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Dynamics of nutrient cycling on post-harvested white spruce sites in interior Alaska

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University of Alaska Fairbanks, 1990

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DYNAMICS OF NUTRIENT CYCLING ON POST-HARVESTED WHITE SPRUCE SITES IN INTERIOR ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska in
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By

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DYNAMICS OF NUTRIENT CYCLING ON POST-HARVESTED WHITE SPRUCE SITES IN INTERIOR ALASKA

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ABSTRACT

Various field and laboratory methods were used to characterize nutrient cycling on two mature white spruce sites, one recently harvested site and three 14-year-old harvested white spruce sites colonized by different plant communities and presenting different intensity of soil disturbance. Study sites were chosen on upland south facing sites and presented conditions of reduced environmental variability. Soil analysis showed no changes in pools of soil nutrient unless the forest floor was removed. On the other hand, some differences in the dynamics of nutrients were seen: (1)- sites where the forest floor was removed showed low N mineralization rates; (2)- N mineralization rates appeared faster in the surface soil of the recently harvested site than in mature white spruce sites; (3)- the surface soil of sites regenerating to aspen showed the highest N mineralization rates of all 14-year-old sites. Field soil temperature, and field soil moisture content as well as N and lignin concentrations of the forest floor could not explain the differences in N mineralization rates between sites. This suggests that species colonization may influence N dynamics and that N cycling rate on regenerating sites is controled by a small pool of rapidly cycling N.

The determination of nutrient uptake and return by vegetation growing in the field indicated that nutrient cycling was much faster in 14-year-old aspen stands than on any other regenerating or mature site.

The measurement of element availability with ion exchange resin bags indicated an increased leaching of nitrate, phosphate and sulfate at springtime, the second summer following harvesting. Poor correlations were obtained between conventional soil testing and ion exchange resin bag determinations.

Comparisons between field and laboratory nutrient availability indices indicated that sites colonized by sprouting aspen exhibited the highest N cycling rates seen in this study. This observation makes aspen an interesting species to consider for mixed species management strategies.

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CHAPTER ONE

GENERAL INTRODUCTION

White spruce is currently the only tree species commercially exploited for timber in interior Alaska. As this resource is limited but also renewable, interior Alaska's forest industry will depend more and more on second growth forests.

White spruce forests are found in late successional stages of the floodplains and in late successional stages of south aspect upland sites. The present study is limited to the study of upland sites. In these ecosystems, secondary succession is usually initiated by fire (Van Cleve and Viereck 1981). Therefore, the harvest of the forest is likely to create, for the first stages of regeneration, an environment different from the one usually seen at the beginning of secondary succession in the natural life history of these ecosystems.

Little is known about the state of regenerating harvested white spruce sites in interior Alaska as their harvesting history is short. Serious problems between competing vegetation and regenerating white spruce are common (Zasada 1986). In similar forest types in Canada (Dobbs 1972) and northern Finland (Sundman et al. 1978), reforestation has frequently failed for unknown reasons.

The object of the present study was to develop a better understanding of nutrient dynamics in post-harvested white spruce sites. Forest managers often limit the evaluation of the effects of forest harvesting and site preparation on site productivity to the monitoring of the short term growth and survival of planted seedlings. As nutrient requirements, at this early stage, are low and increase exponentially thereafter (Miller 1984; Perry *et al.* 1982); the early performance of planted seedlings is a poor indicator of the productive capacity of the soil resource and of the long term effect of these silvicultural practices on site productivity.

In the present study, a variety of approaches are used to describe nutrient cycling on post harvested sites ranging from 0 to 14 years. They give a overall perspective of nutrient dynamics in these ecosystems and a better understanding of the factors controlling the storage and availability of nutrients. This information should be useful to the preservation and improvement of soil fertility in an intensive forest management regime.

Short term effects of forest harvesting on nutrient cycling

The short term pattern of nutrient dynamics after a clear-cut is generally believed to be the following: There is a pulse in the rate of soil organic matter decomposition and element mineralization due to improved soil temperature and moisture level and due to the presence of large quantities of fresh organic debris. In addition the uptake of nutrients by the vegetation is lower because of reduced vegetation cover, thus nutrient availability is higher as well as the potential for nutrient loss by leaching. In this context, a rapid establishment of secondary successional vegetation along with a rapid microbial population response can greatly reduce the rate of nutrient loss (Bormann *et al.*, 1974; Marks, 1974; Vitousek and Walker, 1987).

From the numerous nutrient cycling studies conducted after forest harvesting, it is known that this general pattern is not always observed. As stated by Vitousek and Walker (1987), there seems to be less solid mechanism-based theory concerning patterns of resource availability in secondary succession than in primary succession. Slower mineralization rates or no change in the mineralization rates have also been observed after the removal of the forest as well as a decrease in microbial and microarthropod biomass. Binkley (1984a) observed no change in the rate of N mineralization in the soil of a harvested forest on a high elevation site. Lower mineralization rates as well as a decrease in microarthropods density were observed on xeric sites after clear cutting (Abbot and Crossley 1982; Blair and Crossley 1988; Seastedt and Crossley 1981). Lower mineralization rates on whole tree harvested sites as well as a decrease in bacterial biomass were observed by Hendrickson *et al.* (1985). Finally, lower mineralization rates and lower microbial biomass were observed by Entry *et al.* (1986) on clear-cut sites where the slash had been removed.

In interior Alaska white spruce forests the low precipitation regime and the high C:N ratio of the soil organic matter (Van Cleve and Harrison 1985) could prevent or delay the nutrient mineralization pulse often seen after a clear-cut. Gordon and Van Cleve (1983) did not find any increase in the rate of N mineralization for a period of two years following a clear-cut.

According to Vitousek and Walker (1987), in ecosystems of low productivity (if we compare for instance tropical forests> temperate forests> boreal forests) the pulse of N supply after disturbance is of less magnitude, is delayed, and lasts for a longer period of time than in more productive ecosystems.

Long term effects: the recovery of nutrient cycles in a successional context

The pattern of plant succession after a fire on upland white spruce sites has been described by Van Cleve and Viereck (1981). The general pattern can be described as follows: There is a rapid colonization by herbaceous species followed by the rapid growth of shade intolerant deciduous tree species. Finally white spruce starts to colonize the deciduous stand and later dominates because of its tolerance to shade and its longer life.

However, if a seed source from species that usually come later during the succession were available and soil conditions suitable, this general pattern of plant succession may not be seen. Shade intolerant deciduous species or even white spruce can develop directly following fire (Van Cleve and Viereck 1981). The climax of this successional pattern is a white spruce stand. However, the path leading to the spruce stand can vary in length and species composition. This situation is similar to the ones described by Christensen and Peet (1984) and by Margalef (1968) where the community composition became increasingly predictable as succession proceeded.

