populations since other potential nitrate sinks (leaching, plant uptake) are considered to be non-existent. In heavily compacted mineral soils or soils with a high moisture content, this assumption may be violated if denitrification (N_2 loss across the plastic) is an active process. Incidentally, I should also point out that 2 of the 5 ecosystem studies on "net nitrogen mineralization" cited above did not report the thickness of polyethylene bags employed. The range for the remaining three varied from 0.04 to 0.1 mm in thickness. All were beyond the range tested in this study raising again the question of the effects of the technique on nitrogen mineralization processes and hampering comparison among studies.

I feel that the method employed in this study adequately indicates a true "net" movement of nitrogen into the NH_4-N pool. Movement into the NO_3-N pool is addressed separately through nitrification estimates. This proved to be

valuable in the development of the process model discussed in a later section. (I do recognize, however, that my estimates of nitrogen mineralization will underestimate actual N-movement out of the organic pool, especially where nitrification is high). Regardless, "net nitrogen mineralization" can be easily determined if desired by adding together the separate mineralization and nitrification rates (Appendix II).

Nitrification was virtually non-existent in the control stand in both the forest floor and mineral soil. Thus comparison of the nitrogen mineralization value from this study with the net nitrogen mineralization values from some of the other ecosystem studies in Table 1 is made somewhat easier. When forest floor mineralization is examined the two Picea ecosystems studied in this investigation fall into the lower range of values reported from other coniferous ecosystems around the world. Within the genus Picea, both the P. glauca and P. mariana sites are comparable, in terms of nitrogen mineralization, to a Picea spp. examined at high latitudes in Sweden but much less than temperate Picea sites in Germany and Scotland. Forest floor mineralization for the white birch stand examined in this study was the least of all hardwood ecosystems reviewed. In mineral soil, the mineralization rate in interior Alaskan white spruce is very low, being lowest among Picea systems reviewed, including one Swedish site. The value (5 kg/ha/yr) is somewhat comparable to a Swedish Pinus sylvestris ecosystem, but very low when

all coniferous sites are examined. The low value obtained for white spruce may partially reflect the depth of profile chosen (5 cm, as discussed previously). Variability in depth to bedrock and mineral soil profile depth chosen among researchers makes comparison of mineral soil mineralization rates and pool sizes on an areal basis more difficult than comparison of forest floor parameters.

Few studies report on the effects of clear-felling on mineralization rates, although other cultivation effects have been studied (Table 1). Nonetheless, some review articles on general trends (cf. Vitousek, 1981) and the specific effects (Glavac and Koenies, 1978a, 1980; Matson and Vitousek, 1981) of clearcutting on nitrogen mineralization and nitrification are available. The latter study, however, does not report data on an areal basis although concentration estimates (ug/100g) are reported.

Mineralization rates given for the forest floor of Picea spp. clearcuts in Germany, though, exceed those for interior Alaska clearcuts by a factor of 5 (Glavac and Koenies, 1980) to 10 (Glavac and Koenies, 1978a) times. It is not known, however, whether these authors were utilizing net nitrogen mineralization or simply ammonification in their estimates.

In general, there appears to be some latitudinal control on nitrogen mineralization rates which is likely related

to global temperature patterns. Superimposed upon this pattern is a complex mosaic of other effects including forest (vegetative) cover type, local soil moisture relationships, and degree of disturbance. The forest floor net nitrogen mineralization value obtained in this study (2.48 (mineralization) + 0.06 (nitrification) $g/m^2/yr$ = 25.4 kg/ha/yr) for mature white spruce may be compared to estimates for other cover types in interior Alaska. When net nitrogen mineralization is plotted against annual foliage production, a strong linear relatioship results as reported by Flanagan and Van Cleve (1983) (Figure 18). The P. glauca stand examined in this study lies within the range of nitrogen mineralization values estimated for other P. glauca sites (intermediate amongst other species) using the k-index. This is indirect support for the estimation of nitrogen mineralization from the product of k, the decomposition constant, and the mass of N in the forest floor. Yarie (1983), in applying the FORCYTE yield model to taiga white spruce forests, found net nitrogen mineralization estimates of about 25 kg/ha/yr (June-September) for the forest floor in mature white spruce. This value was calculated within the model from decomposition-nitrogen relationships and was not directly measured. The model also predicted an increase in net nitrogen mineralization to 45 to 50 kg/ha/yr after harvesting with an eventual decline to pre-harvest levels as the stand ages. Under a management regime of thinning and other silvicultural

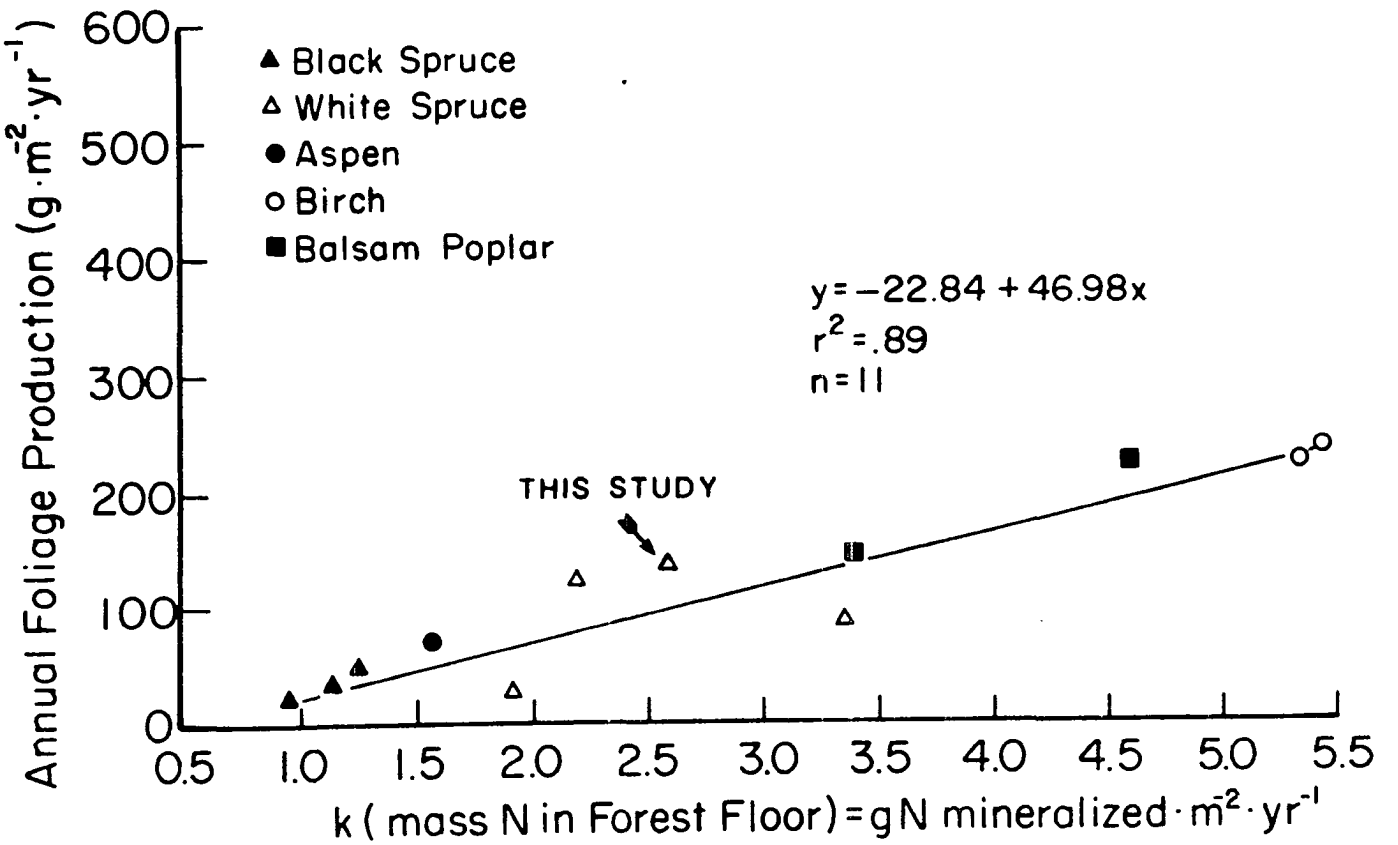


Figure 18. Relationship of annual foliage production to the amount of net nitrogen mineralized per year. This study was not included in the original regression (Flanagan and Van Cleve, 1983). Annual foliage production for this study was estimated from Van Cleve et al. (1983).

activities this decline would be less (to 30-35 kg/ha/yr). These values are roughly in accord with the forest floor net nitrogen mineralization values found in this study. Increased net nitrogen mineralization was not noticed until 2 to 3 years after harvesting, however. The values reported by Yarie (1983) and found in this study are within but towards the lower end of the range of nitrogen mineralization values (9-125 kg/ha/yr) reported for coniferous ecosystems worldwide (Gosz, 1981).

Controls on Nitrogen Mineralization

It was not a specific purpose of this study to examine in detail the relationship between nitrogen mineralization and the physical and chemical factors controlling its magnitude, although it was certainly of interest, especially where differences in these factors between areas or times within the season were noted. The environmental characteristics measured in the three intensive study sites were step-wise regressed upon a variety of nitrogen mineralization and nitrification estimates (see NUMERICAL AND STATISTICAL ANALYSES - Nitrogen Mineralization and Nitrification). The daily rate of mineralization or nitrification ($g/m^2/day$) was determined to be the best dependent variable. No significant relationships were apparent using any combination of the (independent) environmental factors for the forest floor in either clearcut (Table 20). This was also the case when the clearcuts were pooled to increase sample size. In the mineral

Table 20. Regressions of nitrogen mineralization and nitrification on a variety of environmental factors as selected by step-wise regression.

		r^2
	Forest Floor	
Control	Nmin = 0.03151 - (0.17821E-3 x M) + (0.87461E-3 x T)	0.84*
	Nit = -0.001 + (0.9296E-5 x M)	0.52*
	Mineral Horizon	
Control	Nmin = 0.0083 + (0.01875 x R) - (0.46859E-3 x B) - (0.15317E-4 x DD)	0.89*
	Nit = 0.00098 - (0.62058E-4 x M)	0.74*
Cut 1977	Nmin = 0.04057 - (0.14425E-2 x M) + (0.20336E-2 x P)	0.79*
	Nit = -0.00051 + (0.42644E-3 x P)	0.74*
Clearcuts	Nit = -0.00036 + (0.42543E-3 x P)	0.47**

Nmin = nitrogen mineralization rate ($g/m^2/day$)
Nit = nitrification rate ($g/m^2/day$)
M = moisture content (%)
T = soil temperature (^oC)
R = soil respiration ($g\ CO_2/m^2/hr$)
B = moisture content within bags (%)
DD = degree days ($^oC, 0^oC$ base)
P = precipitation (cm)
E = exponent
*,** = significant at $p<0.05$, 0.01 respectively

horizon, no significant regressions were found within the youngest (1978) clearcut but both nitrification and mineralization correlated well with moisture-related factors in the oldest (1977) clearcut (Table 20). Only nitrification could be correlated significantly with an environmental parameter when the clearcuts were pooled.

When negative mineralization and nitrification estimates were removed from the dependent variable array, regressions were improved in almost all cases. However, since these negative values may represent true instances of immobilization (for negative mineralization) or microbial uptake/denitrification (for negative nitrification) these improved regressions were not utilized and are not reported here.

Significant regressions were obtained for both mineralization and nitrification in the forest floor and mineral soil of the control (Table 20). Since only the mineral horizon and not the forest floor of the 1977 clearcut showed significant regressions between mineralization and nitrification and certain physical variables, it was decided not to incorporate the physical variables into the clearcut model (Appendix VI); the amount of information added by the inclusion of these rate equations for the mineral horizon was overshadowed by the fact that significant rate equations could not be developed for the forest floor. (It was not apparent why this was so; day to day fluctuations of greater

magnitude than those occurring in the control area may have had some effect. Certainly, a larger n would have helped). Thus, only the nitrogen cycling model from the uncut area (Appendix V) was tested utilizing nitrification and mineralization rate equations governed by measured physical factors.

Some interesting but rather weak information on the controls of temperature and moisture on nitrogen mineralization is illustrated in Figure 19. Forest floor nitrogen mineralization rates from all study sites, by horizon, are plotted against moisture content for the August, 1979 incubation period. When the deeper (O22) horizons are examined it would appear that there is a strong inverse linear relationship between moisture content and N-mineralization rate. As the forest floor becomes increasingly moist nitrogen mineralization rate declines until it eventually becomes negative (immobilization - black spruce site). Federer (1983) has reiterated the well known fact: anaerobic conditions tend to reduce mineralization. (It should be pointed out that, despite a common sampling time, soil temperatures in black spruce, even in the forest floor, will be less than those from white birch and white spruce sites. Thus temperature may act in conjunction with moisture content to reduce mineralization). The upper horizons (O1, O21) and the top 5 cm of organic material in the disturbed sites do not appear to

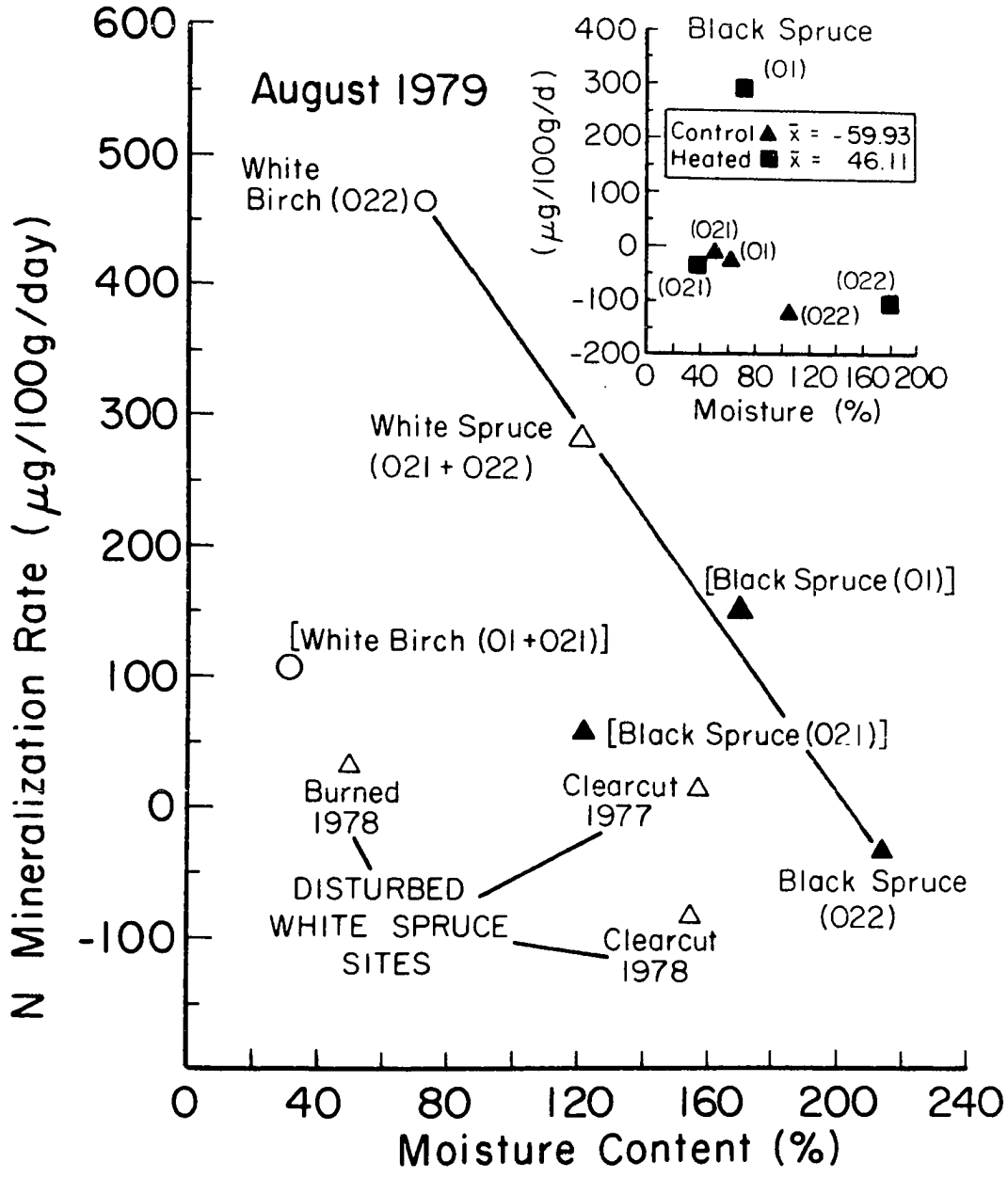


Figure 19. Nitrogen mineralization rate as a function of forest floor moisture content for a variety of sites investigated. The relationship suggested by the diagonal line is not a result of regression. Upper horizons illustrated by [] and disturbed white spruce sites should be excluded from this hypothetical relationship. The inset illustrates the effect of temperature on N-mineralization rates in the forest floor of the semi-intensive black spruce site.

follow this pattern. This would suggest that moisture content may be the more important factor deeper in the forest floor where the influence of solar radiation may not be as strongly felt and soils are colder.

Further support for this hypothesis can be seen when the data from the "heated-control" experiment in black spruce is examined (Figure 19, inset). Although increased soil temperature significantly increased nitrogen mineralization rate (all horizons pooled) from -59.93 to 46.11 ug/100g/day ($p<0.05$), this increase was almost wholly due to increased mineralization in the Ol horizon. Increased soil temperature did not enhance mineralization in either the 021 or 022 horizon. Moisture content, as previously suggested, may be the stronger control here. Temperature may be more important in the upper layers where solar radiation can exert a stronger influence.

This might be especially true in taiga forests at high latitudes where temperature is a major control on terrestrial ecosystem processes. In more temperate regions, this hypothesis might not hold. Federer (1983), for example, working in the northeastern United States was unable to quantifiy the depth effects of temperature and aeration on nitrogen mineralization. He did note that decreasing temperature with depth did control the gradual reduction in mineralization but that this could not account for all the variation observed.

The information presented here in support of these ideas is at best, hypothetical. I should point out that the diagonal line in Figure 19 is not a regression line and that the samples from the white spruce control include the lower portion of the O21 horizon. In addition, both data sets are small and only represent an incubation period of one month (August 1979). The patterns are interesting but probably more complicated than is inferred here. It would be worthwhile to investigate further the effects of these primary controls and their interaction on nitrogen mineralization over a wide array of site conditions.

One complicating factor to the above discussion is that the quality of the organic matter itself may exert tremendous control on nitrogen mineralization. For example, Federer (1983) suggested that organic matter is harder to decompose at deeper depths. Conceivably this could be due to increased organic matter polymerization with age. When average N-mineralization rate in the forest floor was regressed on average forest floor lignin concentration, a non-significant relationship was found (Figure 20), although the trend was correct. When forest floor lignin-nitrogen ratio (9.5 for white birch and between 21 and 30 for all coniferous sites) was used as the independent variable, a tighter spread of data resulted, but this was still non-significant. An even poorer relationship was found with cellulose. However, the sample size was small and again limited to one sampling

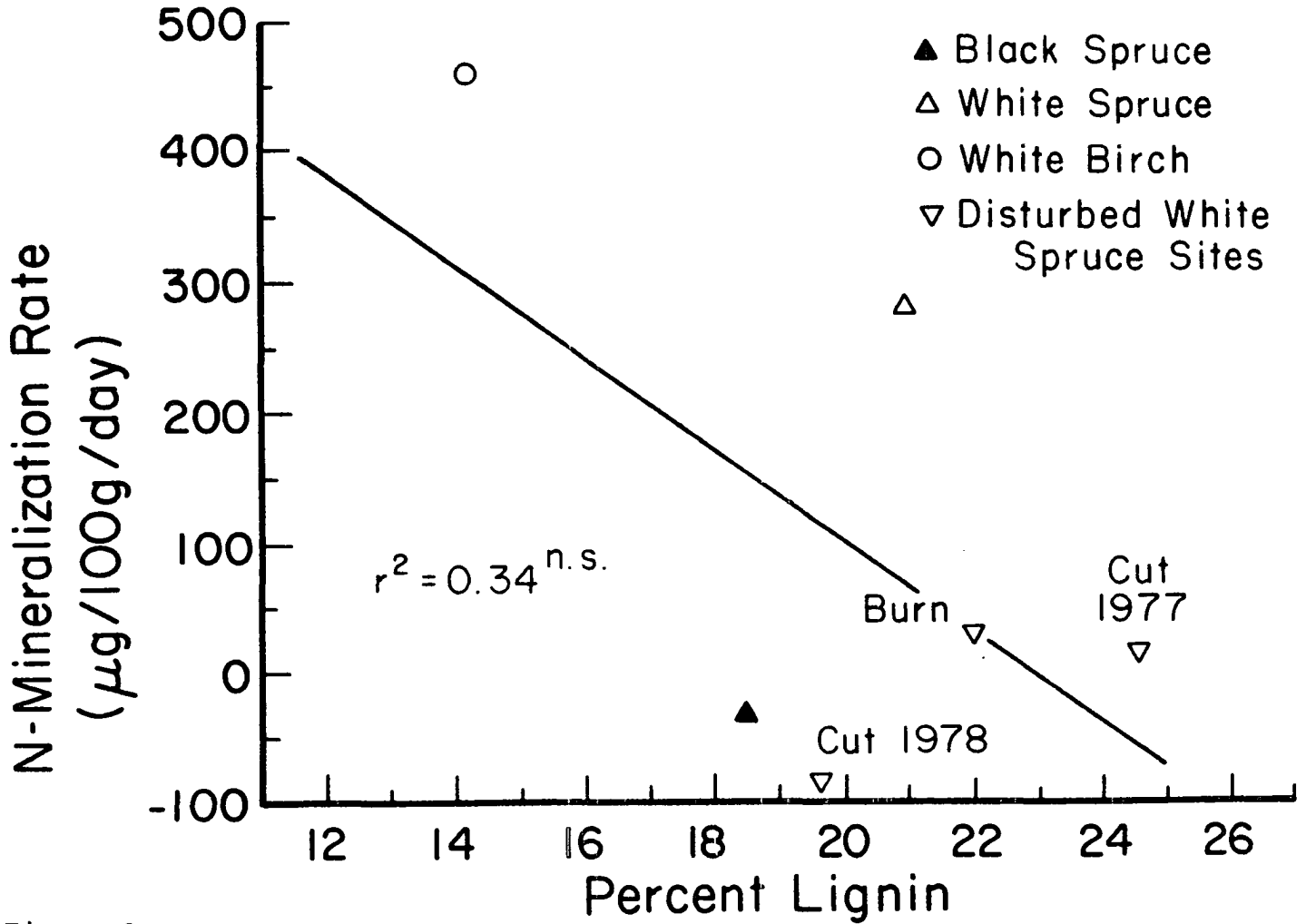


Figure 20. Relationship of N-mineralization to lignin concentration (%) in the forest floor of all study sites.

period. Previous work has indicated that decomposition rate and lignin in the O22 horizon are inversely related (cf. Flanagan and Van Cleve, 1983). This relationship appears to hold for the site examined in this study; a tighter experiment with a larger n would help to confirm this.

Ammonium availabiltity has previously been suggested as a control on nitrification (cf. Vitousek, 1977; Vitousek and Reiners, 1975, and many others). Actually, for autotrophic NO_3-N production, this is an axiom: there must be a substrate to oxidize. Regressions of after-incubation nitrate values (area averages) on pre-incubation ammonium values did not confirm this. Although significant relationships (r^2=0.60**, 0.82**, 0.68**, 0.46* for the 1978 clearcut, 1977 clearcut, both clearcuts together and the control, respectively) were found when forest floor and mineral horizon data were pooled for analysis, the relationship was non-significant for all instances when individual horizons within areas were examined. The variables employed in the regression may have been more highly correlated in the situation where NH_4-N is limiting. Nonetheless, the results from the pooled horizon data (higher n than regression using one horizon) were encouraging. In retrospect, regression utilizing N-values from individual bags rather than area averages as the sample unit might yield more information. The amount of NH_4-N lost and the amount of NO_3-N gained could also be used as an independent and dependent variable, respectively.

Seasonal Distribution of Subsample Nitrogen

Results for available nitrogen analysis for the forest floor and mineral soil (sub- and incubated samples) are shown in Figure 21. The block of bars on the far left illustrate NH_4-N and NO_3-N levels from mid 1979 through May, 1981, (22 continuous months of incubation) for the control area. Similarly the blocks in the center and on the right express the same factors over the same period for the 1978 and 1977 clearcut respectively. Since subsets of this data (in a variety of combinations) were used in the development of the model, the values in Figure 21 are reported in g/m^2. Statistical analyses were performed on data both in this form and on a concentration basis (Appendix III). Results were the same regardless of which form of data was used. This was despite the fact that expression on an areal basis widened the distance between forest floor data from the control area and the clearcuts due to decreased depth of organic matter and thus increased bulk density in the clearcut areas. Mineral soil data was not affected since bulk density was unaffected by harvesting. In addition, a standard mineral soil depth of 5 cm was used in all areas.