The strict facilitation pathway described by Connell and Slatyer (1977) cannot explain community changes: The establishment and growth to maturity of a white spruce stand may not need the early influence on the site of other plant species. However, it is unknown whether or not, in the present context, successional species can have an influence on the productivity of a late successional community. This aspect is frequently neglected in successional models which are often limited to the explanation of species replacement and do not consider the productivity of successional stages.

It is a well known fact that the rapid colonization and growth of secondary successional species reduce the loss of nutrients following disturbances (Likens *et al.* 1978; Marks 1974; Vitousek and Walker 1987). Rapid seed dispersal, vegetative expansion, low nutrient use efficiency and high growth rate are some mechanisms contributing to the rapid colonization by secondary successional species as well as to the regulation of nutrient cycling (Boring *et al.* 1981; Gholz *et al.* 1984; Likens *et al.* 1978).

Another role of colonizer species is not as frequently mentioned; the litter quality (chemistry and structure) of early and mid-successional plant species often differs from late successional species and may promote a faster decomposition and cycling of nutrients (Covington 1981; Cromack and Monk 1975; Federer 1984; Vitousek and Walker 1987). Spruce litter depresses soil nitrogen availability because it decays and mineralizes nitrogen slowly and has a high immobilization potential as a result of its high lignin and phenolic and low nitrogen content (Carlyle and Malcolm 1986; Flanagan and Van Cleve 1983; Gholz and Fisher 1984; Mellilo et al. 1982; Piene and Van Cleve 1978; Van Cleve and Harrison 1985). It might therefore be desirable, for the productivity of a white spruce stand, to grow on a site where soil properties had been altered by early successional species even if their influence is not a si *ne qua non* condition for white spruce establishment.

Considering that the growth of white spruce stands and other boreal forests is often nitrogen limited (Krause 1982; Van Cleve and Oliver 1982; Van Cleve and Zasada 1976) and that the maximum nutrient requirement by white spruce stands is not achieved before canopy closure (Miller 1984), it is possible that successional species play a role in the maintenance and improvement of soil fertility for a considerable length of time.

Sound forest management decision must account for the overall influence of successional species on a site. Their dual role, as competitors with commercial species for limited resources and as soil fertility modifiers, should not be overlooked.

HYPOTHESES

Central Hypothesis

The harvest of a white spruce forest promotes changes in the patterns of nutrient dynamics. The duration and extent of these changes vary with soil conditions and the type of vegetation colonizing the site.

Working Hypotheses

1-The rates of soil organic matter decomposition and of N mineralization are greater following disturbance because of improved soil temperature and moisture regime. These rates are maintained during the first stages of revegetation.

2-Gross nutrient supply is greater after disturbance due to higher mineralization rates. However, secondary successional plants can effectively compete for this resource, reducing the potential for losses as well as the element supply to white spruce seedlings.

3-The distribution of nutrients in the ecosystem, their availability, as well as the gap between nutrient supply and demand, are affected by the type of vegetation colonizing the harvested area.

STUDY AREA

The study area is located in the Bonanza Creek Experimental Forest. Sites were chosen within an area of 10 km2 and presented homogeneous conditions of aspect, microclimate and pedology. Soils are classified as Typic Cryochrepts (Fairbanks silt loam). The parent material is windblown silt free of permafrost.

The local climate is continental, showing low annual precipitation, low humidity, low cloudiness and large diurnal and annual temperature ranges (Slaughter and Viereck 1986). The frost free summer averages 97 days.

All sites were selected on gentle south facing slopes. Aspect is considered to be the single most important determinant of vegetation productivity because of its critical importance on microclimatic conditions at this high latitude (64° 45') (Van Cleve and Yarie 1986).

The homogeneous nature of the parent material, in addition to the dry and cold climate, made soil conditions exceptionally constant between sites. These conditions greatly reduce the risk that differences between sites are caused by geological or pedological characteristics and enable a more accurate observation of the effect of disturbance and vegetation colonization on soil nutrient status.

Field sites were chosen from a chronological sequence. Three different stages in this sequence were studied: (1)- mature white spruce sites which represent the culminating point of plant succession (Van Cleve and Viereck 1981) (2)- less than one year old clear-cuts which are characteristic of the reorganization phase of ecosystem development after disturbance (Bormann and Likens (1979), and (3)- fourteen year old clear-cuts which are characteristic of the aggradation phase of ecosystem development (Bormann and Likens 1979). Two mature white spruce stands and three 14 year old clear-cut sites were selected. Only one recent clear-cut was available. The regenerating sites originated from mature white spruce forests. The clear-cut sites were not burned during or after the harvesting operations.

The vegetation composition of mature white spruce sites and of the recently harvested site was homogeneous. Therefore, there has not been any attempt to stratify these sites. On the contrary, 14-year-old sites showed a highly heterogeneous vegetation composition. To control this variability, these sites were divided into four ecological types which were typical of vegetation composition and surface soil conditions (table 1.1). Portions of these sites that were not sampled with this procedure are considered as being marginal (like roads, skid trails and landing areas) or intermediate between the 4 types (like open woody vegetation areas). The 4 ecological types under study on 14-year-old sites are:

(a)-**Undisturbed**: a sparse vegetation cover is developing on undisturbed forest floor originating from the harvested white spruce stand. The moss layer of the mature white spruce forest is still present. On these surfaces, invasion by seed germination is low (Zasada 1986) and the surface

Table 1.1
Sampling design and intensity of sampling

Ecological types	Area (m2)	Number of sampling units	Intensity of sampling (area(m2)/sampling unit)	Site number
Mature w.spruce				
(1)	10000	10	1000	0-1
(2)	5000	5	1000	0-2
Harvested sites (year 1)	5000	15	333	1-1
(year 14)				
Undisturbed				
(1)	1500	10	150	2-1
(2)	900	5	180	2-2
Grass				
(1)	750	10	75	2-1
(2)	300	5	60	2-3
Scraped				
(1)	330	5	66	2-2
(2)	1500	10	150	2-3
Aspen				
(1)	266	5	53	2-1
(2)	300	5	60	2-2
(3)	4000	10	400	2-3

soil is not densely rooted. Few herbaceous species are colonizing the area. The most frequently encountered species are fireweed (*Epilobium angustifolium*) and horsetail (*Equisetum* spp.).

(b)-Grass: This type is heavily colonized by bluestem (*Calamagrostis candensis*). It is found on partially disturbed organic surfaces (Zasada; 1986). The organic layer is thick and so heavily rooted that it is very difficult to tear apart. Fireweed (*Epilobium angustifolium*) is also present on these sites.

(c)-Scraped: On these sites, the forest floor was scraped off following the harvesting operation. A sparse vegetation cover is developing. White spruce (*Picea glauca*) seedlings are abundant. Few balsam poplar (*Populus balsamea*) as well as some herbaceous species (mostly bluestem) are developing.

(d)-Aspen (*Populus tremuloides*) regeneration: This is the only woody vegetation type that was studied on stage 3 sites. Although paper (*Betula paperyfera*) and alder (*Alnus tenuifolia*) can regenerate on these sites (Zasada 1986), they were not present in significant amounts to be included in this study. The aspen clumps that were selected were dense enough to prevent the growth of a thick herbaceous layer. The sparse understory was composed of *Equisetum* spp., *Calamagrostis canadensis, Rosa acicularis* and *Viburnum edule.* A few observations indicated that these clumps did not develop from an aspen forest but have evolved as root sprouts from sparsely distributed aspen in the harvested white spruce stands. Records of the State of Alaska Forest Service show that the volume of aspen wood harvested on these sites was low. Aspen stumps were rare and did not form dense clumps. In the surrounding unharvested forest aspen were also sparsely distributed. Furthermore, typical aspen forest floor, where the growth of the moss layer is inhibited by the shade created by deciduous leaf litter (Van Cleve and Viereck 1981), was not found even on small areas.

The distribution of these ecological types on 14-year-old clear-cut sites showed a mosaic pattern. This distribution largely reflected the intensity and distribution of disturbance that occurred during the harvesting operation.

On these sites aspen clumps, as well as areas where the forest floor had been scraped, could easily be identified and were selected in at least two different clear-cut area.

On the contrary, dense grassy vegetation and vegetation growing on undisturbed organic surfaces were found only on small areas widely scattered among the clear-cut areas. To locate these types, a survey was conducted on areas of the 3 sites that had not been selected or discarded yet. Both types (undisturbed surface and grass) were found extensively on two of the three sites.

Sampling units from the aspen and scraped types were randomly selected from the identified clumps with a number of replicates per site, related to the size of the clump. Sampling units of grass and undisturbed types were randomly selected from the transect lines with a number of replicates per site, related to the area cover by a given type. The total number of sampling units per type, including stage 1 and stage 2 and stage 3 a, b, c, and d types ranged from 15 to 20. Each ecological type was studied on at least two different sites. In the following chapters, unless specified, the total number of sampling units will be considered. A summary of the information on the sampling design is presented in table 1.1.

CHAPTER 2

EVOLUTION OF SOIL FERTILITY ON HARVESTED WHITE SPRUCE SITES

ABSTRACT

Nutrient availability was assessed on unharvested white spruce sites, on a recently harvested site and on 14-year-old post-harvested sites colonized by different plant communities. These sites were all found on gentle south aspect slopes covered with a loess deposit. Conventional soil chemical analysis, laboratory and field net nitrogen (N) mineralization incubations, a greenhouse bioassay as well as the measurement of field soil temperature, moisture content and tongue depressor decomposition rates were performed in order to describe soil fertility. Field and laboratory net N mineralization rate determinations, as well as the greenhouse bioassay indicated a great decline of soil fertility on 14-year-old sites where the forest floor had been scraped despite the fact that the treatment produced warmer soil temperatures. The recently harvested site showed, compared to the mature white spruce sites, increased N mineralization rates both in the field and under controlled conditions. However, the greenhouse bioassay showed poor growth of seedlings growing on soil from the recently harvested site. This phenomenon could be caused by biological factors not controlled in this experiment. Field and laboratory N mineralization estimates, as well as the greenhouse bioassay, indicated that aspen regeneration had the highest N mineralization rates of all 14-year-old types considered in this study. Surface soil chemical characteristics, as well as soil temperature and water content, only poorly explained differences in N mineralization rates across types. This suggests that on regenerating sites sharing similar physiographic conditions, species colonization may influence N dynamics by litter effects, and that N cycling rates are perhaps controlled by a small pool of rapidly cycling N.

INTRODUCTION

It is generally believed that, apart from the tropical rain forest (Allen 1985), the nutrient capital of a forest ecosystem is little affected by harvesting (Ballard 1978;

Hornbeck and Kropelin 1982; Waring and Schlesinger 1985). Nutrient losses by exportation of biomass (Hornbeck and Kropelin 1982; Weetman and Weber 1972) added to the losses by leaching following disturbance (Hornbeck and Kropelin 1982; Mann *et al.* 1988, Martin and Harr 1989) are generally low enough that the number of years needed to replace them by inputs is less than the forest harvesting cycle (Waring and Schlesinger 1985). However, little is known about the processes, mechanisms, and rates by which nutrients are made available for future stands following disturbance (Hornbeck and Kropelin 1982).

There is a short and a long term response of soil fertility to forest harvesting. The short term effect is related to the large input of nutrients and fresh organic matter added to the soil during the harvesting operations, to the reduction of plant uptake of water and nutrients, and to the modification of soil temperature and soil moisture regime created by the absence of a plant cover (Bormann *et al.* 1974; Stone 1973). These conditions can either increase (Entry *et al.* 1987a and b; Johnson *et al.* 1985, Likens *et al.* 1978), not change (Burger and Pritchett 1984, Wallace and Freedman 1986), or decrease (Abbot and Crossley 1982; Bird and Chatarpaul 1988; Hendrickson *et al.* 1985; Whiteford *et al.* 1981) soil organic matter decomposition and nutrient mineralization. They generally favour nitrification (Likens *et al.* 1969; Vitousek *et al.* 1982; Vitousek *et al.* 1979).

The long term response is mostly related to the modification of the soil environment by plant communities. Plants can modify nutrient availability to future stands by their influence on soil microclimate (Gokceoglu 1988; Harcombe 1975; Van Cleve *et al.* 1983; Viereck *et al.* 1983), by differential nutrient uptake rates, amounts of nutrient returned in litterfall and nutrient storage in perennial tissues (Alban 1982; Alban *et al.* 1978; Ruark and Bockheim 1987; Yount 1975), by the palatability of their litter to microorganisms (Covington 1981; Damman 1971; Federer 1984; Flanagan and Van Cleve 1983; Hix and Barnes 1984; Howard and Howard 1980), and by the production of allelochemicals (Rice 1984).

The objective of the present study was to evaluate the very short term (first year) and longer term (14th year) changes in soil nutrient reserves and availability on post-harvested white spruce sites subjected to different site preparation treatments and colonized by different plant communities.

Materials and Methods

A variety of methods were used to assess soil nutrient availability: (1)-Soil was analyzed using standard laboratory procedures, (2)- N mineralization was measured in the field using the buried bag technique (Eno 1960) together with the characterization of soil temperature, soil water content, and decomposition rates of tongue depressors; N mineralization was also assessed under controlled conditions in the laboratory, (3)- an independent measurement of the potential soil element supply to plants was conducted using a greenhouse bioassay.