For both the forest floor and mineral soil in the uncut situation the concept of an ammonium-dominated climax ecosystem (Rice and Pancholy, 1972) can be seen (use only subsample bars for comparison). In such systems, NH_4-N is

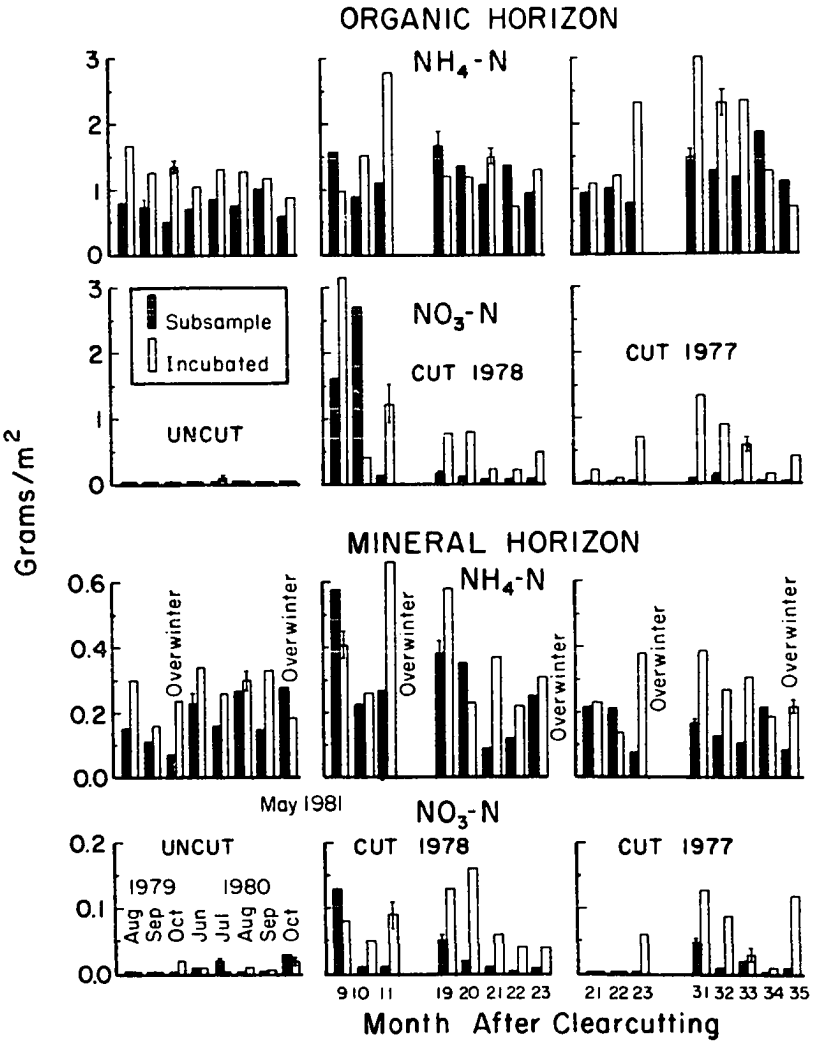


Figure 21. Distribution of available nitrogen (NH_4-N, NO_3-N) in the forest floor and mineral horizon of all intensive study sites for all sampling periods. Subsample and incubated levels are given. Some typical standard errors are illustrated.

probably the preferred nitrogen species by plants (and possibly by microbes) since less energy must be expended to incorporate NH_4-N, as opposed to nitrogen in NO_3-N, into protein structures (Haynes and Goh, 1978). Little nitrate is present in the soil system, a likely result of low nitrification rates, although it has been suggested that high nitrification rates with correspondingly high rates of NO_3-N uptake could also lead to a similar distribution of available nitrogen in the soil (Vitousek, 1977). Whatever the reason, the ammonium to nitrate ratio (Table 21) for the forest floor in the uncut area is very high, relative to the youngest (1978) clearcut although the oldest (1977) clearcut also has a high NH_4-N/NO_3-N ratio. In the mineral horizon NH_4-N/NO_3-N ratios are roughly equivalent across areas. The white spruce forest floor NH_4-N/NO_3-N ratio from this study is far greater than that from another upland white spruce site studied previously. No explanation is available. However, it is interesting to note that the greatest spread (1000:1) between levels of NH_4-N and NO_3-N occurred in the very ammoniun-dominated forest floor of the black spruce stand.

Unincubated forest floor ammonium levels (instantaneous net pool size) in the forest floor from the control varied from 0.5 to 1.0 g/m^2 (~5,000-10,000 ug/100g dry soil) and in the mineral soil from 0.1 to 0.3 g/m^2 (~150 to 550 ug/100g), indicating a wide variation in background ammonium levels.

Table 21. Ammonium/nitrate ratios for the forest floor and mineral soil of selected study sites.

	NH_4/NO_3 ($S_{\bar{x}}$)[a]	
Forest Floor		
Intensive Sites		
Clearcut 1978	9.81	(2.39)
Clearcut 1977	170.79	(83.72)
Control	162.60	(92.45)
Semi-intensive Sites		
Burned White spruce	107.14	(58.63)
Black spruce	1157.75	(1021.38)
White birch	105.53	(25.18)
Mineral Soil		
Intensive Sites		
Clearcut 1978	18.91	(4.30)
Clearcut 1977	9.77	(3.87)
Control	11.90	(2.65)
Semi-intensive Sites		
Burned White spruce	89.87	(34.48)
Black spruce	n.d.[b]	
White birch	683.76[c]	
Data on file[d]		
White spruce (upland)	9.56	(1.29)
White spruce (floodplain)	7.88	(1.08)
Balsam poplar	73.69	(25.46)
sandbar, Tanana river	1.11	(0.28)

[a] does not include cases where nitrate was not found
[b] mineral horizon not sampled - frozen
[c] approximation only. Nitrate found in only 7% of samples
[d] Forest Soils Laboratory study, 1977-1978

In the 1978 clearcut, ammonium levels varied from about 0.75 to 1.5 g/m^2 (~4300 to 8400 ug/100g) in the forest floor and from 0.1 to 0.6 g/m^2 (200 to 1300 ug/100g) in the mineral soil. In the 1977 clearcut ammonium in the forest floor also ranged from 0.75 to 1.5 g/m^2 (3900 to 9400 ug/100g), and in the mineral soil, from 0.1 to 0.2 g/m^2 (4900 to 9400 ug/100g).

Nitrate levels, as previously mentioned, were extremely low in the uncut area (less than 0.1 g/m^2 for both the forest floor and the mineral soil). However, NO_3-N levels were substantially higher in both clearcuts. Almost 3 g/m^2 (14,000 ug/100g) were found in some cases in the forest floor of the 1978 clearcut although the 1977 clearcut had very little (<0.5 g/m^2 or <400 ug/100g). In the mineral horizon, the NO_3-N levels reached almost 0.15 g/m^2 (300 ug/100g) for the 1978 clearcut and 0.05 g/m^2 (100 ug/100g) for the 1977 clearcut.

Separate 3-way analyses of variance on subsample NH_4-N and NO_3-N data sets by horizon, study area and sampling time showed all three factors and interactions to be highly significant for both forms of nitrogen. A multiple classification analysis on NH_4-N showed 56% of the variation in the total data set to be due to horizon, 3% due to sampling time and only 1% due to area. No discernible trends (80% error) were found when NO_3-N was examined. The results from the analysis for NH_4-N illustrates the importance of the forest floor

horizon as a potential supplier of nitrogen to the site, even after disturbance.

Year to year differences in NH_4-N and NO_3-N in the forest floor and mineral soil of all of the intensive sites were tested using the t-statistic (Table 22). Forest floor NH_4-N was consistently higher in 1980 than in 1979 for all areas. However, for mineral soil NH_4-N, and NO_3-N in both the forest floor and mineral soil, the results were variable and no distinct patterns were apparent. Even for forest floor NH_4-N the differences were not large. Since seasonal differences were noted in the control areas as well as the clearcuts these differences likely represent year to year variation in background NH_4-N levels possibly attributable to variation in rainfall N-content and degree of canopy wash. Since the 1980 season had 5 sampling periods and the 1979 only 3, another contrast was conducted, this time utilizing only the 3 incubation periods that were similar between seasons. Generally, the same patterns were repeated but again variability obscured any distinct trends or differences. For both NH_4-N and NO_3-N in both horizons from all areas, a single-factor ANOVA showed sampling time to be a significant effect. However, multiple-range testing revealed no consistent patterns within area or horizon.

Subsample NH_4-N and NO_3-N are compared across areas by sampling period in Table 23. Results were variable. For forest floor NH_4-N the control differed from both clearcuts

Table 22. Distribution of NH_4-N and NO_3-N in the forest floor and mineral soil of the three intensive study sites, by year, (ug/100g ($S_{\bar{x}}$)).

	Forest Floor			
	NH_4		NO_3	
	1979	1980	1979	1980
Clearcut 1978	5950.03 (525.39)	6486.36 (350.06)**	7464.59 (1118.16)	507.54 (46.53)**
Clearcut 1977	4688.61 (238.85)	7033.03 (291.58)**	34.76 (11.03)	197.01 (24.07)**
Control	6935.31 (419.86)	8100.58 (321.79)**	0 (0)	88.97 (7.82)**
	Mineral Soil			
Clearcut 1978	801.85 (59.38)	528.15 (32.85)	102.75 (34.88)	37.88 (5.44)
Clearcut 1977	339.37 (27.42)	289.42 (13.35)**	0 (0)	32.22 (3.62)**
Control	219.18 (12.88)	422.29 (26.41)**	0 (0)	24.86 (7.19)**

** significant at $p<0.05$

Table 23. Distribution of sub-sample NH_4-N and NO_3-N in the forest floor and mineral soil by study site and sampling time (ug/100g).

	Sampling Period	Clearcut 1978	Clearcut 1977	Control
		Forest Floor		
NH_4	1	4924.56	7859.89[a]	8329.79[a]
	2	5203.95[a]	4333.28[a]	7531.71
	3	3988.86[a]	5603.97[b]	4944.42[a,b]
	4	7640.54[a]	8377.56[a]	7218.30[a]
	5	6512.12[a]	6886.73[a]	8888.46[a]
	6	5929.82[a]	5372.15[a]	7543.96
	7	9424.81[a]	6967.01	10600.28[a]
	8	5654.88	4787.97	6137.83
NO_3	1	23.76[a]	8162.07	0[a]
	2	38.95[a]	13582.00	0[a]
	3	41.16[a]	649.68	0[a]
	4	357.38	809.39	96.56
	5	627.28	363.51	121.44
	6	46.69[a]	315.26	98.86[a]
	7	12.85[a]	356.42	19.92[a]
	8	196.22[a]	448.36	108.41[a]
		Mineral Soil		
NH_4	1	444.94[a]	1278.40	294.68[a]
	2	411.43[a]	513.65[a]	220.79
	3	162.90[a]	599.56	142.02[a]
	4	344.52[a]	836.51	444.31[a]
	5	266.74[a]	782.57	301.75[a]
	6	221.66[a]	194.36[a]	515.39
	7	431.00	256.91[a]	289.28[a]
	8	182.43	558.88[a]	553.28[a]
NO_3	1	0.00[a]	283.94	0.00[a]
	2	0.00[a]	17.82	0.00[a]
	3	0.00[a]	19.00	0.00[a]
	4	96.20[a]	105.52[a]	25.90
	5	12.65	51.39[a]	34.82[a]
	6	31.86	14.63	0.00
	7	0.00[a]	0.00[a]	0.00[a]
	8	24.42[a]	18.19[a]	55.95[a]

[a] No significant difference exists between areas with the same superscript ($p<.05$). This data is presented in a different format in Appendix III. Standard errors can be found there. Sampling periods are also described in in Appendix III.

on only 3 out of 8 sampling dates. At other times, the control differed from only one of the two clearcuts, usually having higher NH_4-N concentrations. During June and July there was no difference between areas. For forest floor NO_3-N, the control rarely differed from the 1978 clearcut but most always from the 1977 clearcut. Conversely to that found for NH_4-N, all three areas differed from each other only during June and July. Ammonium-N in the mineral soil of the control differed from both clearcuts on only two occasions and the trend was not consistent. Usually the control differed from one clearcut but not the other. The same vague results were evident for NO_3-N in the mineral horizon.

The purpose of testing subsample available nitrogen levels across areas and sampling year was to establish a basis for comparison of mineralization and nitrification rates. It was desirable to know by how much, if any, substrate (time-zero) levels of NH_4-N and NO_3-N differed between areas as this could conceivably affect these rates. It should be remembered that even instantaneous subsample N values reflect mineralization and nitrification rates up to that point in time. The variability in NH_4-N and NO_3-N across areas, while not consistent, is enough to suggest that these two processes are working differently in the areas examined. However, baseline differences in available nitrogen levels are not large or consistent enough to suggest to

what extent mineralization and nitrification are affected by harvesting.

Mineralization and Nitrification Rates

Mineralization and nitrification rates were calculated by subtracting subsample from incubated NH_4-N and NO_3-N values (Appendix III) and dividing by the number of days of incubation. In only a few instances were subsample estimates not significantly different from incubated estimates. However as can be seen from Figure 21 not all of the incubated estimates were higher than subsample estimates indicating that some immobilization had occurred. The absolute differences between subsamples and incubated samples by sampling period and area are given in Appendix IV. Also included there are estimates of the number of bags per incubation period showing positive gains. These are summarized in Table 24. Note that the differences presented in Appendix IV are not exactly the differences obtained by subtracting subsample from incubated values (Appendix III). This is because Appendix III represents averages of sampling periods with variable n. The differences in Appendix IV were calculated by direct subtraction. The n of each subset was adjusted wherever missing data in one subset (incubated or subsample) precluded subtraction.

The data presented in Table 24 are interesting. Almost 90% of the bags in the control forest floor showed positive gains. Those that were negative must have been so only

Table 24. Percentage of bags showing positive gains in NH_4-N or NO_3-N after incubation.

	Forest Floor		
	Clearcut 1978	Clearcut 1977	Control
NH_4	59.3	69.3	89.0
NO_3	77.2	81.6	40.6
	Mineral Soil		
NH_4	71.5	73.8	81.4
NO_3	74.7	56.2	40.1

slightly since the positive increases were more than enough to ensure that positive gains in NH_4-N occurred during all sampling periods (Figure 21, NH_4-N, forest floor). A smaller percentage of bags in the clearcut areas showed positive gains resulting in negative changes for some sampling times. This is likely the result of increased nitrification. More than 75% of the bags in the clearcuts showed positive gains in NO_3-N; only 40% did in the control. This resulted in measureable amounts of NO_3-N being produced in the clearcut areas (Figure 21). The same basic pattern of gains in nitrogen by bags is also evident in the mineral soil although to a lesser degree than in the forest floor. The data in Table 24 give an indication of the changes that occur within the forest floor after harvesting. These changes do not appear to be as drastic in the more "buffered" mineral soil.

Nitrate is much more prevalent in the disturbed areas and it is possible that it is preferentially taken up by many of the the plant species growing there. Plants with a large photosynthetic capacity, such as those found in disturbed situations, might be expected to have a net energy balance which would allow the expenditure of energy necessary to push the oxidation state of nitrogen from +5 to -3, as it occurs in ammonium and many protein associations. Middleton and Smith (1979), working with grasses, indicate that the difference in total energy costs for nitrogen uptake is only 8% greater when the nitrate form is assimilated in favour of the

ammoniacal form. The excess NO_3-N found in the harvested areas is likely assimilated as Calamagrostis becomes established on the site. Under higher precipitation regimes, NO_3-N could also be rapidly leached from the site (or at least moved downward in the profile). Data from the soil solution samplers did not confirm this (Table 16). On the other hand, early successional plants may follow a strategy of preferentially utilizing reduced nitrogen (NH_4-N) in favour of NO_3-N, thus saving energy which could be used for carbon fixation and growth. The form in which nitrogen is taken up is important when considering the ability of white spruce seedlings, for example, to compete effectively for nitrogen with other species of plants. This discussion refers solely to nutrition; mechanical site-preparation (e.g. scalping) is one way to ensure good white spruce survival in the presence of competition.

Nine to 11 months after harvesting, NO_3-N levels are extremely high and varied, especially in the forest floor. (Compare to NO_3-N levels in the control). Thereafter, they decline to relatively low levels, although remaining higher than in the mature forest. In all cases except for one, nitrification substantially increased NO_3-N levels in incubated bags both in the forest floor and mineral soil. After the 19th month following harvesting the levels of NO_3-N from incubated samples were always higher than subsamples taken from the site for the next incubation period. This

indicates that NO_3-N is being rapidly leached from this system or taken up by plants. Nitrate-N is excluded from root uptake and is unable to leach from the samples incubated in polyethylene bags and is essentially "captured" for analysis.

Seasonal patterns of nitrification after harvesting are illustrated in Figure 22. A simple inverse linear regression has been fitted to these data and is presented in Figure 23. Estimates of nitrification taken during the summer were, in all cases, significantly higher than spring and fall estimates. The lack of nitrate in the control area suggests that nitrifier populations are under possible chemical control by climax vegetation as suggested by Rice and Pancholy (1972). In addition, between nine and 40 months after clear-cutting the maximum rate of nitrification does not appear to be related to time after harvesting but rather to seasonal (climatic) phenomena. These patterns of fluctuating rates should be superimposed upon a general decline in absolute levels of soil NO_3-N (Figure 21) as nitrate produced is lost from the forest floor.

Seasonal patterns of nitrogen mineralization after harvesting are illustrated in Figure 24. Although the highest value in each sequence illustrated in Figure 24 was always significantly different ($p<0.05$) from the lowest value, seasonal patterns are not readily apparent. It does appear that mineralization trends shortly after cutting

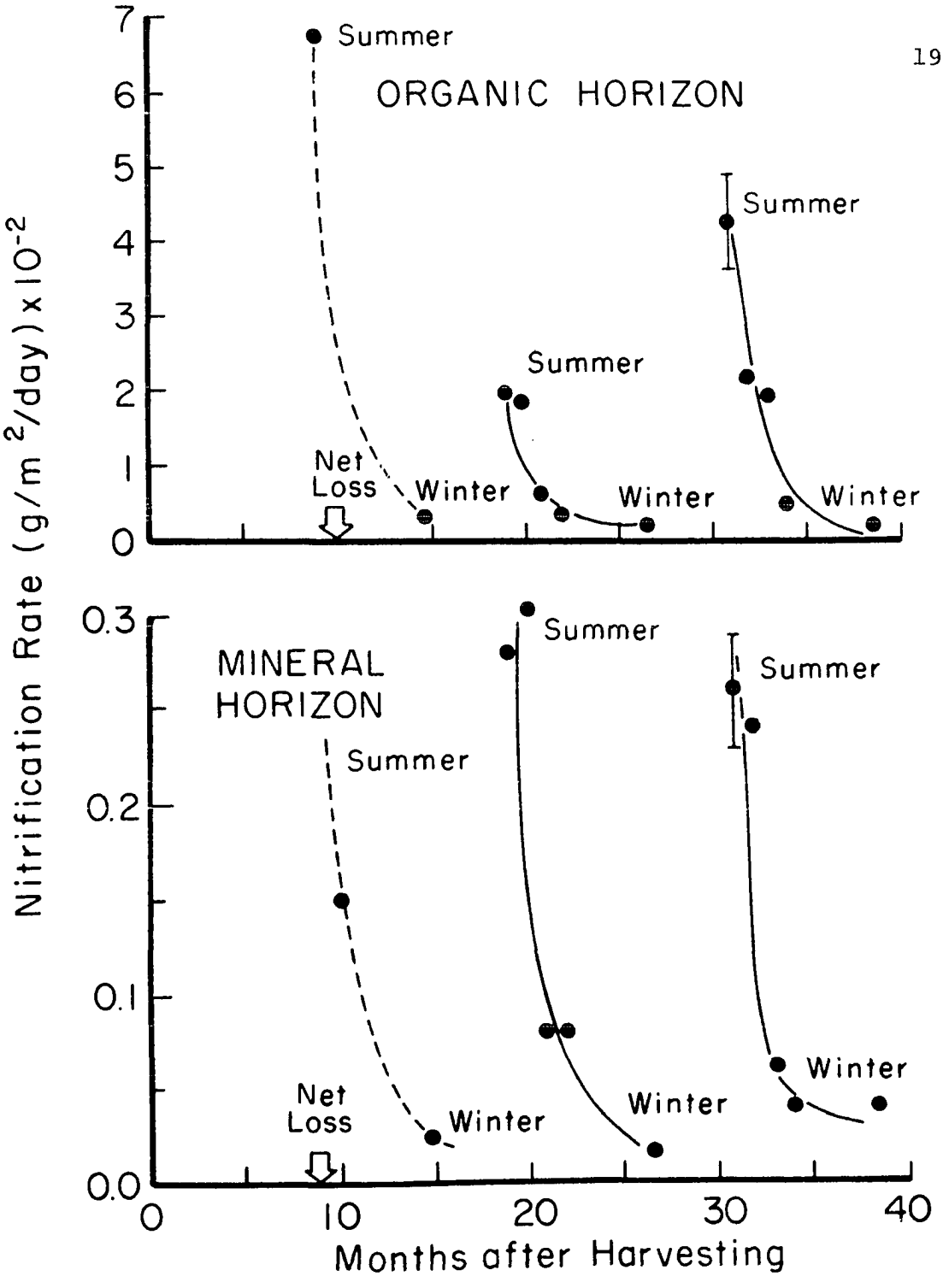


Figure 22. Seasonal patterns of soil nitrification in the forest floor and mineral horizon following harvesting of interior white spruce stands. Two typical standard errors are illustrated. The dashed line represents the theoretical decline in nitrification between months 10 and 15, ignoring the net loss in each case.

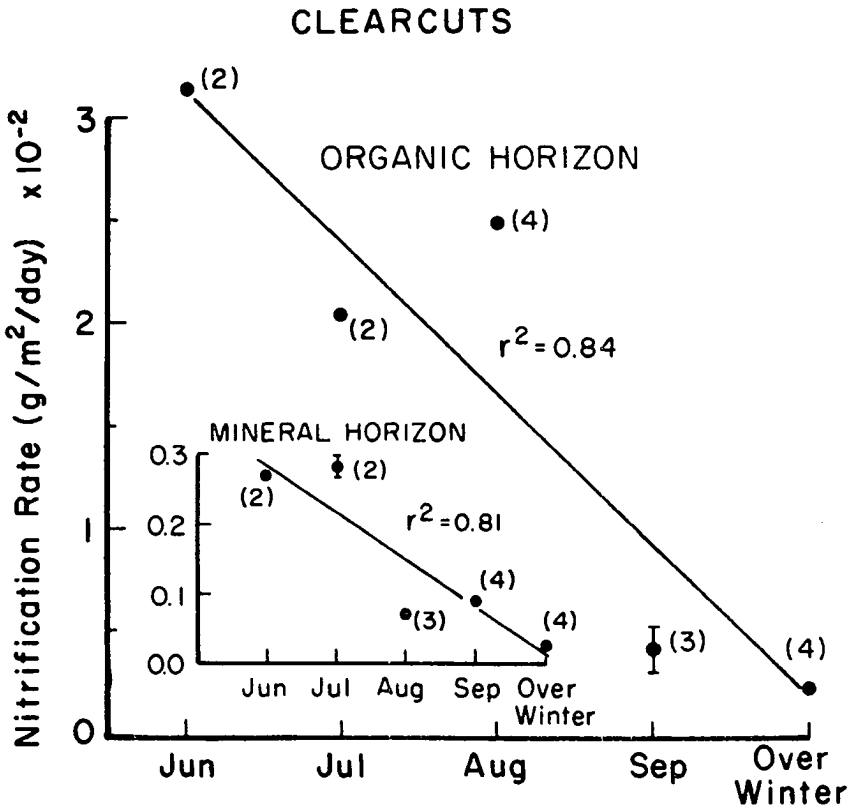


Figure 23. Relationship of soil nitrification rate to time within season for the forest floor and mineral horizon of harvested white spruce sites in interior Alaska.