1-Site description

Six sites were selected in the Bonanza Creek Experimental Forest. The forest is located 25 km west of Fairbanks, Alaska in the Yukon-Tanana uplands. All sites originated from closed mature white spruce stands (Viereck *et al.* 1990) growing on well drained south facing slopes. Soils are classified as Alfic Cryochrepts. Two mature white spruce sites, one recently (less than a year old) harvested white spruce site and three 14-year-old clear-cut strips were selected. Fourteen-year-old sites were later stratified floor (undisturbed), (2)-grass, (3)-scraped forest floor (scraped) and, (4)-aspen clumps (aspen). Undisturbed, grass and scraped types were found on two of the three sites while the aspen type was found on all three sites. Each ecological type except the recently harvested site were studied on at least two different sites. The number of sampling units per ecological type and site was proportional to the area of the type and varied between 5 and 10. For a more complete description of the sampling design and of the ecological types under study, the reader is referred to the general introduction.

2-Sample harvesting, preparation and standard soil analysis

In mid-August, one volumetric sample of the surface soil horizon was collected. In most cases this sample was representative of the total forest floor, however on scraped sites, this horizon had a low organic matter content. The top 5 cm of the soil of scraped sites were collected and considered as the surface soil horizon. In addition the 10 first cm of the underlying mineral soil were collected from each replicate sampling unit. These samples were air dried and sieved at 2 mm. Total N, P, K, Ca and Mg content of the surface soil was determined as described by Van Cleve and Viereck (1972). Extractable P as an index of plant available P was determined on a dilute acid flouride extraction (Jackson 1958). Exchangeable cations were extracted with neutral, 1 M ammonium acetate and measured by direct current plasma emission and by atomic absorption.

Carbon content was estimated using a Leco induction spectophotometer-furnace (Tabatabai and Bremner 1970). Lignin was determined using methods described by Allen (1974). This parameter was not measured on the surface soil of the S sites because of their small organic matter content. Organic matter was determined by ashing subsamples at 400°C for 7 hours. Soil pH was determined on a saturation paste in deionized water.

3-*In situ* net N mineralization, net N mineralization potential, soil temperature, soil moisture content, and tongue depressor decomposition rate

Field net N mineralization was measured using undisturbed soil core sections incubated in polyethylene bags (Eno 1960). Five sampling units per site and ecological types were randomly selected. In each one, and at every sampling date, a core was extracted with a 15 cm diameter corer. Each core was vertically sliced into two sections. One section was brought to the laboratory for immediate extraction and was brought to the laboratory for immediate extraction and analysis of time 0 mineral N content. The other section was placed in a 0.4 mil polyethylene bag with as little disturbance as possible and left in the field until the end of the incubation period when time 1 mineral N content was determined. Each core was divided into two horizontal sections: (1)-the surface soil (this layer was, in most cases, the total forest floor except on scraped sites were it constitued the 5 cm of the surface mineral soil) and 2- the layer of mineral soil from a depth of 5 to 10 cm. This depth was chosen to avoid boundary effects or contamination with forest floor material.

One set of samples was installed in mid-September and left overwinter. The other sets were left in the field for sequential periods of 6 weeks during the frost free period. When brought to the laboratory, samples were sieved at 4 mm to remove large roots, cones and pieces of wood. Five grams of fresh forest floor material and 10 grams of fresh mineral soil were extracted with 50 ml of 2 N KCl. Samples were shaken for an hour, filtered and then analyzed for NH4+ and NO3- on an autoanalyser using methods outlined by Technicon (1976).

Net N mineralization potentials were determined in the laboratory by incubating surface soil samples during 50 days at a constant temperature of 20°C and at a water content corresponding to half of the water holding capacity. These values ranged from 260% to 290% dry weight for forest floor materials and approximated 50% dry weight for surface mineral soil. The sampling design was the same as in the buried bag field incubation except that no non-surface mineral soil sample was included. Samples were collected in mid-September. A 5 gram (dry weight) subsample was immediately extracted and analyzed for the determination of Time-0 NO3- and NH4+ content. Thereafter, 5 gram (dry weight) of surface soil material were placed in 125 ml plastic bottles sealed with 0.4 mil polyethylene and then placed in an incubator. At the end of the incubation period, NH4+ and NO3- were extracted and analyzed as described previously to determine Time-1 mineral N. Net nitrogen mineralization, both in the field and in the laboratory experiment, was estimated as being : (T1 NO3+NH4)-(T0 NO3+NH4). Net nitrification was estimated as being (T1 NO3)-(T0 NO3).

At every field sampling date, the water content of a fresh subsample was determined gravimetrically by oven drying forest floor samples at 60oC and mineral soil samples at 105oC. These results were used as an estimation of soil *in situ* water content as well as a correction factor for the determination of N mineralization on a soil dry weight basis.

Field soil temperature was measured biweekly during the growing season at a depth of 10 cm with dial thermometers. Five temperature readings were taken per date, ecological type and site.

Birch wood tongue depressors were individually weighed and one was installed at mid-depth in the forest floor at each sampling unit in mid-September. They were retrieved from the field exactly one year later. They were then oven dried to a constant weight, gently cleaned, and weighed.

4-Greenhouse bioassay

The greenhouse bioassay technique is considered to be an integrative approach to the measurement of soil fertility. It allows the separation of the nutrient supplying potential of the soil from the effect of *in situ* soil temperature and humidity and from the effect of plant competition. However, some biological effects such as pathogenic interference, mycorrhizal infection, and microbial competition may be confounded with the effect of soil chemical quality (Perry *et al.* 1982). Greenhouse bioassays may be more sensitive than field bioassays, revealing nutrient deficiencies that would not be detectable in the field until regeneration reaches an advanced age (Perry and Rose 1980) and nutrient requirement becomes high (Miller 1984).

The methodology used is that of Van Cleve and Harrison (1985) and Van Cleve *et al.* (1986). At every sampling unit, the surface soil (as defined previously) was collected with a 15 cm diameter corer. Cores from a respective type were separately pooled per site to obtain enough material for the bioassay. The green moss layer of the white spruce site was discarded. All samples were air dried and sieved at 4 mm but not ground. One thousand two hundred grams of quartz sand were mixed with 100 g of forest floor material and placed in a 15 cm diameter plastic pot underlain by a saucer. To account for the large difference in density between forest floor materials and the surface mineral soil of scraped sites, a sample of 500 g of this latter was mixed with 1200 g of quartz sand. The other materials were not significantly different in density from each other. Paper birch (*Betula papyrifera*) was seeded in this mixture. Paper birch was chosen because of its association with all forest types and because of its rapid growth (Van Cleve and Harrison 1985). Three seedlings were allowed to grow in each pot for a period of 3 months. Pots were watered biweekly with distilled water. A constant photoperiod of 21 hr, typical of interior Alaska mid-summer conditions was applied. Light intensity was approximately 200 uE m-2 s-1. Air temperature was maintained between 20 and 25°C.

At the end of the growing period the seedlings were gently removed from the mixture and the root systems washed with distilled water. Seedlings from each pot, within a treatment, were pooled to provide sufficient tissue for the analysis. The biomass was separated into 3 components: leaves, stems and roots. Plant material was dried at constant weight at a temperature of 65°C and then digested and analyzed for N, P, K, Ca, and Mg content as described in Van Cleve and Viereck (1972).