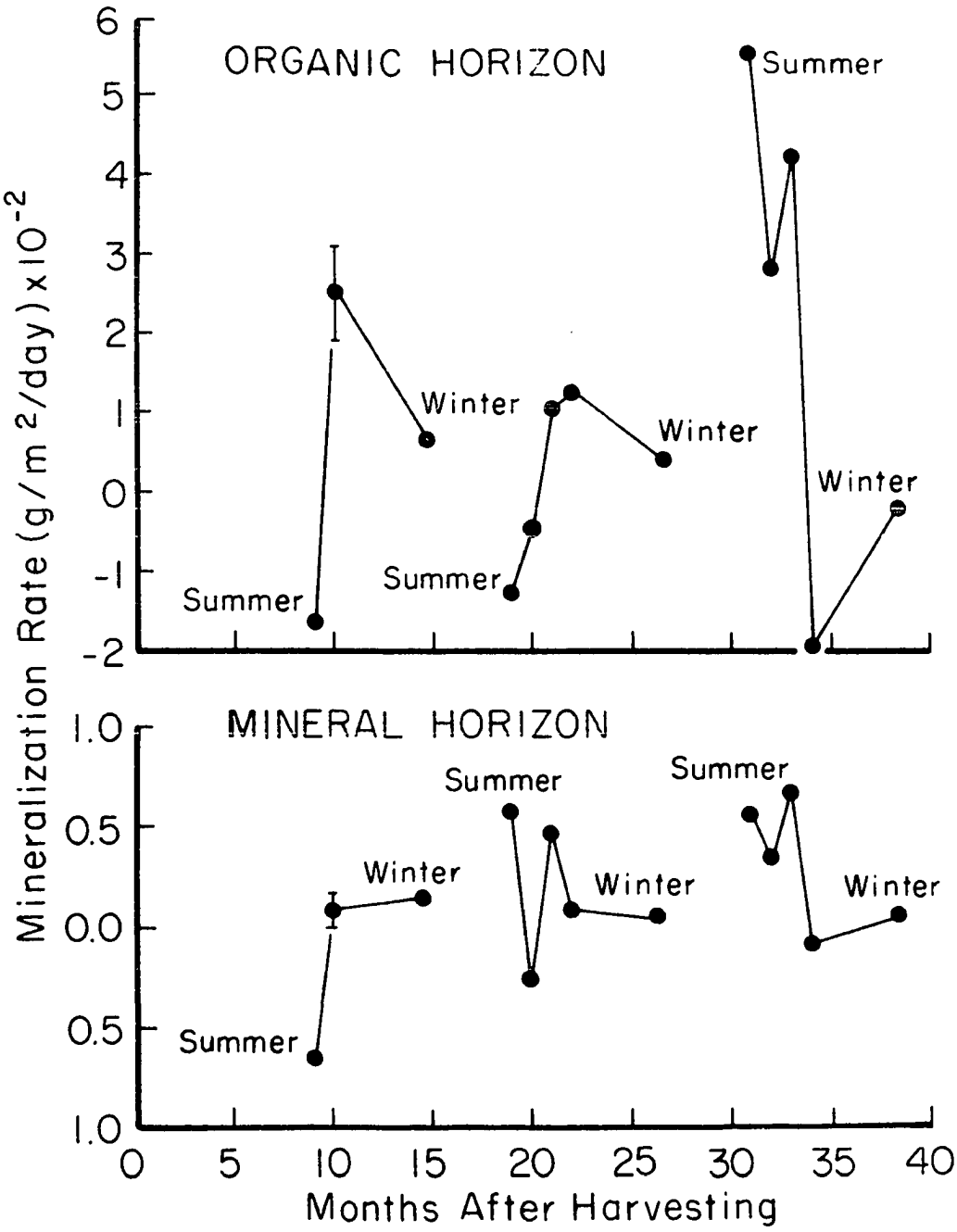


Figure 24. Seasonal patterns of soil mineralization in the forest floor and mineral horizon following harvesting of interior white spruce stands. Some typical standard errors are illustrated.

(winter>summer) progressively reverse until approximately three years after harvesting, when summer rates are higher than winter rates. ("Winter" refers actually to the late fall before freeze-up and the late spring period immediately prior to the removal of bags.) This is very interesting. Since seasonality of nitrification is so pronounced almost immediately after harvesting (Figure 22) and the trends are repeatable, these changes in mineralization rates (by definition, thus reflecting net changes in the NH_4-N pool) cannot be a consequence of changing nitrification rates.

One possible explanation is that shortly after harvesting few changes in the chemical quality of the decomposable substrate would have occurred (see Table 3). Despite almost immediate changes in moisture and temperature regimes, mineralization may be under stronger control by organic matter quality. The "winter" highs portrayed actually represent mineralization rates occurring in early autumn and late spring. During this time the physical structure of the substrate may be under severe stress due to repeated freezing and thawing. There may actually be some physical release of ammonium during this time, accounting for the higher rates of release in the winter. Another factor to consider is that immobilization by organisms responding to immediate decomposition of fine twigs and needles could account for the low summer rates of mineralization (note negative values in Figure 24). However, after several years the decomposition

of readily-decomposed material will slow, thus decreasing immobilization. Temperature and moisture controls on mineralization may become more important. As well, at this time, the organic substrate should have been further weakened by microbial activity and more susceptible to mineralization. Of interest are the findings of Burger and Pritchett (1984) who suggested that N asociated with the organic matter on intensively-treated (silviculturally) sites may be more resistant to decomposition. This was based on the ratio of organic matter to soluble carbon.

Some additional evidence that supports the idea that organic matter quality controls nitrogen mineralization was uncovered when soil solution was fractionated on Sephadex G-25 (see methods for Candler and Van Cleve, 1982: this experiment is still in progress and neither methods or results are fully presented here). In the clearcut areas, the most nitrogen (soluble organic) was associated with compounds having a molecular weight of less than 5000 Daltons (1 D = 1.67×10^{-24} g). However, in the control area nitrogen was strongly associated with high molecular weight compounds (>5000 Daltons). This indicates that harvesting initially causes a breakdown of organic matter into (soluble) nitrogen-rich compounds. Although mobile, these are still molecularly complex and would have to undergo further transformation before plants could utilize the nitrogen confined therein.

Nitrogen mineralization rates are compared between the control area and the clearcuts (averaged) by sampling period in Figure 25. Very generally, little substantial difference exists between areas in terms of forest floor or mineral soil mineralization rates in 1980. In 1979, the clearcuts showed less mineralization than the control area in August, although the rates were roughly equivalent during other sampling times that year. A quick perusal of the climatic data in Table 12 provided no reason that this should be so and without more data on organic matter quality these low mineralization rates must be attributed to random seasonal fluctuations.

Analyses of variance were performed on both mineralization and nitrification rate and on the total NH_4-N or NO_3-N produced on incubation across areas. The results are presented in Table 25 but before discussing these, several points should be made. Bartlett's test for homogeneity of variances rarely indicated that variances between groups were sufficiently homogeneous to allow further testing. However, in addition to being able to withstand even large deviations from normality in the populations being considered, the "analysis of variance is robust enough to operate well even with considerable heterogeneity of variances, as long as all n_i are equal or nearly equal" (Zar, 1974; p. 135). In this particular instance all sample sizes were equal (n=8).

As well, the values presented in Table 25 are averages of the 8 sampling periods (Figure 25) within areas. Thus,

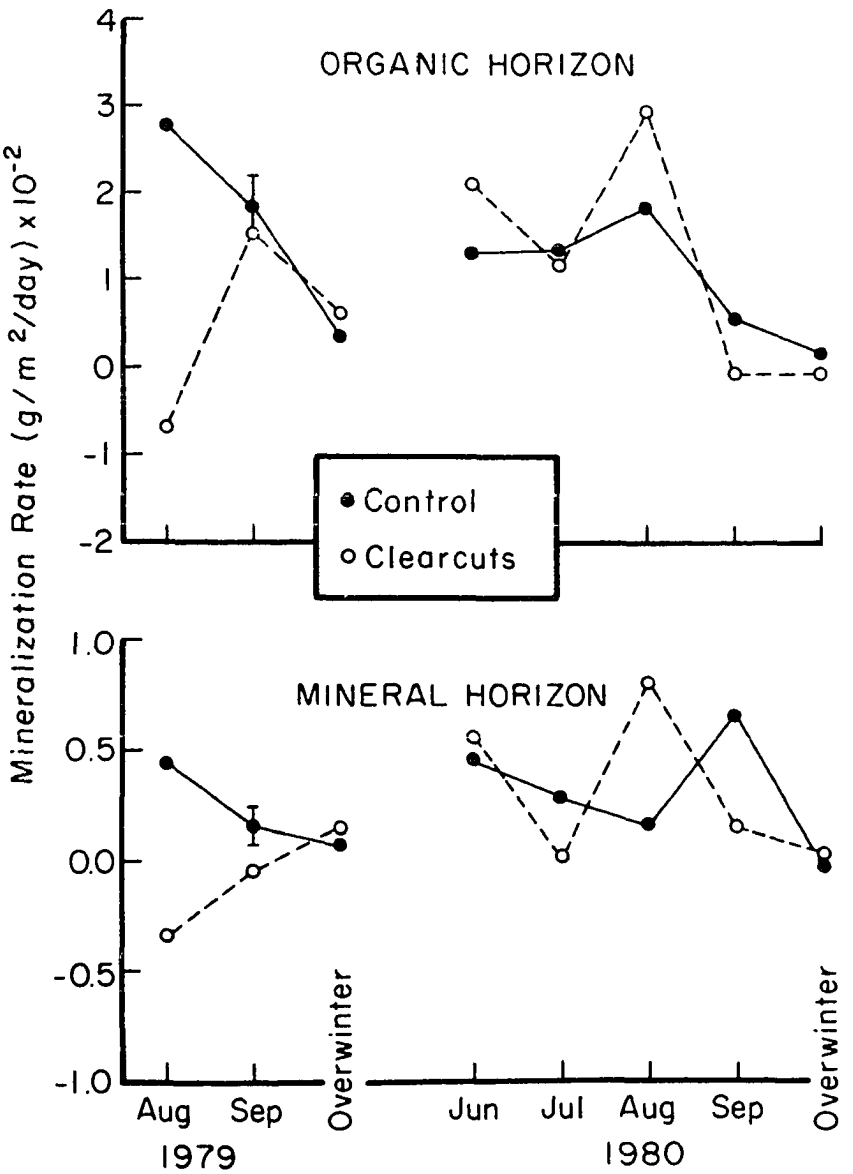


Figure 25. Comparison of mineralization rate (forest floor and mineral horizon) between the control area and the clearcut areas (average of two). Some typical standard errors are illustrated.

Table 25. Nitrogen mineralization and nitrification rates and total NH_4-N or NO_3-N produced during incubation from the forest floor and mineral soil of the three intensive study sites (g/m^2/day ($S_{\bar{x}}$)).

	Clearcut 1978	Clearcut 1977	Control
		Forest Floor	
Mineralization	-0.0002 (0.0056)[a]	0.0151 (0.0087)[a]	0.0128 (0.0032)[a]
(NH_4-N produced)[b,c]	0.1970 (0.2603)[a]	0.5822 (0.3023)[a]	0.5157 (0.0883)[a]
Nitrification	0.0008 (0.0162)[a]	0.0128 (0.0051)[a]	0.0002 (0.0002)[a]
(NO_3-N produced)[b]	0.2428 (0.4908)[a]	0.5023 (0.1342)[a]	0.0090 (0.0054)[a]
		Mineral Soil	
Mineralization	0.0016 (0.0018)[a]	0.0019 (0.0011)[a]	0.0027 (0.0008)[a]
(NH_4-N produced)	0.0893 (0.0648)[a]	0.1005 (0.0418)[a]	0.0931 (0.0279)[a]
Nitrification[c]	0.0012 (0.0005)[a]	0.0008 (0.0004)[a]	-0.0001 (0.0001)[a]
(NO_3-N produced)	0.0428 (0.0169)[a]	0.0428 (0.0142)[a]	0.0011 (0.0042)

[a] No significant difference ($p<.05$) between areas with values having the same superscript

[b] Total amount of NH_4-N (or NO_3-N) produced during the incubation period (g/m^2; n=8)

[c] Two of out four multiple range tests employed (main ANOVA n.s.) showed control to be significantly different from the 1978 clearcut

the analysis of variance was performed with a very small n (8). Each point (Figure 25) however, is an average of between 20 and 30 field determinations (some typical variability in this estimate can be seen in the standard error bar in Figure 25). Theoretically, it would have been possible to determine mineralization and nitrification rates for all bags thus increasing the n to between 160 and 240 when averages across areas were compared. However, I chose to use the smaller n for several reasons. First, even with an n of 20 to 30 per area per horizon, microsite diversity is such that variability is still very high. Some indication of this can be seen when the standard errors in Appendix III and IV are examined. The values therein are based on n=30. There was some doubt that even the use of the larger sample size could overcome variability in the data. Second, the use of the smaller sample size is generally more conservative. Significant relationships will be revealed if they exist, not because they are a residual of large sample size (cf. Robertson, 1982a). Finally, the use of the larger sample size almost implies that this information is useful and necessary in application to forest management - that we know enough about microclimate and mineralization on a m^2-basis to be able to determine the best planting sites for white spruce seedlings. This is not the case. Operationally, selection of sites should favour the most protected ones - expanding

root systems should naturally locate areas of high mineralization.

There will be times during the growing season when more available nitrogen is in the clearcuts than is taken up by white spruce seedlings (or other vegetation). Similarly, there will be times when plants may be stressed due to lack of mineral nitrogen (symptoms: chlorosis) although soil moisture content is probably the more important factor. What seems important then is the average rate of nitrogen supply and the total amount of nitrogen supplied to the site on a periodic basis over the growing season. I feel the results of the test as designed give a good indication of this.

As expected, no significant difference in mineralization rates in either the forest floor or mineral horizon was found between areas. This was also the case when the total NH_4-N produced on incubation was examined, although in the forest floor the main ANOVA was only slightly non-significant ($p<.05$): 2 of the 4 multiple range tests employed showed the control produced more NH_4-N than the 1978 clearcut. When forest floor nitrification rates were examined no significant differences were found among areas; neither was the NO_3-N produced greater in the clearcut areas. However, in the mineral soil, the amount of NO_3-N produced was greater in both clearcuts when compared to the control. In addition, the nitrification rate was only slightly non-significant;

several multiple range tests showed the clearcuts to have higher nitrification rates.

I do not consider statistical significance to be a prerequisite to the formation of a theory; one cannot conclusively say from a statistical association, or lack thereof, that a cause-effect relationship exists. I do feel confident that, as indicated by the statistical analysis in Table 25, the mineralization estimates for the three areas do not differ among themselves. This statement is more correct if the clearcuts are averaged and compared to the control area (Figure 25) since the control area appears to have a higher mineralization rate than the 1978 clearcut by itself (Table 25; 64 times greater, although the standard error for the latter is quite high). On the other hand, despite the results of the statistical analyses, it is obvious that at least during part of the growing season nitrification rates are enhanced in the clearcut areas. In the forest floor the average nitrification rate (over all sampling periods) is 4 and 64 times greater than nitrification in the control area for the 1978 and 1977 clearcuts respectively. In the mineral soil, nitrification estimates from the same 2 clearcuts are 12 and 8 times greater than nitrification in the control. When the seasonal pattern of nitrification is considered (Figure 22) it is easy to see that summer rates of nitrification in the clearcuts are higher than nitrification in the control (essentially 0 in both forest floor and mineral soil

over the entire season). However, when averages are considered, the low n in the ANOVA is a factor contributing to the conclusion presented in Table 25: there is no difference in nitrification rate among areas.

Interestingly though, it should be noted that if the instances of negative rates are removed from the ANOVA (further reducing n) so that only positive mineralization and nitrification rates are considered, the results indicate that there is again no difference in mineralization rates between areas. Additionally, nitrification rates are much higher in both horizons for the clearcut areas when compared to the control. However, as previously discussed in Controls on Nitrogen Mineralization negative rates are valid and the results obtained by ignoring them are not presented here.

When the net nitrogen mineralization rates (g/m^2/incubation period) as defined by Nadelhoffer et al. (1983) for total available nitrogen are calculated and compared across areas some interesting patterns of nitrogen supply emerge (Appendix II). For both clearcuts the combined processes of ammonification and nitrification supply more nitrogen to the site about 50% of the time than these same processes in the control. This is true for both the forest floor and mineral soil. Note that since nitrification in the control area is essentially negligible, the most important process of nitrogen supply in this area is ammonification. Thus, comparing the youngest clearcut (1978) to the control, the patterns of

supply from two essentially different mechanisms are very similar on a seasonal basis (20.5 vs. 25.6 kg/ha/yr). So despite an apparent shift in the composition of microbial populations due to disturbances, approximately the same amount of nitrogen becomes available on an annual basis. Under higher precipitation regimes NO_3-N may be rapidly leached from the system and the net amount of nitrogen made available may eventually consist to a large extent of ammonium. A net decline in total available nitrogen supplied to the site may thus occur after harvesting. However, since NO_3-N leachate losses were not that high, this is probably not the case here.

The depression/resurgence of the supply mechanisms for both harvested sites, as contrasted between 1979 and 1980, reflect seasonal fluctuations in both nitrification and ammonification. The patterns suggest that shortly after harvesting, soil nitrogen mineralization processes are governed more by substrate chemistry than by environmental influences. As time progresses, nitrogen may occasionally be supplied to the site at a rate greater than would occur in the uncut situation (66.0 vs. 25.6 kg/ha/yr). This is exemplified for the rate of supply in 1980 for the older cut (cut 1977); the rate, at least for the summer months (June-August) is at least twice that of the control area in both the forest floor and mineral soil. Soil processes may be under strong climatic control at this point in time after harvesting, although

decomposition of roots and other organic debris left on the site will certainly have commenced and variations in the C/N ratio of newly-deposited litter from pioneer plants may also be asserting an effect.

One of the interesting things to note from Appendix II is that net nitrogen mineralization in the control forest floor never exceeds 1 g/m^2 in any particular incubation period. In the mineral horizon the upper limit is 0.20 g/m^2. As well, immobilization is virtually non-existent: only 1 instance (mineral horizon, overwinter) was found. Both clearcuts, on the other hand, have net nitrogen mineralization values exceeding those of the control on several occasions (>2 g/m^2/period in the forest floor). Both the mean value (g/m^2/period) averaged over all incubation periods and the yearly estimates of net nitrogen mineralization (kg/ha/yr) tend to indicate that, in the forest floor, harvesting does not affect net nitrogen mineralization until several years after the fact. In the mineral horizon, the rate appears to increase almost immmediately. This is not due to leaching: use of polyethylene bags for incubation precludes this. If substrate quality is the controlling factor during the early stages after harvesting, this may simply indicate that nitrogen is mineralized in the mineral horizon from a less complex organic matrix, possibly a result of soluble organic nitrogen leaching (Figure 15). However, these patterns are obscured

by completely opposite trends on a month to month basis, and by the difficulty of comparing clearcuts of different ages with different rates of "aging" over an extended period of time (22 months of continuous incubation). It is interesting to note, however, that the average mineral horizon net nitrogen mineralization value of the 9 forest cover types measured by Nadelhoffer et al. (1983) is 14 times that found in this study for mature white spruce. Two to 3 years after harvesting this differential had been reduced to 5 times, still a substantial difference. (As previously discussed, I feel there are some inherent problems with the use of the net nitrogen mineralization concept.)

Net nitrogen mineralization rates were converted to a daily basis ($g/m^2/day$), averaged for the clearcut areas and compared to the uncut situation to give an indication of the effects of harvesting in general upon nitrogen supply. This is illustrated in Figure 26 (cf. Robertson, 1984). The data for the mineral horizon are variable, but the same patterns discussed with reference to Appendix II can be seen in the forest floor. For up to two years after harvesting (1979) the same amount of nitrogen may be supplied to the site, albeit through different processes (ammonification plus nitrification).

As the clearcuts age and climatic controls on nitrogen supply become more important than substrate chemistry, nitrogen supply to the clearcuts may exceed that to the uncut

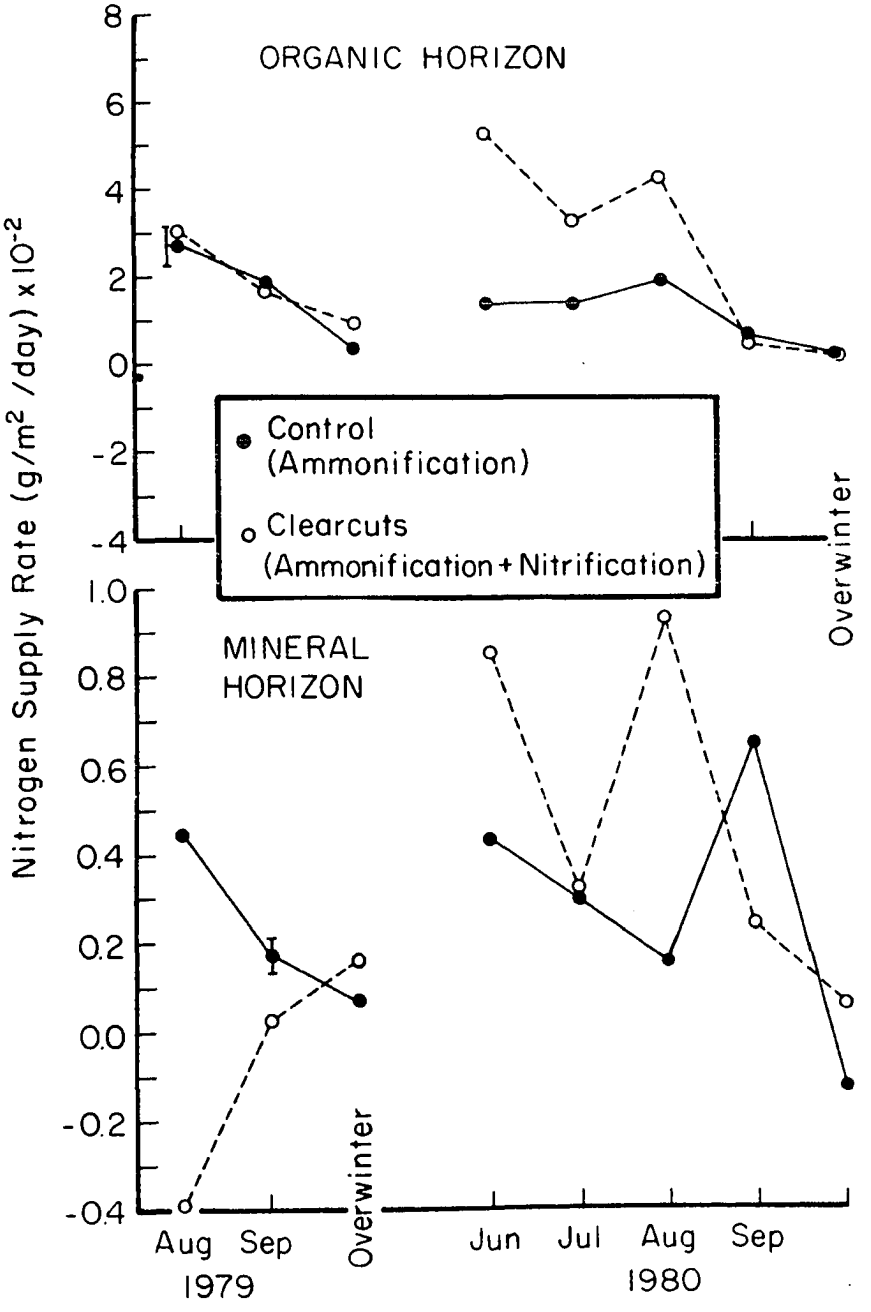


Figure 26. Nitrogen supply rate compared between the control area and the clearcut areas (average of two) for both the forest floor and mineral horizon. N-supply rate for the control area is wholly ammonification; for the clearcuts it is calculated by summing the ammonification and nitrifcation rates. Two typical standard errors are illustrated.

area, especially during the summer months. Matson and Vitousek (1981) also evaluated clearcutting effects upon nitrogen mineralization processes. They found similar increases in nitrification which they attributed in part to the initial population size of nitrifying bacteria. They also indicated that net nitrogen mineralization was increased in one clearcut over the control after a period of only 1.5 years. Very generally, this study supports their results.

It becomes very hard to predict what the nature of nitrogen supply from the site's soil resource to a growing forest might be 100 years from now, given the wide range of management options available and their effects on soil properties. For example, C/N ratio, a strong control of microbial and chemical activity, can be changed drastically simply by time and type of harvesting and post-harvesting site treatment, such as chipping of slash. The nature of the competing vegetation will also be important. In the long-term, seeding, planting, mulching, herbicides, thinning, fertilization, non-treatment, etc., will all have differing effects upon soil nutrient supply. Ultimately, as with most aspects of forestry, the final question to be asked is: can the management strategy be continually repeated successfully on the variety of site qualities encountered in a given region every 100 years? As well, is it possible to have rotations within which nitrogen availability is not an im-

portant limiting factor to growth, and where successful forestry could be realized in a shorter period of time?

Certainly, management decisions based on previous knowledge of the impact of site preparation, seedfall, seedling recruitment, stand growth and soil fertility are invaluable. As far as the latter is concerned, for example, it would be desirable to know what the mineralization rates are of nitrogen in the soil immediately after harvesting. It is also important to know, for the most common management regimes, what levels of soil nitrogen supply might be expected at the end of rotation, just prior to the second cut, based on the uptake rate of the currently growing forest, and the mineralization rate of soil N in an aging ecosystem. We do know that within certain temperate coniferous forest ecosystems it may take 10 to 30 years to replace, through de-novo inputs to the system, the total nitrogen lost from the site under conventional logging (Gordon, 1979). Under whole-tree logging, or in climatically-cool regions such as Alaska, this period may be much longer. We also know, in general, the percentage of nitrogen (or other nutrient) capital in various components of the northern forest and other forests of the world, including the forest floor, and what proportion is removed under various types of logging. This will aid in answering questions as to the long-term effects of specific types of logging such as whole-tree.

Information on the rate of nitrogen mineralization in relation to other element recycling is also becoming available. Sulphur, for example, is mineralized at a much faster rate than nitrogen (Tabatabai and Al-Khafaji, 1980). From the management point of view, the rate of supply of nitrogen and other nutrients to seedlings of a desirable species and the survival of these seedlings is of utmost importance. Thus N-mineralization should be evaluated as a strong component of a nutrient replenishment/depletion model, where the nitrogen available for seedling uptake reflects the net amount available after supplying competing vegetation and losses to other unavailable pools and pathways.

Aspects of Nitrogen Cycling Modelling

An attempt to model nitrogen cycling incorporating soil nitrogen mineralization and nitrification rates established in this study for a mature white spruce forest site and adjacent recently harvested areas in interior Alaska, was of limited success. Nonetheless, the exercise was an extremely useful one, and if the results achieved did not meet the original expectations, some valuable peripheral information was obtained. In this section, I present the conceptual models developed for both uncut and harvested sites.

The language chosen for modelling was DYNAMO, a Fortran-based compiler developed at M.I.T. for simulating "dynamic feedback models of business, economic and social systems". However, any continuous system described by differen-

tial or linear equations can be simulated using DYNAMO. Through the use of time-subscripts on pools and rates that describe a very simple form of integration, the user is easily able to comprehend how iterations of the cycle are performed. A complete description of DYNAMO and DYNAMO-useage is given by Pugh (1976).

The models developed in this study employed linear equations (Appendix V) or linear constants (Appendix VI) for the various rates controlling nitrogen pool-sizes. These simple models could have easily been solved using matrix algebra. However, by using DYNAMO, keeping track of instantaneous pool sizes was greatly facilitated. The real strength of DYNAMO, however, lies in its ability, through time-subscripting, to deal with simple continuous models described by differential equations. To illustrate this, I developed a relatively simple nitrogen cycling model utilizing rate equations taken from the agricultural literature. This model is described in Figure 27.

The levels in the various pools are controlled primarily by the mineralization (net, includes immobilization), nitrification, and nitrate immobilization rate equations. The former are given in Figure 28; the latter takes the following form:

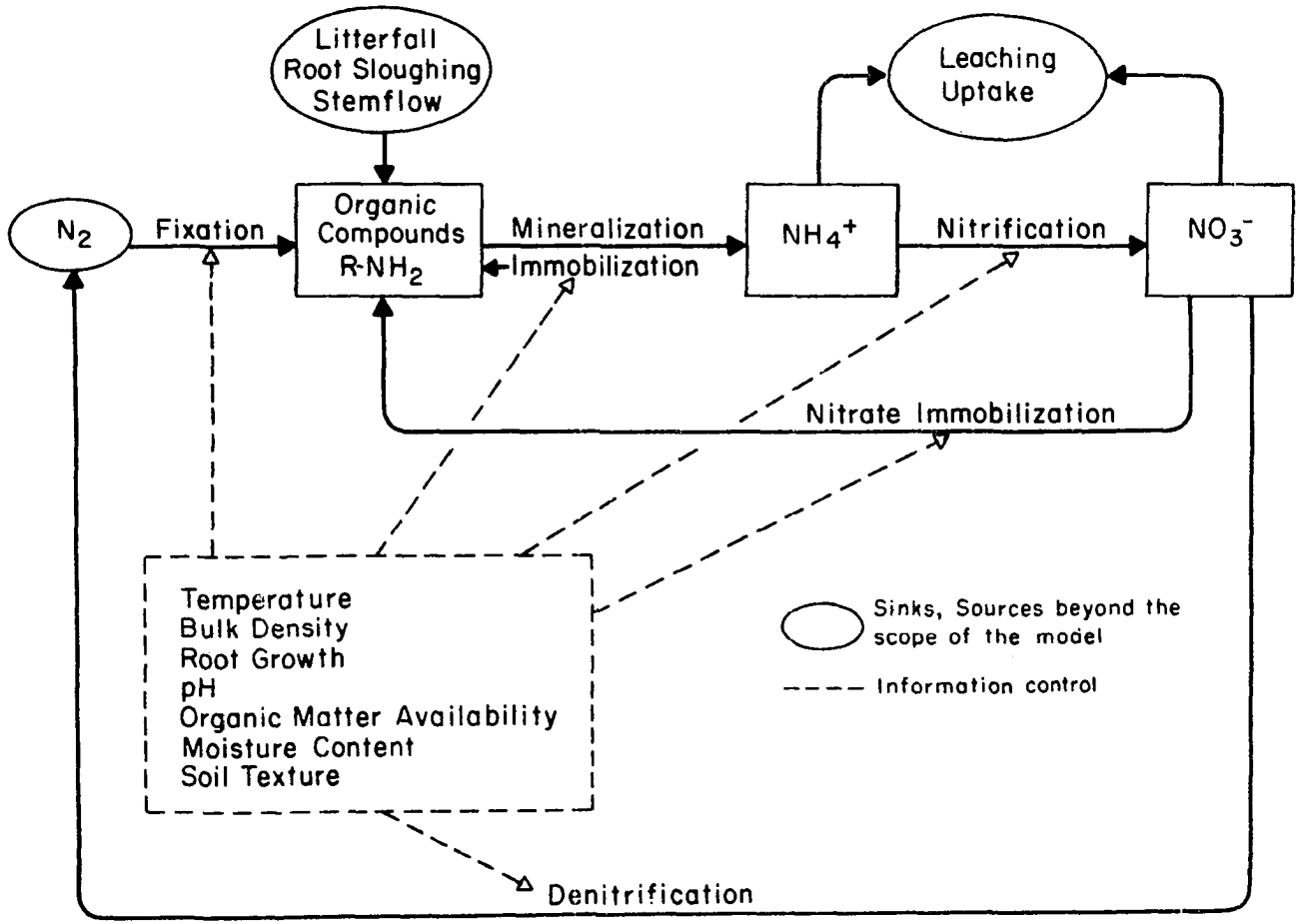


Figure 27. Conceptual model of a simple nitrogen cycle showing major controls on rate equations. Rates were derived from the agricultural literature.

NO_3-immobilization rate = 0.0 +(1.52 Temp)/(Org-N)^2 + 3.23 x 10^{-15} exp(Temp)-[0.0049 Temp (Org-N)-(NO_3-N]/(Org-N) (4)

where Temp = soil temperature (^oC)
(average over length of simulation)

Org-N = organic nitrogen pool (ug/g soil)

NO_3-N = nitrate nitrogen pool (ug/g soil)

and the rate units are ug/g/day

These three equations are taken from Tanji and Gupta (1978) and were developed for irrigated croplands. (These authors also give a good discussion on the use of different types of models in nitrogen cycling). All of these rate equations are defined in terms of precursor and end-product pool sizes.

Tanji and Gupta (1978) also assumed N-fixation to be proportional to the rate of crop root growth:

$$N\text{-fix} = K \cdot Rg \qquad (5)$$

where K = 0.011 (constant)

Rg = root growth (cm/day)

In the present study, root growth was initially estimated by setting N-fix equivalent to an estimate of N-fixation presented by Van Cleve et al. (1971). Denitrification was estimated using a composite equation derived from Bartlett et al. (1979), Cho and Mills (1979) and Tanji and Gupta (1978). Different forms of this equation, based on the Hagin-Amberger model (Hagin et al., 1976) were utilized on various runs of the model. Generally speaking then, the nitrogen cycling processes are governed by the factors given in Figure 27

(inset). Nitrogen-fixation is governed by root growth. Ammonification, nitrification and immobilization are governed by temperature, precursor and end-product pool-sizes, and denitrification is governed by the manipulation of theoretical coefficients representing the following controls on nitrogen mineralization: temperature, organic matter availability, pH, moisture content, texture, and precursor pool-size. Each equation is further controlled, through a small manipulation within the program, by bulk density, allowing both "organic" and mineral soils to be examined. This type of system is very DYNAMO-compatible and has strong predictive powers.

The theoretical result of running the model for 90 days is shown in Figure 28. To observe the speed at which the model cycled nitrogen, the initial values chosen for the three nitrogen pools were taken from this study and were representative of those pools found in the forest floor under mature white spruce. The results shown in Figure 28 represent the pool levels found over 90 days under "optimal" environmental conditions: alkaline pH, temperature 20°C, and organic matter readily available. Soil moisture and texture acted as controls on denitrification only. Since many agricultural soils have a relatively high bulk density with a certain amount of incorporated organic matter (the amount of which can be controlled within the program), the model was run with a bulk density of 1.25 g/cm^3. Using lower bulk

Mineralization Rate =

$$0.892 + 0.00216\,(\text{Temp.}) + 0.027(\text{Org.-N}) + 0.392\,\text{Log}_{10}(NH_4\text{-N})$$

Nitrification Rate =

$$4.64 + 0.00162\,(\text{Temp.})\,(NH_4\text{-N}) + .00162\,\text{Log}_{10}(NH_4\text{-N}) - 2.51\,\text{Log}_{10}(NO_3\text{-N})$$

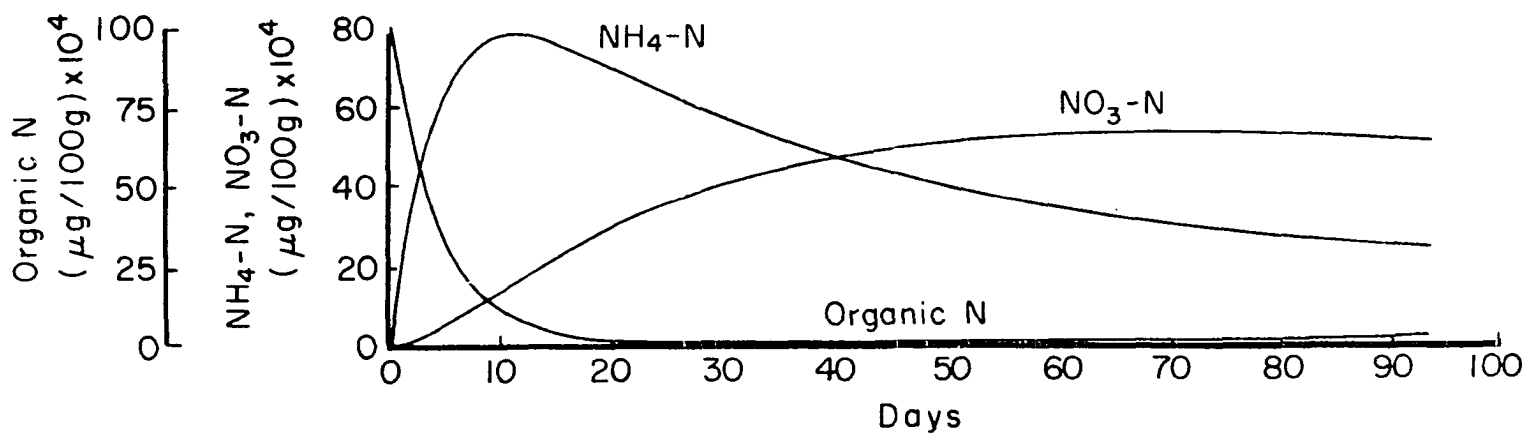


Figure 28. Theoretical result of running the model described in Figure 27, utilizing the DYNAMO programming language. The system portrayed is representative of an agricultural mineral soil. See text for details and information on controls of other nitrogen pathways.

densities, such as those found in the forest floor of mature forests, would result in much higher rates of mineralization and nitrification. The same patterns would be apparent.

There is an immediate decline in the organic-N pool as ammonification proceeds. Once the NH_4-N pool is maximized, nitrification increases, resulting in increased levels of NO_3-N. Denitrification and nitrate immobilization act in tandem to reduce these increases in NO_3-N and, after 40 days, to bring about an increase in the organic-N pool. (Denitrification feeds the organic pool indirectly through N_2). The pool sizes shown after 20 days are supposedly representative of an extremely intensive agricultural system: very little organic matter, high bulk density and high inputs of NH_4-N and NO_3-N. They are perhaps somewhat exaggerated.

Under lowered temperatures ($10^{o}C$), acid conditions and lack of organic matter, all processes were slowed. The main effects were attributable to reduced temperature; the peaks came later, declines were lower and the organic-N pool showed a steady increase. The denitrification process was also separately checked for sensitivity to pH. As expected, under acid conditions, the denitrification process was slowed and the NO_3-N pool declined at a much slower rate; this decline was much greater under alkaline conditions.

It is interesting to note that the pool levels were changed from being representative of a mature forest to a wholly agricultural system in about 90 iterations (days).

Although Tanji and Gupta (1978) acknowledge that their equations fall "short of employing the vast reservoir of knowledge" available "on soil N transformations", the equations appear to be quite representative of a wide array of conditions encountered in the field and effectively summarize many of the diverse models employed in the mathematical modelling of soil nitrogen transformations. This indicates that if such equations were available for forested situations, predictive models using DYNAMO would be relatively easy to create and also extremely useful.

Calculations and Assumptions for N-cycling Models

The development of the nitrogen cycling models proved to be extremely interesting and at the same time, because of lack of information on some required parameters, very frustrating. Despite a wealth of information available on nutrient cycling in white spruce forests in interior Alaska (cf. Van Cleve et al., 1983; other Forest Soils Laboratory data on file) many components had to be estimated from other sources. This naturally introduced a source of error into the models (Figures 29, 30; Appendices V, VI).

Pool sizes are expressed as g/m^2; rates are expressed as $g/m^2/year$. Soil total nitrogen was converted from % estimates by multiplying by a conversion factor that incorporated bulk density and horizon depth. These same conversion factors were used to calculate pool sizes for available soil nitrogen (NH_4-N, NO_3-N). The initial concentration for these

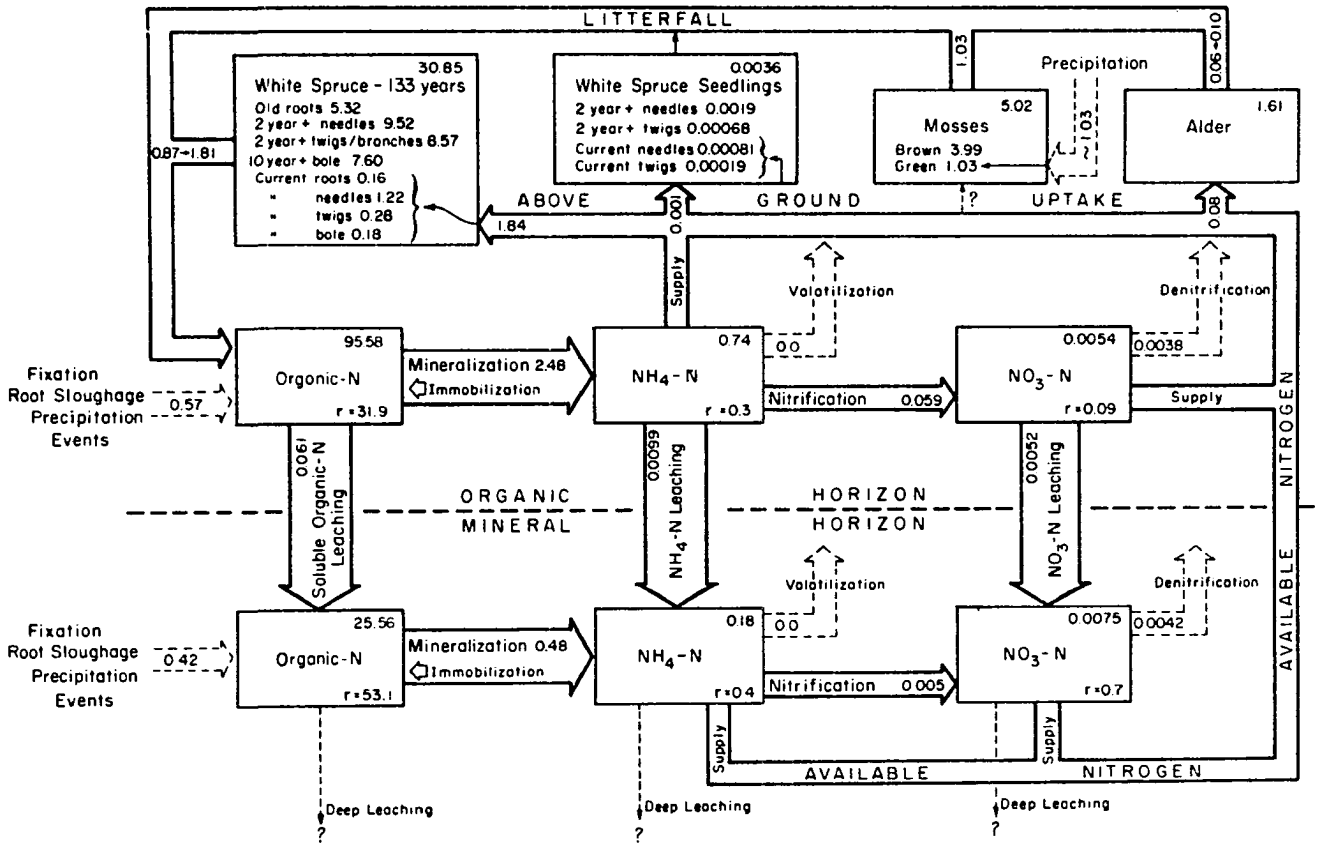


Figure 29. Conceptual model of the nitrogen cycle of a 133-year-old white spruce stand growing on upland loess in interior Alaska. Total pool sizes are in g/m^2 (upper right corner of each box). Rates are in $g/m^2/yr$. Two rates in the same pathway separated by an arrow indicate a changing rate to age 183 (50 year span). r = residence time in the pool (years).

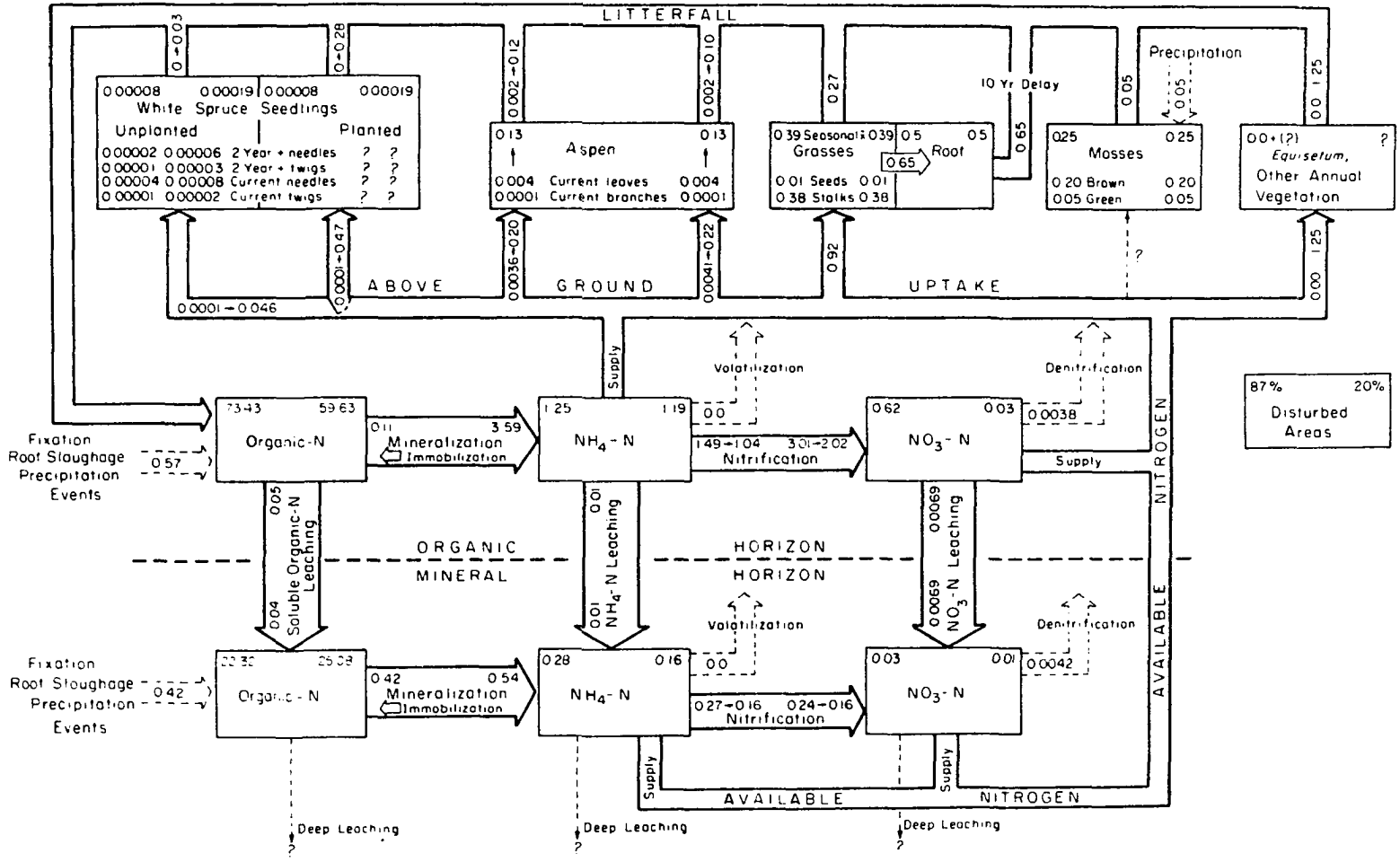


Figure 30. Conceptual model of the nitrogen cycle described in Figure 29, shortly after harvesting (2 - 4 years). Two clearcuts are described. The value in the top right corner of the pools, or on the right hand side of the rate equation represent the older (1977) clearcut. Those on the left describe the younger (1978) clearcut. Pool sizes are g/m^2; rates are expressed as $g/m^2/yr$. Two rates in the same pathway separated by an arrow indicate a changing rate to age 183 (50 year span).

pools, however, was an average of all sampling period subsamples.

Moss production in the uncut situation was estimated from Anon. (1979b). Standing crop for mosses was very roughly back-calculated from Binkley and Graham (1981) who found that for Hylocomium splendens in a coniferous system much farther south, 18% of the standing crop was net production. Nitrogen estimates were obtained for green moss segments by multiplying green biomass by % nitrogen. Nitrogen (%) in brown moss biomass was estimated by averaging values given by Tamm (1953), Weber (1982) and Weetman and Timmer (1967). The latter authors did not report brown moss nitrogen concentration (%) but this was estimated from their data using manipulations of the ratio of dead to green moss, the biomass of green moss, and the N content (kg/ha) of brown moss.

For total nitrogen in white spruce seedlings (control), the total weight (g) per seedling of biomass components (current and 2 years and older needles and twigs) was estimated. Using a value of 3500 seedlings/ha (Viereck et al., 1983), the total weight of each component on an areal basis was obtained. (The value from Viereck et al. (1983) was for a single stand also in the Bonanza Creek Experimental Forest. Seedling density was much lower than this in the control stand; thsi value was picked to represent a "typical" stand in the interior. Regardless, the seedling N component of the model (both biomass and uptake) was very small relative to

the mature forest). This was then multiplied by N-concentration of seedlings collected from the study sites to give g/m^2 of N in seedling components. For total N in mature white spruce trees, the current yearly increment in biomass (needles, twigs, boles) from Van Cleve et al. (1983) for a 134-year-old stand (average of 4) was multiplied by the appropriate N-concentration. For older tissues, biomass was estimated by subtracting the annual increment from the total standing crop, also from Van Cleve et al. (1983). Standing crop and N-uptake for large white spruce root systems was estimated from white spruce-mixed wood data presented by Gordon (1983). Gordon's top/root N-ratio was calculated and used in conjunction with top N-estimates for the white spruce in this study to get standing crop in roots. Bole N-contents and uptake estimates were then compared to these root-N estimates and an educated guess at annual uptake for roots was made. Nitrogen in alder components (standing crop and increment) was taken from Van Cleve et al. (1971) for 20-year-old floodplain stands and corrected for the lower density of alder in the upland white spruce system. All total pool sizes for N in trees, mosses and seedlings are the summations of individual components.

Litterfall for mature white spruce trees was derived from Van Cleve et al. (1983). Alder litterfall was estimated as a % of this and moss litterfall (return) was made equivalent to N-gains from uptake (minimal) and precipitation in-

puts. Litterfall of mature white spruce was incremented from litterfall production curves derived from Van Cleve et al. (1983). Litterfall increments for alder were estimated from Van Cleve et al. (1971). Uptake for all trees and seedlings was set equivalent to the sum of N-contents in current tissues. Initially, uptake in mosses was assumed to come solely from substrate-N. Binkley and Graham (1981) suggested that moss layers received sustantial N in this manner since their estimates of throughfall-N could not account for the N-content of the moss layer. However, it is commonly thought that mosses receive much of their N from precipitation inputs due to the lack of a true vascular system (see discussion in Weber, 1982). In this model, moss N-content was thus assumed to come directly from throughfall inputs.

In the clearcut areas, biomass of fully stocked stands of Calamagrostis (225 g/m^2: Mitchell, pers. comm., 1984) was corrected for % stocking in each clearcut. The aboveground return of N to the site was considered to be dead stalks and seeds. Biomass and nutrient content of the latter were estimated from information provided by the Palmer Research Station, University of Alaska Agricultural Research Station. Nitrogen (%) for stalks was derived from crude protein estimates given by McKendrick (1979). McKendrick (pers. comm., 1984) and Penning de Vries (1983) both indicate a seasonal decline in N-concentrations in stalks of grasses with the onset of fall; much of this N is returned to

roots. Nitrogen concentrations from mid-summer (1.25%) were used to estimate uptake; N-concentration from early fall (0.35%) were used to calculate N-return to the site in stalks. This was added to N-return from seeds (for total return) and subtracted from uptake to give a yearly amount of N returned to roots. It was assumed that roots remained alive for 10 years, thereafter decomposing and releasing N to the site. Uptake by other vegetation (Equisetum, Rosa, etc.) in the clearcuts was determined, based on % cover observations, by comparison to uptake rates for other components in both the cut and uncut situation.