5-Statistical analysis

Soil temperature measurements, soil moisture content, laboratory and field net N mineralization determinations as well as results from the greenhouse bioassay were subjected to a nonparametric statistical test because of the small sample size (n=4 or 5), and thus the inability to test reliably for normality. The Kruskal-Wallis test (Kruskal and Wallis 1952) was used to test differences among site-type. The multiple comparisons test described by Zar (1984) was used when the Kruskal-Wallis test indicated significant differences. Results from other analysis were subjected to one way analysis of variance (ANOVA) to test differences among type-site. When necessary, data was subjected to a logarithmic transformation which succeeded in the homogenization of variance. The Waller Duncan multiple range test was used to indicate significant differences between means (Waller and Duncan 1969). Stepwise forward regressions, as all other statistical analysis were performed on SAS (1985).

RESULTS

1-Surface soil characterization

1-1 Element content, lignin content, pH and total mass

The carbon concentrations and percent organic matter of the surface soil were relatively uniform between ecological types except in the scraped type where they were much lower (table 2.1). Lignin concentrations and pH did not show any difference between ecological types (table 2.1). Total weight of the surface soil layer presented high variability and little significant difference between types. Values for both grass sites were high (table 2.1). Scraped sites were not included in this last comparison because on these sites, the depth of this horizon was subjectively determined at a fixed value of 5 cm.

Table 2.1
Characteristics of the surface soil in the six ecological types under study.

Ecological types	% organic matter	pH	C (%)	lignin (%)	total weight (g.m-2)
Pr>f	0.0001	0.61	0.0001	0.16	0.0271
Mature					
w.spruce	a	a	a	a	b
(1)	75.2±8.6	5.7±0.27	33.5±5.3	29.2±3.9	6773±170
	ab	a	a	a	b
(2)	65.6±16.6	5.53±0.41	33.1±4.8	29.0±3.1	8493±326
Harvested	b	a	a	a	b
sites	57.7±12.4	5.74±0.45	29.5±6.6	25.7±3.9	11049±530
(year 1)					
(year 14)					
Undisturbed	a	a	a	a	b
(1)	63.6±15.2	5.50±0.17	31.8±8.2	29.5±5.7	11613±629
	a	a	a	a	ab
(2)	69.5±16.1	5.73±0.16	34.5±4.9	27.5±3.7	14080±545
Grass	b	a	a	a	ab
(1)	54.7±12.6	5.83±0.52	29.5±6.0	25.5±4.9	12540±1422
	ab	a	a	a	a
(2)	65.8±22.5	5.61±0.32	27.8±9.5	24.3±4.4	18987±1071
Scraped	c	a	b		*
(1)	6.8±1.3	5.49±0.16	3.6±0.9	N.D	25222±1012
	c	a	b		*
(2)	8.28±3.4	5.57±0.28	5.4±3.27	N.D.	24503±572
Aspen	b	a	a	a	b
(1)	55.9±14.4	5.76±0.36	28.9±7.5	25.7±4.7	10613±335
	a	a	a	a	b
(2)	60.2±13.8	5.59±0.29	31.1±7.1	26.3±4.5	10800±308
	b	a	a	a	b
(3)	58.7±7.6	5.70±0.35	30.2±4.2	28.2±2.1	7253±532

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

* treatments not included in the analysis of variance.

Surface soil N concentrations were relatively uniform among ecological types except on one mature white spruce site and on both scraped sites where they were low (table 2.2). Undisturbed and scraped sites showed the lowest P concentrations (table 2.2). Scraped sites had the lowest C:N and C:P ratios. No difference was seen in the C:N ratios between other sites. Undisturbed sites had high C:P and lignin:P ratios. Lignin:N ratios were high on one mature white spruce site but did not differ significantly among other types. Concentrations of total K, Ca and Mg did not differ among types (table 2.3). These analysis were not performed on scraped sites because their low organic content would have required a different digestion procedure.

On a pool size basis, no clear difference in nutrient storage in the surface soil could be seen between ecological types (table 2.4). Again, scraped sites were not included in these comparisons because on these sites, the depth of the surface soil layer was subjectively determined.

Table 2.2
Concentrations of N and P and ratios to carbon and lignin in the surface soil of the six ecological types under study.

Ecological types	N (%)	P (%)	C:N	C:P	lignin:N	lignin:P
Pr>f	0.0001	0.0001	0.0003	0.0001	0.0011	0.0008
Mature w.spruce (1)	c 0.79±0.37	bc 0.084±0.010	a 54±35	ab 401±71	a 49±30	bc 349±53
(2)	abc 1.04±0.38	bcd 0.084±0.012	a 35±14	ab 408±119	b 31±12	bc 357±93
Harvested sites (year 1)	ab 1.10±0.19	bcd 0.082±0.010	a 28±9	b 360±69	b 24±7	bc 317±45
(year 14)						
Undisturbed (1)	bc 0.91±0.10	edf 0.069±0.020	a 36±10	a 499±192	b 33±1	a 473±198
(2)	ab 1.11±0.10	edf 0.070±0.001	a 31±2	a 493±76	b 25±1	ab 391±54
Grass (1)	ab 1.17±0.19	abc 0.086±0.017	a 25±6	b 355±102	b 22±5	bc 308±85
(2)	abc 1.00±0.29	bcd 0.079±0.008	a 32±23	b 357±141	b 26±17	bc 309±63
Scraped (1)	d 0.19±0.04	ef 0.056±0.008	b 22±5	c 63±12	N.D	N.D.
(2)	d 0.23±0.09	f 0.055±0.006	b 22±7	c 96±54	N.D.	N.D.
Aspen (1)	bc 0.90±0.14	ab 0.095±0.016	a 33±11	b 303±50	b 29±8	c 272±29
(2)	a 1.27±0.14	abc 0.085±0.007	a 24±1	b 365±83	b 21±2	bc 308±51
(3)	ab 1.13±0.23	a 0.100±0.016	a 28±7	b 308±71	b 26±5	bc 288±58

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

N.D.: Not determined

Table 2.3
Concentrations of total K, Ca, and Mg in the surface soil of the 6 ecological types under study (%).

Ecological types	K	Ca	Mg
Pr>f	0.0713	0.2290	0.0758
Mature w.spruce (1)	a 0.32±0.05	a 1.67±0.33	a 0.31±0.06
(2)	a 0.34±0.07	a 1.61±0.31	a 0.29±0.08
Harvested sites (year 1)	a 0.40±0.09	a 1.53±0.34	a 0.38±0.07
(year 14)			
Undisturbed (1)	a 0.33±0.10	a 1.71±0.34	a 0.34±0.12
(2)	a 0.27±0.06	a 1.67±0.31	a 0.30±0.08
Grass (1)	a 0.37±0.08	a 1.55±0.32	a 0.30±0.07
(2)	a 0.38±0.09	a 1.42±0.25	a 0.32±0.09
Scraped (1)	N.D.	N.D.	N.D.
(2)	N.D.	N.D.	N.D.
Aspen (1)	a 0.39±0.07	a 1.68±0.32	a 0.39±0.08
(2)	ab 0.38±0.12	ab 1.89±0.18	ab 0.36±0.09
(3)	a 0.39±0.06	a 1.78±0.13	a 0.37±0.06

Note: Estimates are means ± SE. In each column, values followed by the same letter are not significantly different ($p<0.05$).