Aspen N-content and uptake in the clearcuts were estimated in the following manner. A production curve based on the data of Van Cleve and Oliver (1982) for 25-year-old stands and Van Cleve et al. (1983) for 55-year old stands was constructed and biomass production estimates obtained for the 5-year increments from age 0 to age 70. These were multiplied by the N-concentration of leaves (~1.4%) and then these values were reduced to the stocking level of the clearcuts (~7%). Total estimates for leaves and twigs/branches were obtained in this manner. Total tree N-content and N-return in litterfall on an areal basis was modified from Van Cleve et al. (1983). Litterfall increments for aspen were derived from Van Cleve et al. (1983) and Van Cleve and Oliver (1982).

Moss N-content was corrected from the data obtained for the closed stand by moss-coverage in the clearcuts. The N-

content of white spruce seedlings was treated as before. In addition, 2 possible scenarios with respect to the seedlings were considered. In the first, the clearcuts are not planted and the existing seedlings from natural regeneration survive at about 200 stems/ha, growing into an assumed canopy of aspen. In the second situation, white spruce seedlings are planted at 3000 per hectare (2m X 2m). Mortality reduces this density to 2000/ha, aspen is controlled by mechanical removal or herbicides and a new stand of white spruce is generated. (The mortality assumption presumes that the best planting micros-sites (treated) were available; mortality might otherwise exceed 90% if "forest floor" sites were planted.) Litterfall increments for white spruce seedlings in the clearcuts were derived from Van Cleve et al. (1983).

For the uncut stand, N-leachate estimates on an areal basis were taken from data on file, Forest Soils Laboratory. These estimates, obtained using lysimeter plates of known area, were very close in some instances to estimates of N-leachate on an areal basis calculated by taking the average seasonal total water content (mls) of the profile and multiplying by the N-concentration (ug/ml) obtained in this study through the use of porous cup samplers. For example, the soluble organic nitrogen flux ($g/m^2/yr$) was calculated to be 0.082 (water content-porous cup method). This compares to a direct estimate using plate lysimeters of 0.061 $g/m^2/yr$. However, estimates of NH_4-N and NO_3-N were not as accurate

and therefore conversion factors (from the control area) were used to convert porous-cup concentrations to areal estimates for the clearcut areas. Thus the leachate values ($g/m^2/yr$) in Figures 29 and 30 portray the same pattern of losses from the sites given in Figure 15 and Table 16. Nonetheless, it would be a useful exercise to calibrate the less-expensive porous cup samplers against the plate lysimeters thus providing the potential (less cost) for increasing the number of sample points in any particular area.

Mineralization and nitrification rates for all areas and horizons were calculated by taking the daily rate ($g/m^2/day$) and multiplying by the number of days in the incubation period. These were summed for June, July, August, September and the overwinter period (October-May). The August, September and overwinter periods were averages of the two field seasons. In the control area these (summed) mineralization and nitrification rates were similar to those rates predicted from regression (Table 20). (Rates were not predicted from regression in the clearcut areas - see discussion on Table 20.)

The nitrogen cycle in the 133-year-old uncut stand (Figure 29) was assumed to be in steady-state with respect to soil N-pools. Several external processes regulate this state: volatilization (NH_3), fixation, denitrification and root sloughage. Field determinations of these processes were beyond the scope of this project and thus they were derived

in the following manner. Volatilization was considered negligible due to the acid nature of the soils studied. Denitrification rates were chosen so as to maintain the NO_3-N pools in steady state. Nitrogen fixation and root sloughage were chosen so that the total N pool was stable at least for the first few iterations. (In the model litterfall inputs are always increasing, therefore the total-N pool must always show a slight increase from iteration to iteration).

The upper limit for N-fixation (3.31 $g/m^2/yr$) was calculated from Van Cleve et al. (1971) for pure alder stands to a depth of 18.9 cm. This is the total depth (forest floor: 13.9 cm + mineral horizon: 5 cm) employed in the uncut stand. Nitrogen fixation in the uncut stand, based on the proportion of alder in the understory, was then set at 0.3 $g/m^2/yr$. This value was less than the maximum possible but greater than the 0.1 $g/m^2/yr$ estimated for fixation by moss and lichens in an interior black spruce ecosystem with no alder in the understory (Billington, 1981). I should point out that the pure alder stands used from Van Cleve et al. (1971) were Alnus tenufolia Nutt. and not Alnus crispa. Growth strategies and habitats are very different, but in lieu of a better benchmark, 3.3 $g/m^2/yr$ for the upper limit is probably fairly reasonable.

Root sloughage and precipitation (throughfall) inputs were then determined by difference to be 0.27 $g/m^2/yr$. The total fixation-root sloughage and denitrification inputs were

held constant and also used in the development of the N-cycle models in the clearcuts. Even though there is no evidence to suggest that these rates are the same in the clearcut areas as the control, the fact that the rates were held constant between areas allowed other rates and pool sizes to be examined in terms of the effects of harvesting upon them.

Finally, one basic difference between the two models (cut vs. uncut) should be mentioned. The N-cycle model for the control contains mineralization and nitrification rates that are linear functions of soil moisture content, temperature and respiration in the forest floor and mineral soil. This makes it slightly more adaptable to other forest ecosystems than the clearcut model, the rates within which are strictly linear constants.

Both models are similar in that uptake removals (or supply) from each available pool (NH_4-N, NO_3-N in both horizons) are calculated as a function of the pool size itself at each iteration (see note in Appendix V - this is not shown in the listing given there). Since uptake and supply must both be calculated before the iteration is performed (a function of DYNAMO), the possibility also exists that supply may deplete certain pools, especially those with very little nitrogen (e.g. NO_3-N). Thus, there is also a check in each model that analyzes the lag between supply and uptake and shunts the difference, when required, back into the available pool.

In the following section a nitrogen cycling model for a mature white spruce stand in interior Alaska is presented. I also briefly describe the potential effects of harvesting upon this model in terms of the potential stability of the forest over the next 50 years.

Nitrogen Cycling in Mature White Spruce Forests

The nitrogen cycle for a mature white spruce forest in interior Alaska is conceptualized in Figure 29. As indicated previously, much information was gleaned from the construction of this model, even though some information pathways were derived from studies and situations extraneous to the present one. Despite this, the development of the model showed that the calculated rates fit together well between nitrogen pool sizes portraying, with very little manipulation of external inputs and outputs, a strong steady-state system.

The supply rate from the NH_4-N pool in both horizons was calculated such that the NH_4-N pools remained in equilibrium even when the other inputs and outputs within the system were considered. Both the NO_3-N and organic-N (in essence, the mineralization substrate) pools were also held in this state through the manipulation of external processes controlling them. The estimates used were well within the range of values expected for these processes in coniferous forest ecosystems. The magnitude of the fixation-root sloughage inputs to the organic-N pool, for example, was

relatively small in relation to the size of the pool itself. (This was not the case for the NO_3-N pool in either the forest floor or the mineral horizon. Equilibrium was attained here only when denitrification was greater than 50% of the pool size.)

Residence times for elements in pools were calculated at steady-state by dividing the nutrient pool size by the inputs of that nutrient to the pool. Nitrogen resided longest in organic form, as expected, staying 32 and 53 years in the forest floor and mineral horizon, respectively. This is a rough indication of the higher rates of mineralization that would be expected in the forest floor. The residence time for nitrogen in the NH_4-N pool was about 3.5 months for the forest floor and almost 5 months for the mineral horizon. Nitrogen cycled rapidly through the forest floor NO_3-N pool (1 month) but had a much longer residence time in the mineral horizon (8 months). Generally, this indicates that available nitrogen was removed more rapidly from the forest floor than the mineral horizon. Remember that mineral horizon depth was only taken to 5 cm. Nonetheless, these patterns should hold for the entire profile since increases in the N-pool size (as a result of deeper profiles) should be accompanied by corresponding increases in the rate of supply of nitrogen to the pool on an areal basis.

It is quite likely that the (control) soil N-pools examined in this study are indeed in steady state. The

residence times calculated under this assumption for total N (32-53 years) are bracketed by residence times presented by Gordon (1979) for nitrogen under red spruce in the eastern boreal forest (17-99 yrs). Generally, the gradual build-up of organic matter under stands of white and red spruce proceeds in the former presumably because of long fire rotations and in the latter because of the tolerance of red spruce and its habit of "following itself" in the absence of fire. The residence time of N in the forest floor organic pool under white spruce is actully substantially less than 3 of the 4 red spruce sites described by Gordon (1979). (It is actually very comparable with N residence times under black spruce presented by the same author; recurrent fire is cited as the reason for these shorter times.) Typically, though, the forest floor under red spruce is more acidic than that found under white spruce. Thus, it might be expected that turnover and residence time should be less under white spruce. In addition, on the driest red spruce site listed by Gordon (1979), residence time for nitrogen is even lower than the white spruce stand used in this study; thus the dry climate of interior Alaska may in part be responsible for the lower residence time found in this study, possibly because litterfall or root sloughage inputs may be higher under these conditions.

The residence times calculated for the present study can be compared to those determined by isotope dilution for a

60-year-old white birch ecosystem in interior Alaska by Van Cleve and White (1980). Residence time for NO_3-N in that study varied from approximately 4 to 250 days. Ammonium-N turned over between 4 and 400 days and nitrogen resided in the soluble organic pool for between 54 and 94 days. The authors defined two pools for both NO_3-N and NH_4-N. The smallest and largest numbers presented above represent turnover times for the "rapidly" and "slowly" equilibrating available-N pools respectively.

The system described in Figure 29 is ammonium-dominated with respect to available nitrogen pools; NH_4-N levels in the forest floor exceeding those of NO_3-N by over 100 times. Uptake of NO_3-N by trees has been previously suggested as one reason why mature forest systems have low levels of soil NO_3-N (cf. Robertson and Vitousek, 1981). In this case, however, nitrification rates in both the forest floor and mineral horizon are so low that this cannot be happening. Only the NH_4-N pools are capable of supplying the N required by above-ground vegetation. In addition, the use of the polyethylene bag incubation technique precludes uptake by plant roots; the nitrification rates presented are calculated from before and after differences in NO_3-N levels within bags on incubation. This also suggests that plant uptake of NO_3-N is not an active process, although the model did "allow" excess NO_3-N, what little was available after equilibration, to be shunted into the available-for-uptake nitrogen pathway.

The residence time of N as NO_3-N in the forest floor, suggests, however, that nitrate is continually removed from this pool. If plant uptake is not responsible, and leaching losses are minimal (under this precipitation regime), where is the NO_3-N going? The model shows denitrification to be an active process but microbial NO_3-N immobilization (model component illustrated in Figure 28, but not Figure 29) should also be considered. Recently, Vitousek and Matson (1984) invoked such N-immobilization in preference to plant uptake to account for lack of N-loss from certain, and I emphasize this, disturbed forest sites.

Figure 29 is a good example of a tight nutrient cycle; internal recycling is high and external losses are minimal. This particular N-cycle is fairly typical of the "system" roughly defined as "a series of parts that are interconnected so that if you yank on one part, all the other parts move up and down" (Leak, undated). Although nitrogen produced appears to be at a premium, tree growth is probably not limited by soil N-production, although in younger age-class white spruce it appears to be (Van Cleve and Zasada, 1976). Figure 18 tends to support this statement. Of the three white spruce stands shown (ignore "This Study": foliage production was derived from Van Cleve et al., 1983), the one with the highest annual foliage production was growing on a site with next to the lowest N-mineralization rate. The trees in the particular age class studied may be beyond the

physiological age where large responses to nitrogen (as it becomes available in the system) are possible.

One anomaly in the model deserves discussion. As portrayed now, the bulk of N entering the available pool does so as NH_4-N. The flux into this form is approximately 3 $g/m^2/year$ (2.48 forest floor + 0.48 mineral soil). However, uptake by all vegetative components does not exceed even 2 $g/m^2/yr$. Thus it appears that an extra 1 $g/m^2/yr$ of NH_4-N cannot be accounted for; this would result in a steady increase in the NH_4-N pools, definitely not a characteristic of the steady-state system assumed for this forest. Examination of data from other white spruce forests in interior Alaska (data on file, Forest Soils Laboratory) indicated that most stands greater than 120 years should show steady-state conditions for most essential nutrients. This was confirmed by Yarie (1983).

When the model is examined closely the mineralization rate, at least for the forest floor, does not appear to be excessively high (Figure 18). In addition, current uptake of nitrogen excluding roots for mature white spruce trees is comparable to the estimates of Van Cleve et al. (1983) for 133-year-old white spruce: 1.68 vs. 1.56 $g/m^2/yr$. Actually, uptake in the stand examined in this study is, if anything, somewhat inflated. The biomass estimates from Van Cleve et al. (1983) that were used in conjunction with N-concentration estimates to generate areal pool sizes are actually quite

high; only 3 other stands in Alaska of 20 examined by Yarie and Van Cleve (1983a) had higher standing crops of biomass. The stand data of Van Cleve et al. (1983) also indicates a stocking of over 2000 stems/ha. The stand examined in this study had a density of approximately 700 stems/ha.

When root uptake for mature white spruce was calculated (see previous discussion) uptake into the mature tree pool was increased to 1.84 $g/m^2/yr$. It is possible that this is an underestimate, since root uptake was adjusted by top/root ratios for data from the southern boreal forest (Gordon, 1983). If one considers this and invokes uptake by the small but old aspen-white birch component, by miscellaneous ericaceous plants and by alder roots, none of which are shown in Figure 29, the missing 1 $g/m^2/yr$ of nitrogen can be easily accounted for.

Precipitation inputs, based on data presented for black spruce in the interior by Van Cleve et al. (1983) are not likely as high as the value used in the model (1.03 $g/m^2/yr$) (Figure 29). Thus in order for the moss component to remain in steady-state it is tempting to think that uptake of substrate-N (dashed line, Figure 29) into this compartment is theoretically possible. This same scenario has been presented for Hylocomium splendens under Douglas fir by Binkley and Graham (1981). Uptake in this situation (high precipitation inputs; moist/wet stands) by mosses with non-vascular systems is presumably by external upward capillary movement

of water. Under the dry climatic regime found in interior Alaska, this is highly questionable.

The results of the DYNAMO (linear) model are shown in Figure 31. Very generally, all pools reflect a steady-state situation. Note, however, that there is a continual buildup of nitrogen in the organic form. The seasonality of cycling phenomenon is also demonstrated for the NH_4-N and organic-N pools in the forest floor. Most other pools acted similarly. The fluctuations in the NH_4-N pool reflect not only seasonal variation in mineralization and nitrification rates as predicted from multiple-linear regression of these rates on selected climatic parameters, but also seasonal variation in uptake and leaching, both arbitrarily partitioned throughout the season. The fluctuations in the organic-N pool reflect seasonal variation in litterfall (partitioned), leaching, and mineralization as described above.

Effects of Harvesting on Nitrogen Cycling

The effects of harvesting upon the steady-state nitrogen cycle found in mature white spruce stands are illustrated by the conceptual cycle presented in Figure 30. Pool sizes and rates are presented for both clearcuts (see Figure caption for explanation) but DYNAMO output is presented for only the oldest clearcut (Figure 32). The main difference between the two models (uncut vs. cut) is in the nature of the uptake pools. Nitrogen uptake by mature white spruce trees has been replaced by uptake by Calamagrostis, Equisetum and other

herbaceous and woody vegetation, which, shortly after harvesting, approaches 2 $g/m^2/yr$. This is associated with an increase in available nitrogen in the cleared sites (Figure 32), which is in essence a positive feedback to the proliferation of other lesser vegetation. (Many other factors must also be considered; it would be safe to say that nitrogen is probably not limiting to plant growth at this stage). With growth of aspen and under even a moderate planting regime of white spruce, uptake rapidly approaches 3 $g/m^2/yr$ and the cycling of nitrogen becomes much tighter. Precipitation inputs were chosen, based on throughfall-stemflow estimates of other interior coniferous forests (Van Cleve et al., 1983), so that mosses remained in steady-state before desiccation and death which, judging from % cover estimates for mosses in the clearcuts, is quite prevalent in these sites.

Comparison of the two models (Figures 29-30) is interesting. As previously mentioned major inputs and outputs to the system were held constant in order to effectively evaluate the effects of harvesting on nitrogen cycling. These effects appear to be minimal when the mineral horizon is examined. Average leaching inputs from the forest floor to mineral horizon N pools are equivalent when the uncut site is compared to the harvested ones. In addition, pool sizes and mineralization rates are also of the same magnitude. In fact, the average of the two clearcut mineralization rates

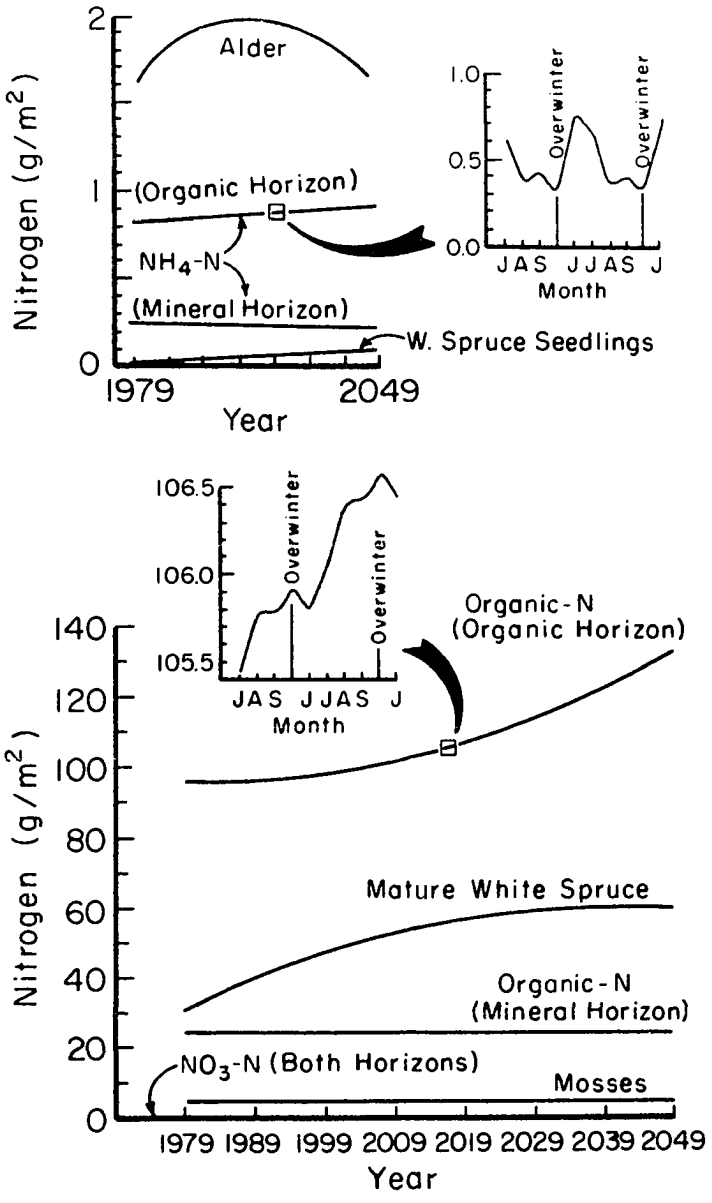


Figure 31. Linear output of the DYNAMO model designed to simulate the N-cycling model presented in Figure 29. See text for details.

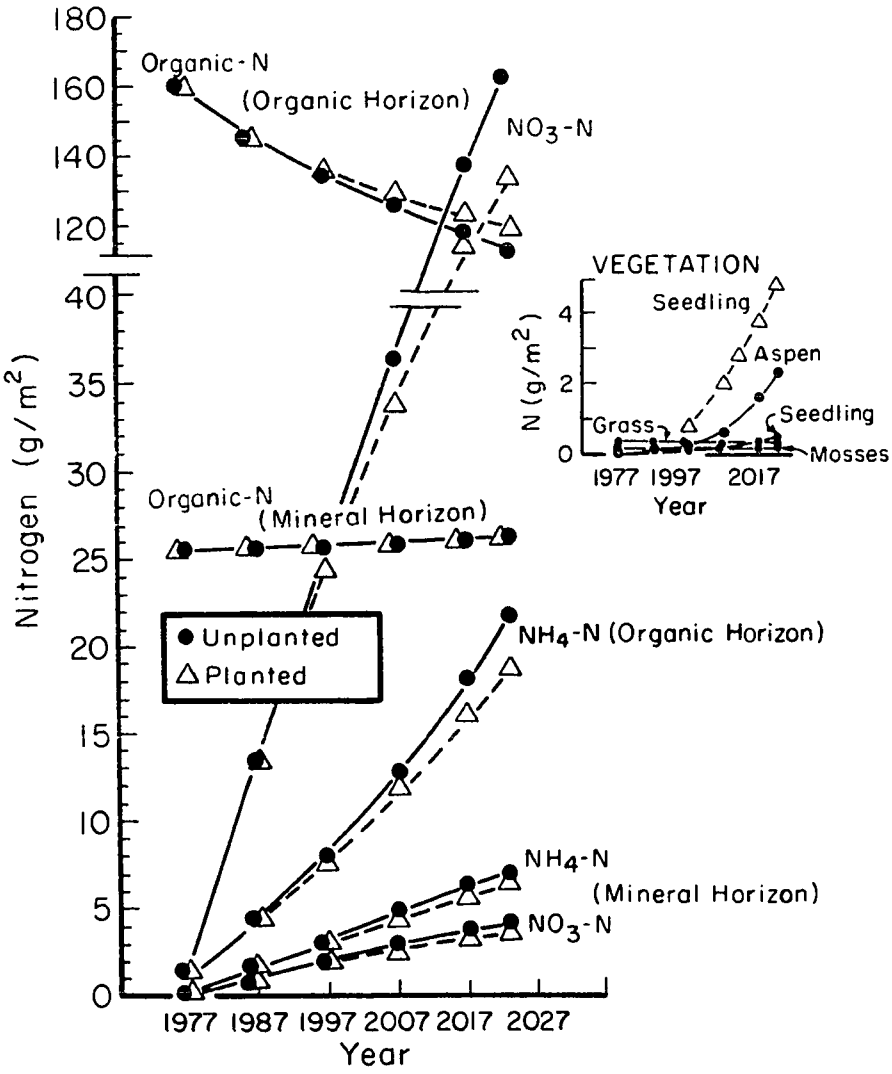


Figure 32. Linear output of the DYNAMO model designed to simulate the effects of harvesting on N-cycling. Refer to Figure 30 and see text for details.

(Figure 20: (0.42 + 0.54)/2=0.48) is identical to the mineralization rate from the control. Average nitrification rates are higher in the harvested areas although from previous discussion (Table 25) there is no statistical basis for this conclusion. The fact that, despite this (assumed) increased rate of nitrification, the NO_3-N pools in the mineral horizon did not differ between the cut and uncut sites, suggests that increased uptake of NO_3-N from this horizon by grasses or other lesser vegetation may be occurring. Nitrate-N immobilization by microbes could also be invoked here as a possible explanation. (The nitrification rate is a net rate, reflecting the total sum of N-movement between the NH_4-N and NO_3-N pools, and doesn't account for N-movement between the NO_3-N and the organic-N pool.) The residence time of N as NO_3-N in the mineral horizon of the control area was actually quite long. Unfortunately, residence times could not be calculated in the harvested areas since steady-state conditions did not exist.

When the models for forest floor pools and rates are compared, it can be seen that the organic-N pools in both clearcuts are substantially higher than that of the control area. Presumably this is a function of large inputs of needle and twig litter upon harvesting. The estimates of organic-N in the clearcuts may actually be too high since the magnitude of the increase ($\sim$60 g/m^2) is about twice the N-

content of the entire standing crop of white spruce! However, as stated previously, estimates of root-N and biomass are somewhat shaky, and perhaps seriously underestimated. Utilizing the data presented in Figure 29 about 23 g/m^2 of N would be left on the site if only the boles of the mature forest were removed. Coupled with N-inputs from the dying moss (5 g/m^2), and other unknown vegetative and fine root compartments (~15 g/m^2?), it is possible to get N-inputs after harvesting of about 40 g/m^2, which would elevate the forest floor organic-N pools in the harvested areas to ~135 g/m^2.

It is interesting to note that even after 50 years, litter inputs to the organic-N pool do not exceed 2.6 g/m^2/year when the site is planted or 2.4 g/m^2/year if it is not. Actually, these values would be somewhat less given that lesser vegetation in the understory, at least in the planted situation, should decline as the stand ages. These values compare favorably with litter inputs for mature white spruce forests at age 130, but are less than inputs of older stands. These reduced inputs result in a lowering of soil organic-N over a 50-year period (Figure 32). An important point can be made here. Harvesting techniques that leave slash and litter on the site will tend to buffer declines in nitrogen that accompany harvesting. Summer whole-tree logging on these sites might result in a serious depletion in soil nitrogen levels in as few as two rotations. These

losses may be partially offset by NO_3-N immobilization by microbes as suggested by Vitousek and Matson (1984). This process is contingent, however, upon the maintenance of high nitrification rates as the "site" ages. There is not sufficient evidence at this time to suggest that this is happening on these sites. In fact, exactly the opposite may be occurring.

Average forest floor NH_4-N levels are much the same when the clearcut areas are compared to the control (no significant difference on many of the sampling dates; Table 23). The average mineralization rate for the clearcut areas is slightly less than that for the control, but this is not a statistically significant difference. Of interest is the fact that the mineralization rates are so different between the 1978 clearcut (0.11) and the 1977 clearcut (3.59 $g/m^2/yr$). This can be attributed to high rates of immobilization after harvesting that must have occurred with inputs of litter having a very high C/N ratio. As the clearcut ages, immobilization slows, and the net movement of N into the NH_4-N pool increases. The mineralization rate may actually be very constant but microbial demand for NH_4-N may lessen its net effect. This same pattern can be seen to a lesser extent in the mineral horizon.

Forest floor nitrification rates are much higher in the clearcut areas than in the control. Additionally, rates of nitrification in the recent clearcut (1978) are less than

those in the older clearcut (1977); again, NO_3-N immobilization may account for this phenomenon. Despite this, however, NO_3-N levels are actually highest in the most recent clearcut (0.62 g/m^2). The fact that the older clearcut showed very low levels of NO_3-N (0.03 g/m^2) despite a high rate of nitrification (3.01 $g/m^2/yr$) suggests again that growth of lesser vegetation was responsible for NO_3-N removals. (Note uptake of annual (lesser) vegetation in Figure 30; 1.25 $g/m^2/yr$ for the 1977 clearcut as vs. 0.00 for the more recent clearcut). The above discussion indicates that N-pools in the mineral horizon, as opposed to those in the forest floor, are more resilient to changes brought about by harvesting.

The effects of harvesting on the major physical and chemical characteristics of white spruce forest sites are summarized in Table 26. These effects are general in the sense that they represent the basic trends of the data, which, for some parameters, varied depending upon the clearcut studied. In addition, for some attributes, the effects of harvesting were not always statistically significant. This was dependent again upon the clearcut studied and time within season.

However, the trends shown in Table 26 appear consistent with the expected effects of timber harvesting: pioneer vegetation is prolific, the integrity of the former forest floor is destroyed and the soil environment is changed in that temperature and moisture are not as "limiting" to

Table 26. The effects of commercial timber harvesting on physical and chemical attributes of interior Alaskan white spruce ecosystems.

Physical Attributes	Effect of Harvesting[a]
presence of associated (lesser) vegetation	greatly increased
continuity of moss cover	greatly decreased
bulk density of forest floor	increased
depth of forest floor	decreased
ambient air temperature/degree days	variable[b]
precipitation reaching forest floor	increased
soil temperature - forest floor	increased
soil temperature - mineral soil	variable
soil moisture content	increased
root/shoot ratio of white spruce seedlings	decreased
Chemical Attributes	
C/N ratio - forest floor	increased[c]
C/N ratio - mineral soil	no change
soil summer respiration-CO_2 evolution	increased
soluble organic nitrogen movement through profile	decreased
pH	no change
mobility of major elements	no change
background NH_4-N levels	no change/variable
background NO_3-N levels	increased/variable
mineralization	no change[d]
nitrification	increased[d]
net nitrogen mineralization	increased[d]
N concentration of current needles, white spruce seedlings	increased
indices of organic matter quality[e]	no change

[a] effects are general: unless noted, the effects are for both forest floor and mineral horizons
[b] dependent upon time within season
[c] one clearcut only
[d] These effects are not statistically true for all times during the season. See discussion in conclusions.
[e] lignin, cellulose, ash, fibre

microbial processes as before harvesting. The microsite environment (microclimate) changes correspondingly; light, temperature and moisture regimes are increased and become more favourable for white spruce seedling development (see root:shoot ratio). Nitrogen availability is also increased on harvesting; this is reflected in increased levels of foliar nitrogen in the current growth of white spruce seedlings found in the clearcut.

The soil system appears well-buffered against harvesting; many factors that control microsite processes are not changed. The C/N ratio in the forest floor, however, is increased, working against mineralization processes. Despite this, increases in the latter suggest that temperature and moisture effects may be as important as organic matter quality, the indices of which did not immediately change. Initially, then, organic matter quality may control overall decomposition and mineralization processes. This is modified at specific times during the season by the effect of increased temperature and moisture. As time from harvesting progresses, the quality of the organic matter substrate should become less important than temperature and moisture in controlling nitrogen mineralization. (This trend will slowly reverse as the forest ecosystem regrows.)

The C/N ratio remained unchanged in the mineral soil although the dynamics of the relationship have been altered; carbon outputs via respiration are increased while nitrogen

(soluble organic) inputs in solution are decreased. The latter may be because of increased mineralization of these low molecular weight compounds and uptake in surface horizons.

Predictive Abilities of the Harvesting Model

In predicting the future, one must deal with either things that change or things that do not. In the case of the latter, it is relatively easy to forecast the future with simple linear models. However, as White (1984) points out: "the trouble is that forecasts have to assume that what is happening at the moment will, more or less, go on happening." Models that must deal with continually changing phenomena are inherently better than such linear models since feedback, either positive or negative, continually forces re-examination of initial or ongoing assumptions. "The difficulty with prediction", from this point of view, "is not that the future turns out differently but that it turns out to be more complex than anyone had expected" (White, 1984).

The levels of the major nitrogen pools in both horizons and vegetation are traced for a hypothetical period of 50 years in Figure 32. This is output from a linear DYNAMO model (Appendix VI) based on Figure 30. The model predicts increases in available-N pools in both horizons, (although the increases in the forest floor far exceed those in the mineral horizon) and in most vegetative components. The organic-N pool is actually quite stable in the mineral hori-

zon but shows a substantial drop in the forest floor, as discussed previously. In addition, the effects of planting are to reduce increases in soil available-N pools due to increased uptake. Increased litter inputs under a planted regime also tend to increase the level of organic-N, at least in the forest floor. This is presumably due to increased litterfall as the plantation grows.

One weakness in this model, as emphasized in the first paragraph of this section is that the nitrogen release rates established early in the development of the clearcut are assumed to continue at their present levels well into the growth of the new stand. The forest floor mineralization rate was held constant (3.59 $g/m^2/yr$ for the oldest clearcut) over the duration of the simulation. However, it was possible to utilize variable nitrification rates with aging of the site by comparing the nitrification rate for the mature forest with those found in the clearcuts and decreasing the clearcut rates by small 5-year increments. Thus, at the end of 50 years forest floor nitrification has decreased in the older clearcut from 3.01 to 2.02 $g/m^2/yr$ and in the younger clearcut from 1.49 to 1.04 $g/m^2/yr$ (Figure 30). (The variation in rates between clearcuts possibly reflects season of harvesting.) At the rates of decline used in the model, both clearcuts will have nitrification rates, at 130 years, similar to the control area (~0 $g/m^2/yr$). However, no information is available on the rate of decline of

nitrification in aggrading forests. Rates of nitrification may actually approach zero very early in the development of the next stand.

This particular model cannot predict what will happen to rates of nitrification or mineralization more than a few years after harvesting. It is likely that mineralization (ammonification) does not increase after harvesting (Table 25). (The total amount of nitrogen moved from the organic pool must increase in order for this statement to be correct since NH_4-N losses to the NO_3-N pool must be "satisfied" - see previous discussion of net nitrogen mineralization.) The mineralization rate given for the forest floor of the oldest clearcut (3.59 $g/m^2/yr$) is not statistically higher than the 2.48 $g/m^2/yr$ calculated for the contol. However, when this higher value is used to re-cycle nitrogen in the clearcut (Figure 32) an extra 1 $g/m^2/yr$ (approximately) is added to the NH_4-N pool, resulting in the increase shown for that pool.

In contrast, the FORCYTE model presented by Yarie (1983) for interior white spruce forests predicts that net nitrogen mineralization will actually increase after harvesting. In fact, this rate is almost 5 $g/m^2/yr$ which compares favorably with the net nitrogen mineralization rate (not ammonification) established for this study (4.3 $g/m^2/yr$, average of forest floor rates for the two clearcuts - Appendix II). The value from Yarie (1983) should actually be

slightly higher than the ones found in this study since Yarie also considered the organic matter content in the mineral horizon to a depth of 70 cm. Yarie also predicted that after about 125 years net nitrogen mineralization rates would stabilize at between 2 and 3 $g/m^2/yr$. This can now be verified by field results obtained in this study for a mature (133-year-old) white spruce stand (2.56 $g/m^2/yr$ - Appendix II).

Although the DYNAMO model (Figure 32) is of doubtful usefulness beyond 1987 (for example) because of reasons discussed above, it does give one view of the disruption of the steady-state conditions that exist in the mature forests. All available-N pools increase; NH_4-N primarily because of reduced uptake, but not increases in mineralization and NO_3-N primarily because of reduced uptake and increased nitrification. If the release rates found shortly after harvesting were maintained for the next 50 years NH_4-N levels would increase from 5 (mineral horizon) to 20 times (forest floor) above those levels found in the control area. Nitrate-N would increase from 5 to over 160 times. These increases are possible, I suppose, considering the low stocking of aspen on the sites. Young, dense poplar plantations have been shown to take up as much as 9 $g/m^2/yr$ (Dawson et al., 1983). In contrast, the total N-content of the aspen in the clearcuts from this study just barely exceeds 2 g/m^2 at the end of 50 years. The model output given in Figure 32 should

be used conservatively to show disruption of the nitrogen cycle in the uncut stand and the increased amounts of available nitrogen. There is no doubt that the development of differential rate equations between precursor and end-product pools would greatly strengthen the model. Under the present circumstances, I would hesitate to look at the model seriously beyond a 10-year output.

Forest Management Considerations

Some forest management considerations in general have been already briefly discussed in other portions of this study. Needless to say there are many silvicultural aspects of both conventional and intensive forest management schemes that will affect nutrient, and more specifically, nitrogen-cycling. I would like to address several of these.

Whole-tree harvesting is just one aspect of intensive forest management, albeit the one that has the most impact on forested sites. Considering first then the question of conventional versus whole-tree logging as the preferred method of timber extraction, it would appear from the standpoint of nutrient (N) supply that the micaceous loess sites of the interior uplands could sustain conventional harvesting of white spruce indefinitely. (Indeed, given the political climate surrounding forestry in the state of Alaska and lack of interest in intensive forest management, this may be exactly what will happen.) Nitrogen cycling data from conventional clearcut areas in the interior indicate that

organic-N pools are increased almost immediately after harvesting due to inputs from slash and litter (Figures 29, 30, 32). This increased pool immediately begins to decline as available nitrogen is released to the site under increased temperature and moisture regimes. Vegetative regrowth on these sites by natural regeneration (all species) or plantations should preclude declines in the organic-N pool to levels below that found in mature forest since litterfall inputs will increase (asymptotically) as the vegetation ages. Nitrogen losses in leachate under the dry climatic regime of the interior should also be minimal. It is interesting to note (from Figure 30) that N-mineralization (ammonification) rates decline immediately after harvesting (0.11 $g/m^2/yr$) but several years later tend to increase again (3.59 $g/m^2/yr$). Conventional harvesting, with its typically high litter and branch inputs will thus tend to initially decrease N-mineralization rates. However, this will be buffered to some extent by increased organic-N inputs, from which N will be released at eventually higher mineralization rates.

I should point out that this discussion follows the schematic model in Figure 30. There is no statistical basis (Table 25) for differences in the rates between clearcut areas or between control and the clearcut areas. (The average of the clearcut mineralization rates actually is equivalent to the rate in the control area). Based on our know-

ledge of C/N ratios and decomposition phenomena, however, these patterns are quite feasible.

Whole-tree harvesting, on the other hand, may have the opposite effect. Mineralization rates could remain stable or increase sharply immediately after harvesting since inputs of litter with a high C/N ratio would be eliminated. In addition, organic-N inputs under whole-tree harvesting would be minimal and limited to those provided by decaying roots. Declines in the organic-N pool would occur immediately due to loss of N inputs in litterfall and (at least) the maintenance of pre-harvest mineralization rates and from levels essentially the same as those found immediately prior to harvest.

Recently, questions concerning the effects of whole-tree harvesting upon nutrient cycles and site resilience in general have been asked but on the whole there is a lack of good studies addressing these effects. Vitousek and Matson (1984) implicate intensive forest management (whole-tree) as a prime factor in elevated N-losses from more southerly forest ecosystems. Many other studies, however, are either in progress, or like this one, predict effects based upon what has happened under conventional logging and what could potentially happen if additional biomass components were removed from the site.

Yarie (1983) has calibrated a large forest growth and yield model (FORCYTE) to interior Alaskan white spruce for-

ests based on nitrogen dynamics. Since the N-mineralization estimates from the running of this model were very close to those found from field studies, it is likely that the model is well-suited to the white spruce forests of interior Alaska, although Yarie does point out that some gains could be made in precision of the model. Nonetheless, it would be interesting to look at the recommendations of that author, especially as they apply to intensive forest management.

According to the model of Yarie (1983), under shortened rotations of 120 years or less, intensified management should result in increased N-availability and site productivity. Decomposition (and associated site-quality parameters) should increase and remain higher than in uncut forests for all rotations up to 120 years. After this period, the forest should function, with respect to N-cycling, at pre-harvest rates.

Under extremely shortened rotations (75 years) Yarie (1983) found that increases in site productivity were accompanied by decreases in forest floor biomass over 3 rotations although the extent of loss was dependent to a large extent on the management intensity chosen. Only the heaviest management regime (3 commercial thinnings at ages 35, 50 and 65) resulted in substantial site degradation. Yarie attributed increases in productivity to increases in rates of decomposition and mineralization within the forest floor and

to large N-inputs from N-fixation during the first 20 years after harvesting.

The parameters in Yarie's (1983) model were initially verified by growing a planted stand of 6000 stems/ha for 200 years and comparing stand biomass with that found in fully-stocked mature white spruce stands. Yarie admits that 6000 trees/ha is unreasonably high for an initial planting density but points out that, under natural regeneration, up to 10,000 stems/ha may persist into the first year. However, most mature white spruce stands will not exceed 2000 stems/ha. Only one stand of 22 examined in interior Alaska by Yarie and Van Cleve (1983a) had over 5000 stems/ha; the particular stand examined was the second youngest (55 years).

A lower density of 4000 stems/ha was employed in the FORCYTE model when the various management schemes were simulated. Since the growth equation used is derived from standard growth and yield tables, mortality within the plantation must be accounted for, but its extent is never known. The model employed in the present study assumed a planting of 3000 stems/ha (2 m X 2 m) with mortality reducing this density to 2000 stems/ha. A density of 4000 stems/ha, as utilized by Yarie (1983) would have removed more available nitrogen from the clearcuts than was removed during the linear simulation (Figure 32) conducted at lower density. The effects of this on N-availability as the stand ages are not known.

Many eastern boreal forest sites have been identified as capable of sustaining conventional logging, but because many of these sites are shallow and underlain by granitic bedrock it has been suggested that they cannot support intensive forest management. On these sites, whole-tree logging at least should be precluded (cf. Weetman et al., 1979). Remember that intensive forest management entails not only more complete utilization of site biomass but also silvicultural aspects such as pre-commercial thinnings and planting of genetically-superior (and more nutrient demanding) forest stock.

In interior Alaska, the upland micaceous loess sites may actually be more resilient than some of the more granitic white spruce sites in eastern Canada. A comparison of nutrient reserves for upland white spruce stands in interior Alaska (Van Cleve et al., 1983) with upland white spruce-mixedwood stands in Ontario (Gordon, 1983) indicates that soil reserves (organic + mineral) are similar for nitrogen and potassium but far greater in Alaska for phosphorus, calcium and magnesium. However, despite the fact that Yarie's (1983) model estimates for N-mineralization are in close agreement with field estimates obtained in this study I hesitate to fully endorse Yarie's conclusions that intensified management can be sustained on these sites indefinitely. I have several reasons for this. First, extension of the model trends for organic-N found in the present study

for even a decade suggests an immediate decline in post-harvest levels, primarily due to the fact that N-mineralization rates are maintained but N inputs to the soil system are reduced due to the absence of litterfall from the mature stand. (Some N will be returned in the litterfall of the competing vegetation.) This post-harvest level is determined in part by the amount of slash and debris left on the site. Second, no simulations of other potentially limiting nutrients have been conducted. Both phosphorus and potassium, for example, have been identified as elements that may become potentially limiting to seedling growth after whole-tree harvesting on good spruce sites (Gordon, 1979). Potassium reserves, at least, on these upland sites in Alaska are similar to those found in Ontario. In addition, as previously discussed, any lesser vegetation on the clearcuts will effectively compete for available potassium with white spruce seedlings (Figure 14). Finally, as Yarie (1983) concedes, the proportions of alder in the shrub layer may not be as great as the 50% used in the FORCYTE model. Certainly, the persistence of alder into mature stands is not always consistent (cf. Viereck et al., 1983; (this study did have ~400 stems/ha at age 133)). There is also no evidence to suggest that alder invades all clearcuts in the same manner; we do not really know what is going to occur at the end of the second and third rotations.

On the other hand, the higher planting densities employed by Yarie (1983) were actually stressing the site more than those employed in the model developed in this study. If the FORCYTE model predicted increased productivity under these higher densities, it is difficult to predict what the effect of lower densities could be. In addition, it is well known that the time to recover to pre-disturbance levels in a secondary succession is usually much less than that required in primary succession (Van Cleve and Viereck, 1981) - in this case about 200 years. This is a long time. While it is true that we do not really know what the impact of 200 years of management on certain sites will be, it can also be said that we also do not know what advances will be made in forest science that will buffer the effects of increased biomass removal on shorter rotations.

The second aspect of intensive management I would like to discuss refers to the role of alder in the N-nutrition of developing plantations, already briefly discussed. Alder inter-planting has been continuously suggested as one means of improving the supply of nitrogen to forest trees in plantation situations. Dawson et al. (1983), for example, in summarizing past research on the subject, gives the example of an intensively-cultured short rotation Alnus-Populus mixture. Height growth of poplar increased with increasing alder in the mix and with closeness to alder. The poplar had

height growth equivalent to that obtained from optimal ammonium nitrate fertilizer. Dawson et al. (1983) speculate that shading or allelochemicals from Populus stress Alnus into releasing nitrogen from N-fixation resulting in N-accretions in Alnus-Populus intermixture.

In Alaska, alder interplanting has been suggested by Yarie and Van Cleve (1983b) as one way of maintaining site fertility. However, they also point out that the beneficial effects of interplanting alder with a highly-productive species such as aspen, as might happen in an energy-plantation, may be short-lived since overtopping of the alder may quickly occur. Under these conditions, alder may not be a positive contributor to the N-nutrition of the stand, although N-fixation may still proceed to a certain extent. This condition is unlikely to occur in white spruce interplantings because of slower spruce growth. However, the benefits of interplanting should be weighed against the economic costs of either the reduced planting densities of white spruce that may be necessary with interplanting or the increases in man or machine-hours necessary to preserve the alder component under intensive forest management (cleanings, pre-commercial thinnings). Young alder may also effectively compete with white spruce seedlings and this could be a problem where alder regeneration is sparse and alder must be planted (Zasada, 1984; pers. comm.). This, of course, is a very site-dependent phenomenon: some floodplain white spruce sites

will regenerate wholly to alder (Zasada, pers. comm., 1984); others on the floodplain consist of dense alder with spruce seedlings and saplings underneath. In addition, soils under alder plantations have a high nitrification potential. However, Hendrickson and Chatarpaul (1984) found that needles of white spruce and other conifers inhibited nitrification in such plantations. Thus benefits accruing to the site from increased N-fixation due to alder interplanting may be offset by reductions in nitrification.

Finally, I would like to comment briefly on two aspects of Alaskan forestry in general. First, while much remains to be done, ecological land classification work in Alaska to date has been thorough and several good overviews exist (Viereck and Dyrness, 1980; Viereck et al., 1983). Community ecosystems in general are well-defined. However, in the advent, perhaps, of intensive forest management in Alaska, it is imperative that the best sawtimber, log and fiber-producing sites be identified within each vegetation type. This does not of course, have to preclude selections and exclusions for ecological uniqueness. As well, while many factors are important, the persistence through preservation of some mature spruce stands in the interior, in addition to a variety of successional stages, might benefit local moose populations in terms of overwinter cover. On these sites, intensive forest management should be thoroughly tested. There are many examples within the state where forested land

has been "assaulted" by agriculture and where, within the physical and chemical constraints (fertilizer additions acknowledged) of the sites, successful growing of agronomic and horticultural crops has been realized.

On sites selected for intensive forestry, such as the Willow Island Project (Institute of Northern Forestry) growth and yield in natural forests should be first determined in order to benchmark potential gains resulting from silvicultural manipulations, improved harvesting techniques and planting of genetically superior stock (cf. the recommendations of Packee (1984) for interior white spruce). The above should be tested across as wide a range of chemical and physical conditions (site-specific) as possible. Chemical and physical controls on tree growth and successful regeneration should also be identified and the silvicultural methods for modifying these controls evaluated.

Second, I feel that past forest practices in interior Alaska, especially within the genus Picea, have to a large extent been dysgenic in nature. By this I mean that most harvesting practices have tended to select against the genes responsible for the largest, straightest and tallest trees. It is imperative that genetically superior stock be identified and preserved. Provenance trials in the interior should be continued and genetically superior plantations for lumber or fiber-production should be created and evaluated not only in terms of biomass production but also in terms of the

increased nutrient demand on the site that must inevitably occur. Studies on nutrient mineralization and cycling in general can play an integral role in helping to address at least this latter concern.

Cultural techniques to ensure that the largest number of trees of the best stock are established on the best micro-sites should also be considered. This entails the use of natural regeneration and the inclusion of hardwoods in management schemes (possibly as nutrient reservoirs) prior to pre-commercial thinning.

SUMMARY AND CONCLUSIONS

It was hypothesized that commercial timber harvesting in the upland mature white spruce forests of interior Alaska affected soil nitrogen mineralization (ammonification) and nitrification rates by changing the major factors that control these processes. The principal controls potentially affected by timber harvesting were thought to be soil temperature and moisture regimes, soil microbiological properties and organic matter (substrate) quality.

Laboratory incubations were initially used to test the gas exchange properties and permeability of the polyethylene bags used in the field incubations (Eno, 1960). The results indicated that thickness of plastic bags over the tested range of 0.015 (0.6 mil) to 0.032 mm (1.25 mil) was not an important factor in determining mineral nitrogen production, when compared to other factors such as temperature and length of incubation. I would like to encourage other workers who utilize polyethylene bags for soil incubations to report the thickness of bag used. I would further like to suggest that those researchers utilizing bag thicknesses outside the range of those tested here test their specific bags for CO_2 and H_2O permeability. Incubations conducted under the effects of a diurnal temperature regime would also provide valuable information on temperature-bag thickness interactions that might occur during field incubations. Length of incubation time

may also be an important factor in determining nitrogen mineralization, especially when incubating "poor types of humus" of low organic matter quality where a lag in ammonium or nitrate release may occur (Tamm, 1971). This phenomenon is evidently quite site-specific. I have had interpretable results in the field and laboratory utilizing monthly incubations but other researchers are advised to determine the optimal incubation period for the specific soil or site under investigation.

This study has confirmed that polyethylene bags (0.015 mm to 0.032 mm thick) provide an easy way to evaluate nitrogen processes *in situ*. The use of N^{15} in conjunction with this methodology could help to identify nitrogen turnover times and immobilization phenomena.

Field experimentation revealed that a pooled sampling technique could effectively lower inherent variabliity in soil available-N data, even with a relatively small sampling size (n=10). Researchers are urged to investigate the variability in background levels of NH_4-N and NO_3-N prior to initiating extensive field sampling designs. In most cases, regardless of design, a large number of point samples will be desirable.

Timber harvesting resulted in higher soil moisture contents in both the forest floor and mineral soil presumably due to a lack of transpiration in the clearcuts. In addition, precipitation reaching the forest floor was, as expect-

ed, higher in the clearcut areas. Harvesting also caused an increase in forest floor temperatures but the effects on ambient air and mineral soil temperature were variable and dependent upon time within season. Similarly, the effect upon degree days was also variable. The best discriminating variable, with respect to treatment, proved to be mineral soil moisture content, being much higher in the clearcut areas. Generally, these changes in the physical characteristics of the site are largely responsible for the noted increases in NO_3 production in the clearcut areas.

Selected chemical characteristics of the forest floor and mineral horizon were generally not different between areas at this point in time after harvesting. The mobility of many elements in post-harvest interior Alaskan forest soils does not appear to be strongly or immediately affected by clearcutting processes, at least under the less than moderate precipitation regime found in interior Alaska. The physical property of the soil most affected by harvesting was the bulk density of the forest floor. Presumably due to slash deposition, compaction during logging and possibly to increased heterotrophic decomposition, the depth and mass of the forest floor decreased after harvesting, resulting in higher bulk densities for the forest floor (or remains thereof) in the cleared areas.