N.D.: not determined.

Table 2.4
Total pool sizes for selected elements in the surface soil of the six ecological types under study (g.m-2).

Ecological types	N	P	K	Ca	Mg
Pr>f	0.0467	0.1022	0.0761	0.1726	0.1762
Mature w.spruce					
(1)	b 54.5±32.1	a 5.7±1.5	a 21.5±7.4	a 111.7±29.9	a 21.1±7.9
(2)	ab 91.9±55.9	a 6.9±2.3	a 28.7±13.8	a 136.5±60.0	a 24.7±12.9
Harvested sites (year 1)	ab 117.6±48.9	a 8.9±3.9	a 46.9±32.1	a 169.3±80.8	a 44.1±31.7
(year 14)					
Undisturbed					
(1)	ab 111.2±77.8	a 8.1±4.8	a 36±16.0	a 200.6±117.7	a 36.5±15.4
(2)	ab 154.1±53.4	a 9.9±3.9	a 39.4±20.7	a 245.4±135.5	a 43.5±24.4
Grass					
(1)	ab 151.6±137.8	a 10.6±8.5	a 48.0±37.3	a 195.0±187.9	a 37.2±25.8
(2)	a 187.5±113.8	a 14.5±7.3	a 72.3±51.8	a 269.2±145.9	a 61.7±47.2
Scraped *					
(1)	* 42.5±10.3	* 14.0±3.2	N.D.	N.D.	N.D.
(2)	* 57.50±12.4	* 13.5±2.7	N.D.	N.D.	N.D.
Aspen					
(1)	ab 98.55±46.5	a 9.8±2.8	a 43.2±20.8	a 171.5±30.9	a 42.5±18.3
(2)	ab 139.7±48.9	a 9.3±2.9	a 38.8±8.6	a 207.1±70.2	a 38.9±14.3
(3)	b 79.0±62.1	a 6.9±4.6	a 29.2±24.8	a 128.6±91.3	a 28.9±26.3

Note: Estimates are means ± SE. In each Column, values followed by the same letter are not significantly different ($p<0.05$).

* treatment not included in analysis of variance

N.D.: not determined.

1-2 Available nutrient

a) Extractable P and exchangeable bases

Concentrations of extractable P showed the same trend as the total P content. The surface soil of undisturbed and scraped types consistently showed the lowest concentrations (table 2.5a).

Exchangeable K and Mg concentrations were relatively constant between types except on scraped sites where they were low (table 2.5a).

Exchangeable Ca was lowest on scraped sites, followed by aspen forest floor, and then by the other forest floor types which showed more or less uniform concentrations (table 2.5a). On a weight per volume basis concentrations of extractable P, exchangeable K, and exchangeable Mg were no longer lower on scraped sites than on other types (table 2.5b). However, concentrations of exchangeable Ca on scraped sites were still lower on a weight per volume basis.

On a pool size basis (table 2.6) the total amount of exchangeable Ca of the mature white spruce sites was roughly

Table 2.5a
Extractable P and exchangeable bases in the surface soil of the 6 ecological types under study (weight per weight basis)

Ecological types	Extractable P ug.g-1	K meq.100g-1	Ca meq.100g-1	Mg meq.100g-1
Pr>f	0.0001	0.0001	0.0001	0.0001
Mature w.spruce				
(1)	60.24±13.44a	2.14±0.44a	47.44±6.65a	8.99±1.48a
(2)	61.77±12.79a	1.35±0.69a	44.84±6.69ab	6.63±1.09b
Harvested sites (year 1)	58.93±20.16a	2.21±1.24a	44.51±8.11ab	7.25±1.31b
(year 14)				
Undisturbed				
(1)	33.53±7.55c	1.32±0.58a	41.35±9.57abc	6.36±1.01b
(2)	40.55±7.09bc	1.46±0.39a	50.02±7.11a	6.99±0.79b
Grass				
(1)	51.86±12.74ab	1.44±0.61a	45.76±14.82a	6.63±1.77b
(2)	62.09±11.12a	1.75±0.67a	42.48±11.61abc	7.49±1.75ab
Scraped				
(1)	10.89±7.03d	0.38±0.06b	1.78±0.32e	2.09±0.31c
(2)	10.46±6.25d	0.47±0.17b	1.92±0.53e	2.72±0.42c
Aspen				
(1)	48.64±9.19ab	1.72±0.15a	34.19±4.79cd	7.53±1.92ab
(2)	55.84±20.86ab	1.65±0.35a	29.77±3.00d	6.16±1.35b
(3)	64.31±9.88a	1.92±0.67a	35.30±8.58bcd	7.60±2.59ab

Note: Estimates are means ± SE. In each column, values followed by the same letter, are not significantly different (p<0.05).

Table 2.5b
Extractable P and exchangeable bases in the surface soil of the 6 ecological types under study
(weight per volume basis)

Ecological types	Extractable P ug.cm-3	K ug.cm-3	Ca ug.cm-3	Mg ug.cm-3
Pr>f	0.0083	0.0893	0.0001	0.0001
Mature				
w.spruce	abc	a	bc	bc
(1)	4.57±1.23	62.6±19.5	712±79	83.0±18.73
	abc	a	bc	d
(2)	4.64±0.92	42.2±26.2	698±206	61.53±16.2
Harvested	ab	a	b	bcd
sites	5.22±1.71	76.6±37.9	804±194	79.0±17.4
(year 1)				
(year 14)				
Undisturbed	c	a	bc	bcd
(1)	3.04±0.63	45.7±16.8	754±189	70.8±14.5
	abc	a	a	b
(2)	4.41±0.88	62.2±19.2	1092±207	92.0±10.7
Grass	abc	a	b	bcd
(1)	4.46±0.93	49.3±21.1	798±259	71.7±25.29
	ab	a	bc	bcd
(2)	5.28±1.42	57.5±19.9	743±314	77.8±28.7
Scraped	ab	a	e	b
(1)	4.02±2.65	54.7±7.04	130±20	92.2±9.4
	bc	a	e	a
(2)	3.61±1.27	63.7±21.5	136±42	116.2±23.5
Aspen	abc	a	cd	bcd
(1)	4.29±1.02	58.3±13.3	602±110	79.6±17.3
	ab	a	d	cd
(2)	4.97±2.11	55.5±8.21	519±66	65.8±18.1
	a	a	bcd	bc
(3)	5.81±1.19	66.9±18.4	637±169	83.42±21.9

Note: Estimates are means ±SE. In each column, values assigned to a same letter, are not significantly different (p<0.05),

Table 2.6
Pool sizes of extractable P and exchangeable bases in the surface soil of the 6 ecological types under study (g.m-2).

Ecological types	Extractable P	K	Ca	Mg
Pr>f	0.0257	0.4132	0.1991	0.2501
Mature w.spruce				
(1)	b 0.41±0.15	a 5.71±2.83	a 63.8±16.0	a 7.51±2.66
(2)	b 0.51±0.17	a 4.69±2.74	a 76.0±27.7	a 6.71±2.56
Harvested sites (year 1)	b 0.63±0.36	a 9.38±5.47	a 102.5±64.3	a 10.00±6.10
(year 14)				
Undisturbed				
(1)	b 0.40±0.27	a 6.26±5.08	a 100.8±74.6	a 9.15±5.73
(2)	b 0.56±0.22	a 8.21±5.08	a 142.7±70.0	a 11.83±4.39
Grass				
(1)	b 0.65±0.59	a 7.43±7.04	a 132.2±88.6	a 9.64+6.83
(2)	a 1.12±0.51	a 11.34±4.30	a 156.6±88.6	a 16.96±9.39
Scraped *				
(1)	* 0.27+0.18	* 3.71±1.17	* 8.8±1.6	* 6.34±1.34
(2)	* 0.22+0.15	* 3.09±0.98	* 9.4±1.4	* 8.42±1.22
Aspen				
(1)	b 0.52±0.20	a 7.04±1.95	a 72.7±22.6	a 9.52±3.42
(2)	b 0.61±0.31	a 6.65±1.56	a 64.5±18.2	a 8.05±3.05
(3)	b 0.43±0.24	a 5.86±2.32	a 58.4±54.2	a 7.69±7.56

* treatments not included in comparaison of variances.

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

equivalent to the amount found in the 14-year-old aspen sites. These amounts were lower than the ones found on both grass and both undisturbed 14-year-old types, but these differences were not significant.

b) Net N mineralization

- *In situ* net nitrogen mineralization

Net N mineralization showed a very high variability on all sites (table 2.7). The recently harvested site showed the greatest cumulative net N mineralization per soil dry weight or per soil volume (table 2.8). Net N mineralization per soil dry weight or soil volume was significantly lower in both scraped sites than in all other surface soil materials. The other 14-year-old regenerating types showed, on the average, a higher net N mineralization rate than mature white spruce sites. However, these differences were not significant. Aspen showed the greatest net N mineralization rate of the 14-year-old regenerating systems. It was followed by grass and then by the undisturbed type. Again, these differences were not significant.

On a pool size basis, no significant difference between types could be seen (table 2.8). Again scraped sites were

Table 2.7
In situ net N mineralization in the surface soil horizon of the 6 ecological types under study (ug.g-1)

	Sampling periods *			
Ecological types	1	2	3	4
pr>f	0.0023	0.0120	0.0059	0.0243
Mature				
w.spruce	b	b	ab	a
(1)	0.91±2.03	5.78±11.4	27.33±15.40	84.54±42.61
	a	ab	ab	ab
(2)	8.86±14.78	19.74±18.16	48.52±38.68	31.70±13.87
Harvested	a	ab	a	ab
sites	158.90±86.08	69.56±42.99	106.42±91.45	60.20±57.24
(year 1)				
(year 14)				
Undisturbed	ab	ab	ab	ab
(1)	19.37±22.65	38.94±36.54	51.66±52.13	36.09±24.63
	ab	ab	ab	ab
(2)	53.88±57.40	39.52±27.95	58.46±79.89	27.81±25.47
Grass	ab	ab	ab	ab
(1)	42.64±68.41	33.83±36.33	70.28±76.98	58.96±74.20
	ab	a	ab	ab
(2)	106±125.07	83.47±57.40	50.69±41.04	29.58±13.84
Scraped	ab	b	b	b
(1)	2.92±3.21	1.99±1.98	5.35±8.65	1.15±0.24
	ab	b	b	b
(2)	2.57±1.92	3.42±2.49	4.01±3.49	1.16±0.53
Aspen	a	ab	a	ab
(1)	118.48±75.13	31.39±42.50	113.36±116.43	24.61±14.12
	ab	ab	a	a
(2)	17.33±15.97	35.97±37.03	115.72±89.96	79.03±73.55

* period 1: September 15, 1988 - May 27, 1989
period 2: May 27, 1989 - July 1, 1989
period 3: July 1, 1989 - August 12, 1989
period 4: August 12, 1989 - September 15, 1989

Note: Estimate are means ± SE. Values assigned to a same letter are not significantly different ($p<0.05$).

Table 2.8
Cumulative net N mineralization in the surface soil of the 6 ecological types under study from one year of field incubation and a 50 day laboratory incubation.

Ecological types	in situ incubation			laboratory incubation	
	ug.g-1.yr-1	ug.cm-3	g.m-2.yr-1	ug.g-1	ug.cm-3
p>f	0.0001	0.0005	0.0698	0.0001	0.0002
Mature					
w.spruce	a	a	a	b	b
(1)	118.6±39.6	8.87±4.65	0.81±0.44	35.4±42.5	2.27±3.01
	a	a	a	ab	ab
(2)	108.8±50.1	8.42±3.79	0.90±0.42	79.0±76.7	6.55±7.72
Harvested	a	a	a	ab	ab
sites	395.0±201.5	36.0±23.9	4.42±3.61	213.6±124.4	18.59±10.83
(year 1)					
(year 14)					
Undisturbed	a	a	a	ab	ab
(1)	146.1±105.3	13.0±9.1	1.51±1.37	131.0±87.2	11.86±7.28
	a	a	a	ab	ab
(2)	179.7±70.8	20.1±7.5	2.49±1.14	71.4±65.9	7.62±7.13
Grass	a	a	a	b	b
(1)	205.7±92.8	19.0±11.1	2.26±1.55	15.0±27.3	1.31±2.35
	a	a	a	b	b
(2)	207.1±139.0	23.5±14.4	5.62±5.52	22.2±38.5	2.18±4.06
Scraped	b	b	a	b	b
(1)	11.4±9.2	3.80±3.1	0.26±0.18	11.4±18.5	3.83±6.17
	b	b	a	b	b
(2)	11.2±4.8	3.76±1.7	0.26±0.11	2.4±1.67	0.80±0.56
Aspen	a	a	a	a	a
(1)	287.8±136.7	25.8±14.0	3.29±2.07	257.8±104.9	23.52±9.74
	a	a	a	a	a
(2)	248.1±176.7	22.4±16.7	2.11±2.04	377.8±38.3	33.54±2.35

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

not included in this comparison for the reason previously explained.