Chemical analyses of soil solution indicated moderate translocation of calcium and magnesium from the forest floor

to the upper mineral horizon in relation to the exchangeable pool sizes for these elements. No differences were noted among areas. Potassium losses from the upper horizons were always greatest under the uncut stand and least under the 1978 clearcut. The 1977 clearcut was always intermediate. However, this hierarchy was not always statistically significant throughout the season. Nonetheless, this pattern is likely the result of not only higher potassium inputs due to canopy wash in the control area but also of increased uptake of potassium by lesser vegetation in the cleared areas and soil microbial immobilization in response to cutting. Soluble organic nitrogen concentrations followed the same distribution as potassium, being highest in the control and least in the most recent cut. This is likely a result of a higher degree of root exudation in the control area, in concert with a higher degree of microbial activity in the clearcut areas.

Year to year variability in the C/N ratios from the forest floor and mineral horizon was high. However, the 1977 clearcut consistently had a higher forest floor C/N ratio than either the 1978 clearcut or the control, presumably because of the large amount of slash left on that site. Carbon/nitrogen ratios in the mineral horizon differed little between areas.

Soil respiration was consistently higher in the clearcut areas than in the control. The largest differences were

always in mid-season, when soil temperatures were highest. This cannot solely be interpreted as an indication of higher microbial activity in the clearcut areas (although this is likely) since these estimates were not corrected for root respiration. However, as an index of the soil's total CO_2 output, the information obtained was useful when the relationship between nitrogen mineralization and specific soil-site characteristics was later investigated.

A bioassay utilizing white spruce seedlings collected from the harvested and uncut areas suggested that enhanced nitrogen levels in the current foliage of the clearcut seedlings resulted from increased nitrogen uptake. Levels of NO_3-N in the clearcut areas were substantially higher than those in the control. This suggests that NO_3-N may be the form of nitrogen utilized. However, without the use of an N^{15} bioassay, this is impossible to determine. The photosynthetic capacity of the seedlings grown in the clearcut areas is likely much greater than those in the control due to a larger proportion of current-year needles. With this increased capacity may come the inherent ability to take up and reduce nitrate effectively.

Significant regressions of nitrogen mineralization and nitrification on soil moisture and temperature were found for both the forest floor and mineral horizon in the uncut stand. These relationships were not always evident in the clearcut areas, especially in the forest floor: fluctuations in the

temperature and moisture regimes in the clearcut areas may have precluded the development of strong relationships. Temperature appeared to be the stronger predicting variable, but this was not true in all cases.

When nitrogen mineralization patterns were examined in black spruce and white birch forest cover types and compared to those for white spruce, some weak but interesting aspects of the controls of N-mineralization were revealed. These indicated that soil moisture may control N-mineralization more than soil temperature at deeper depths while soil temperature might be the stronger factor closer to the surface. However, due to the interaction of these two factors, and the design of the experiment across cover types, it is not possible to conclusively and statistically say that this is so.

In terms of instantaneous pool sizes, both the forest floor and mineral soil of the control area exhibited characteristics of an ammonium-dominated climax ecosystem (Rice and Pancholy, 1972). Ammonium-N pools ranged from 0.5 to 1.0 g/m^2 and 0.1 to 0.3 g/m^2 for the forest floor and mineral horizon respectively. Nitrate-N pools and nitrification rates were very low. According to Vitousek (1977), this same distribution of available nitrogen in soil pools could result under conditions of high nitrification coupled to high NO_3-N uptake rates. However, use of the polyethylene bag technique precludes plant uptake so uptake by mature trees cannot be

invoked here. This still leaves the possibility that NO_3-N is being utilized by microbes. However, it does not seem to make much ecological or evolutionary sense that two entirely different life-forms (microbes and trees) could evolve together into a mature ecosystem dominated by NO_3-N, with only one of these life-forms (microbes) utilizing nitrate. I feel that the evidence is strong enough here to state that the white spruce forest soils of interior Alaska are ammonium dominated, and as such, exhibit very low rates of nitrification.

After harvesting, nitrification substantially increased levels of NO_3-N in both the forest floor and mineral horizon. Seasonality of nitrification was evident, with the highest rates found in mid-summer. These seasonal patterns were not evident for nitrogen mineralization.

Statistically, harvesting did not affect N-mineralization or nitrification rates. This was partially a result of the sample sizes; only eight (n) incubation periods were employed, despite a continuous period of incubation of 22 months. However, when nitrification rates were looked at within season, they were often much higher in the clearcut areas when compared to the control. It is important to understand that while harvesting did not affect mineralization rates (i.e. net production of NH_4-N, or ammonification) more N would have to be transferred from the organic-N pool to "satisfy" increased nitrification. Thus, harvesting did

increase "net nitrogen mineralization". This is consistent with our knowledge of the effects of increased temperature and moisture regimes on decomposition processes after harvesting.

A schematic development of nitrogen cycling models indicated that nitrogen cycling was extremely "tight" in the control area, which exhibited many of the characteristics of a steady-state system. Conventional harvesting disrupted this system to the extent that available nitrogen pools increased, primarily a function of decreased plant uptake (NH_4-N pool) and increased nitrification (NO_3-N pool).

The application of a simulation language (DYNAMO) to the systems was not as successful as originally expected due to the linear nature of the rates governing pool sizes. Nonetheless, some arguments can be made against whole-tree harvesting on short (<100 years) rotations. Conventional harvesting of white spruce on interior micaceous upland sites could proceed indefinitely based on, at least, estimates of nitrogen reserves; this may be conditional upon the increased input of some silvicultural effort. Nutrient budgets for other elements should also be considered.

The modelling methodology employed in this study was not strong enough to predict long-term effects of forest harvesting on these sites. Neither was it possible to provide a predictive mechanism to evaluate potential replenishment and/or depletion of N-supplies with disturbance

beyond saying that, in the short-term, supply of nitrogen to white spruce seedlings planted in the clearcuts should not be a problem.

In the future, it is likely that site preparation on these types of sites will be more prevalent than at present. Prescriptions recognizing that released-by-harvest available nitrogen will be rapidly captured (taken up) by natural regeneration of fast-growing pioneer species will be most successful. In terms of the herbaceous cover, scarification to expose good white spruce mineral soil micro-sites will simultaneously return much of the nitrogen in the plants to the soil. With respect to aspen, short-term "losses" to this component probably are not harmful if litterfall and biomass produced remain on the site. However, it should be remembered that establishment and maintenance of white spruce plantations (at least) is hampered by the presence of trembling aspen stems. Additionally, although aspen may deteriorate at age 50-70, returning nitrogen to the site, it may not be released from slowly decomposing boles for another 50 years or so. In natural ecosystems, this "released-from-aspen" nitrogen can be effectively utilized by white spruce present in the understory, which at this age (70+) is beginning to enter a period of rapid growth. In harvest-plant systems, it may be more desireable to have this "aspen" nitrogen available at an earlier time to support rapid seedling and sapling growth.

Thus, in the short-term, winter harvesting operations or summer harvesting operations that leave limbs and needles on the site will be most beneficial. Scarification is also recommended not only to enhance seedling establishment but also to hasten decomposition of branches. Uptake of nitrogen by annual vegetation (or perennial grasses) should not be a concern under this scenario. The inputs to the soil system of these high C:N residues will work against the availability of nitrogen. However, these trends to immobilization should be adequately offset by increased inputs of mineral nitrogen into the system (mineralization) due to increased temperature and moisture regimes. In addition, immobilization processes should be short-lived as long as debris has been well broken up and dispersed through the upper soil horizon. Whole-tree harvesting or harvesting that removes any biomass other than boles to a harvestable top diameter should be avoided at all costs.

Harvesting does not appear to be detrimental in the short-term (1 rotation) to N-dynamics on these upland white spruce sites. This statement would be more correct if competing lesser vegetation could be eliminated by scarification or herbicides.

In the long-term, uptake by perennial vegetation of nitrogen by undesireable (for harvest) trees, such as aspen, should not pose a problem as long as the biomass produced remains on the site. As mentioned previously, this may be

more desireable under a management scheme employing natural regeneration. Under a harvest and plant situation, this strategy may not be as desireable; mechanical and/or herbicidal cleanings of aspen, such as those conducted in northern Ontario, should be considered.

In terms of the original objectives of this study, it was possible to determine mineralization levels and patterns for the forest floor and mineral soil of white spruce forest sites in interior Alaska. It was also possible to measure these and nitrification rates in adjacent clearcuts. However, depending upon the clearcut studied entirely different effects of harvesting may appear. This is possibly a result of the difference in ages of the clearcuts but given that this difference was only 1 year this is perhaps questionable. A pre-study intensive investigation of substrate factors in each clearcut may have been beneficial to later phases of the project but without really knowing the exact amount of debris left on each site after logging this cannot be said for certain.

One problem in evaluating the effects of harvesting on N-processes may have been the paired design chosen. It might be better to "calibrate" a large section of mature forest in terms of all major N-processes (denitrification, litterfall, root sloughage and (especially) fixation, etc.) for a long period of time (5 years) and then to harvest that same site. The potential control of the organic-N substrate on mineral-

ization processes could also be effectively evaluated in this manner by controlliing the type of logging and hence the amount of slash left on portions of the site.

Finally, Yarie (1983) has stated: "The major gap in the information on white spruce ecosystems used" (in his model) "was the effect of clearing on forest floor nitrogen mineralization rates in comparison to values for the uncut situation. It would be very helpful to know what the... mineralization rates are in clearcuts and uncut forests..." I feel that, to a certain extent, this statement has been addressed adequately by the present study.

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Appendix I

Major elemental concentrations from foliage

of selected vegetation on the three intensive sites.

Appendix I. Major elemental concentrations from foliage of selected vegetation on the three intensive sites (mean (S)).

	(%)				
	N	P	K	Ca	Mg
133-yr-old white spruce (control)					
current needles	0.961 (0.029)	0.220 (0.013)	0.687 (0.036)	0.661 (0.026)	0.142 (0.010)
2 yr+ needles	0.866 (0.025)	0.139 (0.007)	0.384 (0.024)	1.101 (0.031)	0.125 (0.009)
current twigs	0.982 (0.011)	0.180 (0.000)	0.842 (0.006)	0.711 (0.005)	0.110 (0.000)
2 yr+ twigs	0.502 (0.026)	0.098 (0.006)	0.585 (0.031)	0.752 (0.019)	0.075 (0.003)
bolewood	0.055 (0.006)	0.004 (0.001)	0.052 (0.005)	0.228 (0.028)	0.003 (0.000)
White spruce seedlings (control)					
current needles	1.165 (0.046)	0.226 (0.009)	0.933 (0.030)	0.552 (0.036)	0.163 (0.005)
2 yr+ needles	0.913 (0.027)	0.218 (0.009)	0.561 (0.014)	0.799 (0.034)	0.099 (0.006)
current twigs	0.964 (0.032)	0.196 (0.006)	1.003 (0.038)	0.636 (0.030)	0.113 (0.006)
2 yr+ twigs	0.476 (0.023)	0.100 (0.005)	0.510 (0.052)	0.456 (0.019)	0.085 (0.004)
roots	0.366 (0.026)	0.084 (0.006)	0.298 (0.019)	0.372 (0.019)	0.072 (0.006)
(clearcut 1978)					
current needles	1.508 (0.072)	0.314 (0.012)	1.028 (0.062)	0.655 (0.054)	0.147 (0.007)
2 yr+ needles	1.010 (0.050)	0.292 (0.027)	0.647 (0.039)	0.827 (0.074)	0.122 (0.009)
current twigs	0.951 (0.052)	0.229 (0.008)	0.863 (0.055)	0.454 (0.026)	0.150 (0.014)
2 yr+ twigs	0.677 (0.038)	0.146 (0.008)	0.523 (0.026)	0.413 (0.017)	0.113 (0.006)
roots	0.718 (0.035)	0.189 (0.008)	0.431 (0.032)	0.498 (0.031)	0.125 (0.006)
(clearcut 1977)					
current needles	1.391 (0.051)	0.313 (0.013)	0.810 (0.041)	0.601 (0.024)	0.122 (0.007)
2 yr+ needles	1.033 (0.052)	0.300 (0.013)	0.648 (0.024)	0.799 (0.027)	0.081 (0.006)
current twigs	0.940 (0.035)	0.215 (0.006)	0.855 (0.021)	0.384 (0.016)	0.089 (0.004)
2 yr+ twigs	0.514 (0.023)	0.109 (0.008)	0.446 (0.018)	0.420 (0.015)	0.066 (0.004)
roots	0.502 (0.023)	0.145 (0.011)	0.440 (0.022)	0.431 (0.022)	0.067 (0.006)
Trembling aspen (control)					
leaves	1.415 (0.087)	0.424 (0.046)	1.205 (0.176)	2.192 (0.908)	0.522 (0.061)
branches	0.983 (0.098)	0.183 (0.019)	0.536 (0.028)	0.077 (0.124)	0.154 (0.022)
(clearcut 1978)					
leaves	1.274 (0.063)	0.321 (0.042)	0.723 (0.025)	1.838 (0.309)	0.413 (0.108)
branches	0.717 (0.068)	0.157 (0.032)	0.395 (0.018)	0.667 (0.046)	0.039 (0.008)
(clearcut 1977)					
leaves	1.403 (0.057)	0.278 (0.034)	1.079 (0.062)	1.552 (0.191)	0.266 (0.014)
branches	0.761 (0.016)	0.155 (0.014)	0.515 (0.026)	0.957 (0.172)	0.129 (0.015)
All mosses[a]					
(control)	0.913 (0.116)	0.170 (0.013)	0.718 (0.073)	0.618 (0.032)	0.155 (0.023)
(clearcut 1978)	0.906 (0.055)	0.144 (0.007)	0.578 (0.118)	0.680 (0.068)	0.175 (0.016)
(clearcut 1977)	0.894 (0.447)	0.178 (0.020)	0.751 (0.048)	0.740 (0.065)	0.185 (0.012)
Grasses					
(clearcut 1978)	0.494	0.067	0.472	0.398	0.060
(clearcut 1977)	0.545	0.071	0.472	0.372	0.051

[a] For control and 1977 clearcut: Pleurozium, Hypnum, Hylocomium, Polytrichum, for clearcut 1978: Pleurozium, Hypnum, Hylocomium.

Appendix II

Net nitrogen mineralization rates (forest floor and mineral horizon of the three intensive study sites) as defined by Nadelhoffer *et al.* (1983) for all sampling periods.

Appendix II. Net nitrogen mineralization rates (forest floor and mineral horizon of the intensive study sites) as defined by Nadelhoffer et al. (1983) for all sampling periods (g/m^2/period).

Sampling period	(days)	Net nitrogen mineralization		
		Clearcut 1978	Clearcut 1977	Control
Forest Floor				
August 1979	(31)	1.58	0.31	0.86
September 1979	(30)	-2.20	0.29	0.56
Overwinter 1979-1980	(234)	2.39	2.20	0.87
June 1980	(30)	0.22	2.92	0.40
July 1980	(31)	0.45	1.55	0.46
August 1980	(31)	0.72	1.91	0.57
September 1980	(30)	-0.43	-0.43	0.18
Overwinter 1980-1981	(234)	0.70	-0.02	0.34
	Mean	0.43	1.09	0.53
Mineral Horizon				
August 1979	(31)	-0.25	0.00	0.14
September 1979	(30)	0.08	-0.06	0.05
Overwinter 1979-1980	(234)	0.42	1.57	0.19
June 1980	(30)	0.26	0.25	0.11
July 1980	(31)	0.02	0.18	0.07
August 1980	(31)	0.35	0.23	0.06
September 1980	(30)	0.16	-0.01	0.20
Overwinter 1980-1981	(234)	0.07	0.21	-0.08
	Mean	0.14	0.30	0.09
Yearly estimate (kg/ha/yr)	Forest Floor	20.5	66.0	25.6
	Mineral Horizon	7.0	14.0	5.1

Average of mineral horizon net nitrogen mineralization from 9 stands (Nadelhoffer et al., 1983): 69.5.

Appendix III

Ammonium and NO_3-N determinations for subsample and incubated samples from the forest floor and mineral soil of the three intensive sites.

Appendix III. Ammonium and NO_3-N determinations for subsample and incubated samples from the forest floor and mineral soil of the three intensive sites (ug/100g).

	Sampling Period	NH_4 subsample		NH_4 incubated		NO_3 subsample		NO_3 incubated	
Forest Floor									
Clearcut 1978	1[a]	7859.89	(1268.94)	4941.16	(660.60)*	8162.08	(1812.00)	15799.19	(2979.18)*
	2	4333.28	(655.39)	7795.97	(1279.78)*	13582.00	(2098.50)	2132.52	(560.30)**
	3	5603.97	(507.00)	13981.41	(1399.70)**	649.68	(268.99)	6082.16	(1535.72)**
	4	8377.56	(1075.03)	6074.03	(632.24)	809.39	(135.27)	3880.32	(628.84)**
	5	6886.73	(794.92)	6056.34	(573.45)	627.28	(112.96)	4020.98	(773.58)**
	6	5372.15	(616.72)	7618.19	(806.06)*	315.26	(100.69)	1156.95	(301.67)*
	7	6967.01	(653.12)	3746.87	(293.24)**	356.42	(52.70)	1085.43	(250.96)**
	8	4787.97	(451.22)	6574.57	(685.84)*	448.36	(76.30)	2507.36	(476.60)**
Clearcut 1977	1	4924.56	(428.61)	5580.54	(690.95)	23.76	(23.76)	1025.50	(267.30)**
	2	5203.95	(415.59)	6185.30	(557.51)	38.95	(13.18)	466.08	(139.58)**
	3	3988.86	(374.83)	11998.12	(1084.71)**	41.16	(19.82)	3783.96	(850.35)**
	4	7640.54	(767.70)	15511.32	(1455.94)**	357.38	(56.35)	6985.29	(116.30)**
	5	6512.12	(617.54)	11887.21	(982.80)**	363.51	(69.29)	4634.18	(896.80)**
	6	5929.82	(460.76)	12054.26	(757.38)**	46.69	(20.10)	2925.59	(612.89)**
	7	9424.81	(717.05)	6347.10	(668.25)**	12.85	(12.85)	740.78	(230.07)**
	8	5654.88	(376.06)	3519.16	(256.02)**	196.22	(46.80)	2157.64	(459.91)**
Control	1	8329.79	(561.29)	17202.18	(1522.23)**	0	(0)	0	(0)
	2	7531.71	(979.35)	13025.68	(1200.20)**	0	(0)	0	(0)
	3	4944.42	(355.55)	13848.10	(862.77)**	0	(0)	226.58	(18.42)**
	4	7218.30	(621.99)	10904.55	(913.99)**	96.56	(26.22)	108.09	(14.00)
	5	8888.46	(882.74)	13812.83	(1338.34)**	121.44	(10.33)	911.03	(454.29)
	6	7543.96	(476.80)	13179.81	(891.29)**	98.86	(21.36)	61.76	(22.51)
	7	10600.28	(797.52)	12241.88	(1506.46)	19.92	(6.14)	109.21	(24.79)**
	8	6137.83	(386.47)	9154.10	(689.45)**	108.41	(8.35)	124.67	(18.39)
Mineral Soil									
Clearcut 1978	1	1278.40	(115.61)	897.84	(77.74)**	283.94	(102.04)	177.67	(63.82)
	2	513.65	(38.36)	585.18	(41.42)	17.82	(4.17)	114.16	(31.39)**
	3	599.56	(65.68)	1457.86	(135.96)**	19.00	(8.93)	200.51	(47.48)**
	4	836.50	(81.80)	1274.86	(86.29)**	105.52	(20.34)	285.39	(34.47)**
	5	782.58	(75.17)	519.31	(57.42)**	51.40	(8.17)	357.07	(75.61)**
	6	194.36	(14.72)	809.16	(50.87)**	14.63	(1.81)	129.22	(30.02)**
	7	256.91	(20.25)	488.64	(29.84)**	0	(0)	90.81	(25.84)**
	8	558.87	(46.88)	687.74	(73.38)	18.19	(3.91)	81.08	(11.79)**

Appendix III. continued.

Mineral Soil

	Sampling Period	NH_4 subsample		NH_4 incubated		NO_3 subsample		NO_3 incubated	
Clearcut 1977	1	444.94	(48.24)	456.73	(48.92)	0	(0)	0	(0)
	2	411.43	(51.36)	281.54	(26.30)*	0	(0)	0	(0)
	3	162.90	(15.63)	742.60	(64.59)**	0	(0)	123.58	(19.02)**
	4	344.52	(22.12)	775.54	(69.16)**	96.20	(8.38)	256.61	(43.48)**
	5	266.74	(23.81)	530.56	(49.52)**	12.65	(5.26)	181.75	(44.31)**
	6	221.66	(20.08)	622.36	(51.72)**	31.86	(4.43)	65.43	(14.45)*
	7	431.00	(31.48)	382.30	(33.43)	0	(0)	20.80	(5.51)**
	8	182.43	(22.40)	441.79	(43.49)**	24.42	(5.95)	238.11	(42.61)**
Control	1	294.68	(21.84)	573.42	(69.96)**	0	(0)	0	(0)
	2	220.80	(18.16)	317.11	(31.76)*	0	(0)	0	(0)
	3	142.02	(17.46)	475.28	(39.36)**	0	(0)	39.04	(1.70)**
	4	444.31	(67.25)	668.01	(67.79)*	25.90	(3.67)	26.67	(1.07)
	5	301.75	(23.58)	498.75	(35.81)**	34.82	(3.45)	0	(0)**
	6	515.39	(40.84)	585.37	(55.87)	0	(0)	22.16	(4.55)**
	7	289.28	(18.44)	648.30	(58.90)**	0	(0)	8.54	(1.80)**
	8	553.25	(94.15)	372.84	(41.55)	55.95	(32.20)	43.04	(9.56)

[a] Sampling periods (1-8) are, in order, August 1979, September 1979, overwinter 1979-1980, June 1980, July 1980, August 1980, September 1980, overwinter 1980-1981.

*, ** significant at $p<0.05$ and <0.01, respectively.

Appendix IV

Differences in NH_4-N and NO_3-N concentrations (ug/100g) between sub- and incubated samples for the forest floor and mineral soil horizons of the intensive study sites by sampling time.

Appendix IV. Differences in NH_4-N and NO_3-N concentrations (ug/100g) between sub- and incubated samples for the forest floor and mineral soil horizons of the intensive study sites by sampling time (mean (S_x)). The percentage of bags in each case showing positive gains is also given.

Forest Floor

		Clearcut 1978		%+	Clearcut 1977		%+	Control		%+
NH_4	1	-2499.98	(1238.91)	50.0	538.30	(510.83)	64.3	8872.39	(1278.74)	100.0
	2	3658.09	(1711.30)	71.4	996.17	(574.02)	69.2	5516.27	(852.04)	96.6
	3	7938.70	(1214.22)	100.0	8009.27	(1009.73)	96.7	8906.69	(759.37)	100.0
	4	-1997.26	(695.50)	25.9	7870.78	(1040.56)	100.0	3689.25	(644.95)	89.7
	5	-800.38	(478.79)	50.0	5267.54	(879.88)	89.7	4995.67	(1271.12)	86.2
	6	2501.23	(625.01)	92.3	6362.72	(631.69)	96.4	5524.24	(677.02)	100.0
	7	-2621.47	(431.85)	8.0	-2874.88	(982.97)	24.1	1641.60	(1369.82)	55.2
	8	1734.65	(651.53)	76.9	-2135.72	(434.92)	13.8	3255.45	(616.14)	84.6
			Mean	59.3		Mean	69.3		Mean	89.0
NO_3	1	10198.52	(2290.05)	100.0	1008.05	(308.66)	57.7	0	(0)	0
	2	-14326.70	(2383.22)	0	431.84	(154.62)	45.8	0	(0)	0
	3	4106.25	(1060.08)	90.5	3547.42	(905.55)	100.0	220.72	(19.32)	100.0
	4	3182.66	(588.74)	100.0	6162.26	(1108.97)	96.4	11.53	(22.78)	55.2
	5	3393.70	(725.68)	84.6	4029.40	(890.57)	91.7	429.73	(289.85)	25.9
	6	865.50	(260.09)	88.0	2877.23	(603.40)	92.9	-28.29	(18.20)	19.2
	7	620.83	(220.51)	66.7	731.14	(255.84)	79.2	92.90	(26.24)	69.2
	8	1712.01	(377.33)	87.5	1949.46	(457.32)	89.3	12.42	(18.12)	55.2
			Mean	77.2		Mean	81.6		Mean	40.6

Mineral Soil

NH_4	1	-434.09	(125.35)	21.4	-1.24	(36.96)	42.9	263.19	(57.38)	75.0
	2	65.60	(28.90)	62.1	-113.49	(34.93)	31.0	96.32	(27.66)	86.2
	3	774.70	(135.29)	92.6	562.38	(66.27)	100.0	332.38	(40.27)	100.0
	4	417.04	(62.98)	89.7	318.49	(43.60)	100.0	223.70	(51.65)	89.7
	5	-209.43	(65.49)	33.3	246.50	(43.08)	95.6	199.92	(29.25)	92.9
	6	618.50	(42.13)	100.0	384.52	(40.91)	100.0	86.61	(43.24)	57.1
	7	231.73	(21.58)	100.0	-48.70	(28.52)	20.7	355.87	(51.51)	96.3
	8	114.38	(51.18)	73.1	244.16	(29.47)	100.0	-111.59	(98.33)	53.8
			Mean	71.5		Mean	73.8		Mean	81.4
NO_3	1	-106.26	(66.66)	14.8	0	(0)	0	0	(0)	0
	2	96.35	(29.87)	58.6	0	(0)	0	0	(0)	0
	3	163.88	(37.63)	92.0	114.00	(17.02)	100.0	39.04	(1.70)	96.2
	4	197.20	(22.00)	100.0	145.90	(39.83)	69.2	-3.10	(3.78)	52.2
	5	244.72	(61.21)	81.5	172.77	(41.46)	71.4	-38.18	(3.80)	0
	6	102.21	(28.58)	76.0	33.71	(12.23)	58.6	24.97	(5.28)	79.2
	7	90.81	(25.84)	92.9	20.80	(5.51)	50.0	6.25	(1.53)	52.0
	8	62.96	(11.87)	81.5	190.29	(32.96)	100.0	-11.64	(33.13)	41.4
			Mean	74.7		Mean	56.2		Mean	40.1

Appendix V

DYNAMO listing of a simple nitrogen-cycling model for a mature white spruce stand in interior Alaska.

Appendix V. DYNAMO listing of a simple nitrogen-cycling model for a mature white spruce stand in interior Alaska.

```
NOTE      WORKING MODEL OF THE NITROGEN CYCLE STEADY-STATE,
NOTE      WHITE SPRUCE, 130 YEARS TO 200 YEARS
NOTE      POOLS ARE G/M2; RATES ARE G/M2/YR
NOTE      THE MINERALIZATION AND NITRIFICATION
NOTE      FLUXES IN THIS MODEL ARE DRIVEN BY
NOTE      SOIL MOISTURE CONTENT, TEMPERATURE,
NOTE      AND RESPIRATION
NOTE      AS AN EARLY VERSION, THIS PARTICULAR
NOTE      MODEL DOES NOT CONTAIN THE UPTAKE
NOTE      CHECK LATER ADDED (AS FOUND IN THE
NOTE      CLEARCUT MODEL)
NOTE      TO RUN UNDER TIME-SHARING, REMOVE CONTROL CARDS AND TYPE SX/DYNA
NOTE      THE NEXT 4 LINES CYCLE DATA ON AN ANNUAL BASIS (4 MONTHS, 1 OVERWINTER PERIOD)
L     S.K=AUX.J+S.J
N     S=5
A     AUX.K=5*STEP(1,S.K)
A     PER.K=5+TIME.K-S.K
NOTE      THE NEXT 3 LINES CORRECT FOR LENGTH OF PERIOD
A     DAYS.K=FIFGE(C1,C2,PERI.K,5)
N     C1=234
N     C2=30
NOTE      THE NEXT 3 LINES CORRECT FOR NEG. NITRIF. IN MINERAL HORIZON
A     COR1.K=FIFGE(Y1,Y2,PERI.K,2)
N     Y1=0.00
N     Y2=0.010944
NOTE      THE NEXT 6 LINES CORRECT FOR VARIABLE SPRUCE LITTERFALL
A     A.K=1*STEP(.041,50)
A     B.K=1*STEP(.040,100)
A     C.K=1*STEP(.039,150)
A     D.K=1*STEP(.038,200)
A     E.K=1*STEP(.025,250)
A     F.K=1*STEP(.022,300)
NOTE      THE NEXT 6 LINES CORRECT FOR VARIABLE ALDER LITTERFALL
A     G.K=1*STEP(.002,50)
A     H.K=1*STEP(.001,100)
A     I.K=1*STEP(.001,150)
A     J.K=1*STEP(.001,200)
A     K.K=1*STEP(.002,250)
A     L.K=1*STEP(.002,300)
NOTE      SET UP LEVEL EQUATIONS
L     CHECK.K=(SUPNHO.JK+SUPNHM.JK+SUPNOM.JK-
X     UPTMO3.JK-UPTSEE.JK-UPTALD.JK-UPTTRE.JK)*DT
L     TOTNO.K=TOTNO.J+(LITMOS.JK+LITSPR.JK+LITALD.JK+FIRSPO.JK
X     -AMMONO.JK-LEASON.JK)*DT
L     NH4O21.K=NH4O21.J+(AMMONO.JK-SUPNHO.JK-LEANH4.JK-NITRIO.JK-
X     VOLAT.JK)*DT
L     NO3O21.K=NO3O21.J+(NITRIO.JK-SUPNOO.JK-LEANO3.JK-DENITO.JK)*DT
L     TOTNMI.K=TOTNMI.J+(LEASON.JK+FIRSMI.JK-AMMONM.JK)*DT
L     NH4MIN.K=NH4MIN.J+(AMMONM.JK+LEANH4.JK-SUPNHM.JK-NITRIM.JK-
X     COR1.K-COR2.JK)*DT
L     NO3MIN.K=NO3MIN.J+(NITRIM.JK+LEANO3.JK-SUPNOM.JK-DENITM.JK+
```

Appendix V. continued.

```
X     COR1.K+COR2.JK)*DT
L     MOSSN.K=MOSSN.J+(UPTMOS.JK+PREMOS.JK-LITMOS.JK)*DT
L     SEEDN.K=SEEDN.J+(UPTSEE.JK)*DT
L     TREEN.K=TREEN.J+(UPTTRE.JK-LITSPR.JK)*DT
L     ALDERN.K=ALDERN.J+(UPTALD.JK-LITALD.JK)*DT
NOTE      INITIAL VALUES
N     CHECK=0.00
N     TOTNO=95.58
N     NH4021=0.74
N     NO3021=0.0054
N     TOTNMI=25.75
N     NH4MIN=0.18
N     NO3MIN=0.0075
N     MOSSN=5.02
N     SEEDN=0.00362
N     TREEN=30.69
N     ALDERN=1.61
N     TIME=1
NOTE      SET UP RATE EQUATIONS
R     COR2.KL=TABHL(COR,PERI.K,1,5,1)
R     LITMOS.KL=TABHL(LITM,PERI.K,1,5,1)
R     LITSPR.KL=0.174+A+B+C+D+E+F
R     LITALD.KL=0.015+G+H+I+J+K+L
R     FIRSPO.KL=TABHL(FIXO,PERI.K,1,5,1)
R     AMMONO.KL=(.03151-(.17821E-03*MOISTO.K)+(.87461E-03*TEMPO.K))*DAYS.K
R     LEASON.KL=TABHL(LEASO,PERI.K,1,5,1)
R     SUPNHO.KL=TABHL(SUPNH1,PERI.K,1,5,1)
R     LEANH4.KL=TABHL(LEANH,PERI.K,1,5,1)
R     NITRIO.KL=(-.001+(.9296E-05*MOISTO.K))*DAYS.K
R     SUPNOO.KL=TABHL(SUPNO1,PERI.K,1,5,1)
R     LEANO3.KL=TABHL(LEANO,PERI.K,1,5,1)
R     DENITO.KL=TABHL(DENIT1,PERI.K,1,5,1)
R     FIRSMI.KL=TABHL(FIXM,PERI.K,1,5,1)
R     AMMONM.KL=(.0083+(.01875*RESP.K)-(.46859E-03*BAGSM.K)-(.15317E-04
X     *DDAYS.K))*DAYS.K
R     SUPNHM.KL=TABHL(SUPNH2,PERI.K,1,5,1)
R     NITRIM.KL=(.00098-(.62058E-04*MOISTM.K))*DAYS.K
R     SUPNOM.KL=TABHL(SUPNO2,PERI.K,1,5,1)
R     DENITM.KL=TABHL(DENIT2,PERI.K,1,5,1)
R     UPTMOS.KL=TABHL(UPTM,PERI.K,1,5,1)
R     UPTSEE.KL=TABHL(UPS,PERI.K,1,5,1)
R     UPTTRE.KL=TABHL(UPTSW,PERI.K,1,5,1)
R     UPTALD.KL=TABHL(UPTA,PER.K,1,5,1)
R     PREMO.KL=TABHL(PRE,PER.K,1,5,1)
R     VOLAT.KL=0.00
NOTE      ENVIRONMENTAL VARIABLES TO DRIVE MINERALIZATION/NITRIFICATION
A     MOISTO.K=TABHL(MOIST,PER.K,1,5,1)
A     TEMP.K=TABHL(TEMP,PER.K,1,5,1)
A     BAGSM.K=TABHL(BAGS,PERI.K,1,5,1)
A     DDAYS.K=TABHL(DDAY,PERI.K,1,5,1)
A     MOISTM.K=TABHL(MOIMIN,PERI.K,1,5,1)
NOTE      DISTRIBUTION OF RATES ACROSS SEASON (5 MONTHS, 1 O.W.)
T     MOIST=160.96/192.67/113.03/115.47/107.72
```

Appendix V. continued

```
T     TEMP=14.2/16.8/13.6/6.7/-11.9
T     RES=.6081/.7073/.5236/.4007/.1797
T     BAGS=19.8/21.8/20.4/17.2/17.9
T     DDAY=391.0/486.7/422.9/184.7/184.4
T     MOIMIN=21.67/25.38/15.51/12.94/15.29
T     LITM=.26/.26/.26/.26/0/00
T     FIXO=.16/.18/.14/.09/0.00
T     LEASO=.015/.015/.015/.015/0.00
T     SUPNH1=0.59/0.59/0.65/0.58/0.00
T     LEANH=.002475/.002475/.002475/.002475/0.00
T     SUPNO1=.01/.023/.025/.002/.0.00
T     LEANO=.0013/.0013/.0013/.0013/0.00
T     DENITI=0.00/0.00/0.00/0.00/0.00
T     FIXM=.12/.13/.12/.05/0.00
T     SUPNH2=.1545/.1255/.1255/.0865/0.00
T     SUPNO2=.001875/.003875/.004375/.003875/0.00
T     DENIT2=.0005/.0016/.0006/.0005/0.00
T     PRE=.265/.272/.2608/.2322/0.00
T     UPS=.000025/.000025/.000025/.000025/0.00
T     UPTSW=.47/.45/.50/.42/0.00
T     UPTA=.02/.02/.02/.02/0.00
T     UPTM=0.00/0.00/0.00/0.00/0.00
T     COR=0.00/0.017851/0.00/0.00/0.00
NOTE      VARIABLES FOLLOW NOMENCLATURE IN CLEARCUT MODEL
NOTE      WITH THE FOLLOWING ADDITIONS
NOTE      UPTALD=UPTAKE, ALDER
NOTE      UPTTRE=UPTAKE, MATURE WHITE SPRUCE
NOTE      LITSPR=LITTERFALL, MATURE WHITE SPRUCE
NOTE      LITALD=LITTERFALL, ALDER
NOTE      SEEDN=TOTAL NITROGEN, WHITE SPRUCE SEEDLINGS
NOTE      TREEN=TOTAL NITROGEN, MATURE WHITE SPRUCE
NOTE      ALDERN=TOTAL NITROGEN, ALDER
NOTE      ENVIRONMENTAL FACTORS:
NOTE      MOISTO=MOISTURE CONTENT, FOREST FLOOR
NOTE      TEMPO=SOIL TEMPERATURE, FOREST FLOOR
NOTE      RESP=SOIL RESPIRATION
NOTE      BAGSM=MOISTURE CONTENT, WITHIN BAGS, MINERAL HORIZON
NOTE      DDAYS=DEGREE DAYS
NOTE      MOISTM=MOISTURE CONTENT, MINERAL HORIZON
PRINT     TOTNO/NH4021/NO3021/TOTNMI/NH4MIN/NO3MIN/
X         MOSSN/SEEDN/TREEN/ALDERN/CHECK
PLOT      TOTNO=NH4021=1/NO3021=2/TOTNMI=L/NH4MIN=3/NO3MIN=4/
X         MOSSN=M/SEEDN=S/TREEN=ALDERN=A
NOTE      SINCE YEARS=5,LENGTH=350/5=70 YEARS
SPEC      DT=1.0/LENGTH=350/PRTPER=1/PLTPER=1
RUN
END
```

Appendix VI

DYNAMO listing of a simple nitrogen-cycling model for a small clearcut (formerly mature white spruce) in interior Alaska.

Appendix VI. DYNAMO listing of a simple nitrogen-cycling model for a small clearcut (formerly mature white spruce) in interior Alaska.

```
NOTE     WORKING MODEL OF THE NITROGEN CYCLE
NOTE     CLEARCUT 1977
NOTE     POOLS ARE G/M2;RATES ARE G/M2/YR
NOTE     THE MINERALIZATION AND NITRIFICATION FLUXES IN
NOTE     THIS MODEL ARE FIXED (SIGNIFICANT RELATIONSHIPS
NOTE     BETWEEN THESE FLUXES AND SOIL TEMPERATURE,
NOTE     MOISTURE AND RESPIRATION WHERE NOT FOUND)
NOTE     NEXT 7 STATEMENTS FOR VARIABLE ASPEN UPTAKE (LEAF
NOTE     AND BRANCH)
A    A.K=1*STEP(.01,1982)
A    B.K=1*STEP(.0114,1987)
A    C.K=1*STEP(.0148,1992)
A    E.K=1*STEP(.0324,2002)
A    F.K=1*STEP(.0738,2007)
A    G.K=1*STEP(.0522,2012)
NOTE     NEXT 7 STATEMENTS FOR VARIABLE ASPEN LITTERFALL
A    H.K=1*STEP(.0052,1982)
A    I.K=1*STEP(.0072,1987)
A    J.K=1*STEP(.0083,1992)
A    K.K=1*STEP(.0145,1997)
A    L.K=1*STEP(.0166,2002)
A    M.K=1*STEP(.0248,2007)
A    N.K=1*STEP(.0249,2012)
NOTE     NEXT 7 STATEMENTS FOR VARIABLE SEEDLING UPTAKE
A    O.K=1*STEP(.067,1982)
A    P.K=1*STEP(.067,1987)
A    Q.K=1*STEP(.067,1992)
A    R.K=1*STEP(.067,1997)
A    S.K=1*STEP(.067,2002)
A    T.K=1*STEP(.067,2007)
A    U.K=1*STEP(.067,2012)
NOTE     NEXT 7 STATEMENTS FOR VARIABLE SEEDLING LITTERFALL
A    AA.K=1*STEP(.0397,1982)
A    BB.K=1*STEP(.0397,1987)
A    CC.K=1*STEP(.0397,1992)
A    DD.K=1*STEP(.0397,1997)
A    EE.K=1*STEP(.0397,2002)
A    FF.K=1*STEP(.0397,2007)
A    GG.K=1*STEP(.0397,2012)
NOTE     SET UP LEVEL EQUATIONS
L    TOTNO.K=TOTNO.J+(LITMOS.JK+LITSEE.JK+LITASP.JK+LITGRT.JK+LITPLA.JK
X    +FIRSPO.JK-AMMONO.JK-LEASON.JK)*DT
L    NH4021.K=NH4021.J+(AMMONO.JK-SUPNHO.JK.LEANH4.JK-NITRIO.JK-
X    VOLAT.JK)*DT
L    NO3021.K=NO3021.J+(NITRIO.JK-SUPNOO.JK-LEANO3.JK-DENITO.JK)*DT
L    TOTNMI.K=TOTNMI.J+(LEASON.JK+FIRSMI.JK-AMMONM.JK)*DT
L    NH4MIN.K=NH4MIN.J+(AMMONM.JK+LEANH4.JK-SUPNHM.JK-NITRIM.JK)*DT
L    NO3MIN.K=NO3MIN.J+(NITRIM.JK+LEANO3.JK-SUPNOM.JK-DENITM.JK)*DT
L    MOSSN.K=MOSSN.J+(UPTMOS.JK+PREMOS.JK-LITMOS.JK)*DT
L    SEEDN.K=SEEDN.J+(UPTSEE.JK-LITSEE.JK)*DT
L    ASPN.K=ASPN.J+(UPTASP.JK-LITASP.JK)*DT
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Appendix VI. continued.

```
L     GRASN.K=GRASN.J+(UPTGRA.JK-LITGRA.JK-UPTROO.JK)*DT
L     ROOT.K=ROOT.J+(UPTROO.JK-LITROO.JK)*DT
NOTE      CALCULATE DISTRIBUTION OF NITROGEN SUPPLY
A     CONST.K=TABHL(CON,Y.K,1978,2023,5)
NOTE      ON  FIRST RUN,  INSERT 0.00 INTO EACH CELL OF  THE
NOTE      FOLLOWING TABLE. PRINT CHECK, AND THEN RE-INSERT
NOTE      CHECK VALUES INTO THE TABLE TO CORRECT FOR SUPPLY-
NOTE      UPTAKE  LAG.   USE THE ABSOLUTE  VALUE OF CHECK.
NOTE      (A SIMPLE WAY TO ADD THE CHECK VALUES ONTO THE SUPPLY)
NOTE      FIRST AND LAST TWO TABLE ENTRIES ARE ALWAYS 0.00
T     CON=0.00/.077/.0784/.0818/.0884/.0994/.1408/.1192/0.00/0.00
N     Y=1978
A     CORR.K=FIFZE(CONST,0,TEST.K)
A     TEST.K=TIME.K-Y.K+1
L     Y.K=Y.J+V.J
A     V.K=FIFGE(5,0,TEST2.K,3)
A     TEST2.K=TIME.K-Y.K
A     CHECK.K=SUPPLY.K-TOTUPT.K
A     SUP1.K=AMMON0.JK-VOLAT.JK-NITRI0.JK-LEANH4.JK
A     SUP2.K=NITRI0.JK-DENIT0.JK-LEANO3.JK
A     SUP3.K=AMMONM.JK+LEANH4.JK-NITRIM.JK
A     SUP4.K=NITRIM.JK+LEANO3.JK-DENITM.JK
A     TOTSUP.K=SUP1.K+SUP2.K+SUP3.K+SUP4.K
A     TOTUPT.K=(UPTMOS.JK+UPTGRA.JK+UPTASP.JK+UPTSEE.JK+UPTPLA.JK)*DT
NOTE      CORR IS CHECK, THE DIFFERENCE BETWEEN TOTAL UPTAKE AND
NOTE      TOTAL SUPPLY
L     SUPPLY.K=(SUPNH0.JK+SUPNO0.JK+SUPNHM.JK+SUPNOM.JK)*DT+CORR.J
A     F1.K=SUP1.K/TOTSUP.K*TOTUPT.K
A     F2.K=SUP2.K/TOTSUP.K*TOTUPT.K
A     F3.K=SUP3.K/TOTSUP.K*TOTUPT.K
A     F4.K=SUP4.K/TOTSUP.K*TOTUPT.K
A     TOTF.K=F1.K+F2.K+F3.K+F4.K
R     SUPNH0.KL=FIFGE(SUP1.K,F1.K,F1.K,SUP1.K)
R     SUPNO0.KL=FIFGE(SUP2.K,F2.K,F2.K,SUP2.K)
R     SUPNHM.KL=FIFGE(SUP3.K,F3.K,F3.K,SUP3.K)
R     SUPNOM.KL=FIFGE(SUP4.K,F4.K,F4.K,SUP4.K)
NOTE      SET UP INITIAL VALUES
N     SUPPLY=2.2242
N     TOTUPT=2.2242
N     CHECK=0.00
N     TOTNO=159.63
N     NH4021=1.19
N     NO3021=0.0262
N     TOTNMI=25.25
N     NH4MIN=0.16
N     NO3MIN=0.0104
N     MOSSN=0.25
N     SEEDN=0.00019
N     ASPN=0.135
N     GRASN=0.39
N     TIME=1977
N     ROOT=0.5
NOTE      SET UP RATE EQUATIONS
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```
R     LITSEE.KL=0.0+AA+BB+CC+DD+EE+FF+GG
R     LITMOS.KL=0.05
R     LITGRT.KL=LITGRA.JK+LITROO.JK
R     LITGRA.KL=0.27
R     LITASP.KL=0.0021+H+I+J+K+L+M+N
R     LITPLA.KL=1.25
R     FIRSPO.KL=0.57
R     AMMONO.KL=3.59
R     LEASON.KL=0.05
R     LEANH4.KL=0.01
N     NITRIO=3.01
R     NITRIO.KL=TABHL(NITRI,Y.K,1978,2023,5)
T     NITRI=3.01/2.90/2.79/2.68/2.57/2.46/2.35/2.24/2.13/2.02
R     LEANO3.KL=0.0069
R     DENITO.KL=0.0038
R     FIRSMI.KL=0.42
R     AMMONM.KL=0.54
N     NITRIM=0.238
R     NITRIM.KL=TABHL(NITM,Y.K,1978,2023,5)
T     NITM=.238/.229/.220/.211/.202/.193/.184/.175/.166/.157
R     DENITM.KL=0.0042
R     UPTMOS.KL=0.0
R     PREMOS.KL=0.5
R     UPTSEE.KL=0.0001+O+P+Q+R+S+T+U
R     UPTASP.KL=0.0041+A+B+C+D+E+F+G
R     UPTGRA.KL=0.92
R     UPTROO.KL=0.65
R     UPTPLA.KL=1.25
R     VOLAT.KL=0.00
R     LITROO.KL=FIFGE(0.65,0,TIME.K,1987)
PRINT     T/SUP1/TOTSUP/TOTUPT/SUPPLY/F1/SUPNHO/SUPNOO
X     /CHECK/AMMONO/LITSEE/NITRIO
PLOT      TOTNO=T/NH4021=1/NO3021=2/NH4MIN=3/NO3MIN=4/ASPN=A/MOSSN=M/
X         SEEDN=S/GRASN=G/TOTNMI=L
NOTE      TOTNO=TOTAL NITROGEN, ORGANIC HORIZON
NOTE      NH4021=NH4, ORGANIC HORIZON
NOTE      NO3021=NITRATE, ORGANIC HORIZON
NOTE      TOTNMI=TOTAL NITROGEN, MINERAL HORIZON
NOTE      NH4MIN=NH4, MINERAL HORIZON
NOTE      NO3MIN=NITRATE, MINERAL HORIZON
NOTE      MOSSN=TOTAL NITROGEN, MOSSES
NOTE      SEEDN=TOTAL NITROGEN, WHITE SPRUCE SEEDLINGS
NOTE      ASPN=TOTAL NITROGEN, ASPEN
NOTE      GRASN=TOTAL NITROGEN, GRASSES-CALAMAGROSTIS CANADENSIS
NOTE      ROOT=TOTAL NITROGEN, ROOTS OF GRASSES
NOTE      SUP1-4 ARE THE AMOUNTS THAT CAN BE SUPPLIED
NOTE      FROM THE 4 AVAILABLE POOLS (NH4021,NO3021,NH4MIN,NO3MIN)
NOTE      TOTSUP=TOTAL CAPABLE SUPPLY
NOTE      TOTUPT=TOTAL UPTAKE OF SEEDLINGS, GRASSES, MOSSES, ASPEN
NOTE      SUPNHO,SUPNOO,SUPNHM,SUPNOM ARE THE ACTUAL AMOUNTS SUPPLIED
NOTE      FROM THE FOUR AVAILABLE POOLS IN ORDER TO SATISFY UPTAKE
NOTE      AND NO MORE (CALCULATED BY DIVIDING SUP BY TOTSUP AND
NOTE      MULTIPLYING BY TOTAL UPTAKE)
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Appendix VI. continued

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NOTE      RATES: LIT(——) = LITTERFALL OF
NOTE      PLANTS(PLA), ABOVEGROUND GRASSES-DEAD STEMS/SEEDS(GRA), ASPEN(ASP)
NOTE      MOSSES(MOS), SEEDLINGS(SEE), GRASSROOTS(ROO), AND
NOTE      GRASSES-TOTAL (GRT)
NOTE      FIRSPO=FIXATION, ROOT SLOUGHAGE, PRECIPITATION
NOTE      EVENTS FOR THE ORGANIC HORIZON
NOTE      AMMONO=MINERALIZATION RATE, ORGANIC HORIZON
NOTE      LEASON=LEACHATE, SOLUBLE ORGANIC NITROGEN
NOTE      LEANH4=LEACHATE, AMMONIUM
NOTE      NITRIO=NITRIFICATION RATE, ORGANIC HORIZON
NOTE      LEANO3=LEACHATE, NITRATE
NOTE      DENITO=DENITRIFICATION RATE, ORGANIC HORIZON
NOTE      FIRSMI=FIXATION, ROOT SLOUGHAGE, PRECIPITATION EVENTS FOR THE
NOTE      MINERAL HORIZON
NOTE      AMMONM=MINERALIZATION RATE, MINERAL HORIZON
NOTE      NITRIM=NITRIFICATION RATE, MINERAL HORIZON
NOTE      DENITM=DENITRIFICATION RATE, MINERAL HORIZON
NOTE      VOLAT=VOLATILIZATION
NOTE      UPTAKE RATES: UPT(——) -AS IN LITTERFALL-
NOTE      PREMOS=PRECIP. INPUTS TO MOSS
SPEC      DT=1.0/LENGTH=2023/PRTPER=1/PLTPER=1
RUN
END
```