No net NO3- production occurred in the surface soil of control and scraped sites at any of the sampling dates (table 2.9).

Certain chemical characteristics of the forest floor could explain portions of the variance in N mineralization rates (table 2.10). However, these relationships were largely due to the contrasting properties of the surface soil of scraped sites with other surface soil materials. When scraped sites were removed from the calculations, only laboratory N mineralization, extractable P, and exchangeable Ca (negatively) remained significantly related to estimated field available N. In a forward stepwise regression analysis (without scraped sites), only laboratory N mineralization and total Ca concentration (negatively) were selected from soil chemical and microclimatic variables to explain cumulative N mineralization *in situ* (table 2.11). Soil temperature, as well as N and lignin concentrations, were not selected. The R2 of this regression was low (R2=0.21).

Table 2.9
Net NO3- production in the surface soil of the 6 ecological types under study from field and laboratory incubations (ug.g-1)

Ecological types	* In situ incubation					laboratory incubation
	period 1	period 2	period 3	period 4	Cumulative	
p>f						0.0001
Mature w.spruce (1)	0	0	0	0	0	ab 109±102
(2)	0	0	0	0	0	ab 150±136
Harvested sites (year 1)	46±58	33±52	50±57	49±55	178±155	a 413±169
(year 14)						
Undisturbed (1)	26±22	21±30	62±54	20±20	129±82	ab 172±122
(2)	58±71	12±22	33±67	12±19	115±69	ab 112±95
Grass (1)	34±53	13±12	24±33	10±23	80±46	ab 41±45
(2)	56±117	27±60	15±11	0	97±122	ab 53±68
Scraped (1)	0	0	0	0	0	b 15±20
(2)	0	0	0	0	0	b 4±1
Aspen (1)	1±2	3±6	69±87	0	72±87	ab 206±149
(2)	1±3	14±22	63±91	39±67	117±100	a 453±92

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

* period 1: September 15, 1988 - May 27, 1989
period 2: May 27, 1989 - July 1, 1989
period 3: July 1, 1989 - August 12, 1989
period 4: August 12, 1989 - September 15, 1989

Table 2.10
Linear regressions between cumulative field N mineralization estimates and certain surface soil characteristics

Soil Characteristics	Cumulative field N mineralization all treatments (n=55) R2	 P	 Without S sites (n=45) R2	 P
laboratory N mineralization	0.176	0.0001***	0.143	0.0079**
extractable P	0.312	0.0001***	0.103	0.0260*
exchangeable K	0.128	0.0057**	(-) 0.0001	0.9291
exchangeable Ca	0.090	0.0222*	(-) 0.139	0.0090**
exchangeable Mg	0.119	0.0079**	(-) 0.026	0.2730
total N	0.241	0.0001***	0.029	0.2499
total P	0.075	0.0380*	(-) 0.003	0.7020
total K	N.D.	N.D.	0.047	0.1393
total Ca	N.D.	N.D.	(-) 0.064	0.0827
total Mg	N.D.	N.D.	0.034	0.2060
C:N	(-) 0.003	0.6547	(-) 0.049	0.1293
C:P	0.113	0.0098	(-) 0.017	0.3772
lignin (%)	N.D.	N.D.	(-) 0.047	0.1389
lignin:N	N.D.	N.D.	(-) 0.049	0.1312
Lignin:P	N.D.	N.D.	(-) 0.024	0.2940
cumulative soil temperature	(-) 0.180	0.0009***	0.010	0.5004

*, **, *** significant at p<0.05, p<0.01, p<0.001 respectively

N.D.: Not determined

Table 2.11
Stepwise multiple regression analysis of cumulative surface soil in situ N mineralization and soil chemical and microclimatic characteristics (without S sites)

n=45		In situ cumulative N mineralization R2
laboratory N mineralization		0.14
element concentration		
N		
P		
K		
Ca	(-)	0.07
Mg		
C		
lignin concentration		
extractable P		
exchangeable K+		
exchangeable Ca++		
exchangeable Mg++		
cumulative in situ soil temperature		
average water content		
Sum R2		0.21
F		6.17
pr>F		0.0043

- Laboratory N mineralization potential

After 50 days of incubation at constant temperature and water content the net release of N by surface soil materials was greater on the recently harvested site and on both aspen sites than in all other ecological types (table 2.8). The general trend in N mineralization seen with the buried bag technique was followed except for the grass sites which showed, under laboratory conditions, a very low N mineralization potential.

Net nitrate production occurred on scraped and mature spruce sites unlike the field incubation although the magnitude of values, on these sites, was substantially lower than on other sites (table 2.9).

As with the field incubation study, the chemical characteristics of the forest floor could only poorly explain the variation of N mineralization rates under controlled conditions when the spruce sites were not included in the computations (table 2.12). In a stepwise regression analysis only exchangeable Ca (negatively) and exchangeable Mg were selected to explain laboratory N

Table 2.12
Linear regressions between laboratory N mineralization estimates and certain surface soil characteristics

Soil Characteristics	Laboratory N mineralization estimates			
	all treatments (n=55)		Without S sites (n=45)	
	R2	P	R2	P
extractable P	0.255	0.0001***	0.138	0.0093**
exchangeable K	0.063	0.0573	0.0001	0.8632
exchangeable Ca	0.006	0.5640	(-) 0.33	0.0001***
exchangeable Mg	0.105	0.1292*	0.001	0.8190
total N	0.100	0.1531*	0.002	0.7723
total P	0.137	0.0040**	0.041	0.1678
total K	N.D.	N.D.	0.089	0.0390*
total Ca	N.D.	N.D.	0.001	0.7911
total Mg	N.D.	N.D.	0.125	0.0136*
C:N	(-) 0.004	0.6150	(-) 0.031	0.2277
C:P	0.026	0.2222	0.056	0.1050
lignin (%)	N.D.	N.D.	(-) 0.011	0.4670
lignin:N	N.D.	N.D.	(-) 0.027	0.2655
Lignin:P	N.D.	N.D.	(-) 0.044	0.1523
cumulative soil temperature	(-) 0.125	0.007**	(-) 0.002	0.7792

*, **, *** significant at p<0.05, p<0.01, p<0.001 respectively

N.D.: Not determined

mineralization rates when S sites were excluded (table 2.13). Again N and lignin concentrations of the surface soil were not selected.

c) Soil temperature and moisture content

Both scraped sites showed a consistently greater soil temperature than all other sites except at the very beginning and at the end of the growing season where their temperature was equivalent to the other sites (fig. 2.1). Cumulative degree-day summations showed that scraped sites had the highest soil temperature (table 2.14). Values of the recently harvested site were lower than values found on both mature white spruce sites. However, most of these differences are not statistically significant.

The water content of the surface soil of both scraped sites was consistently lower than on other types (table 2.15). Again, no consistent difference could be seen between the other types.

d) Tongue depressors decomposition rates

The decay rates of tongue depressors were not consistent between replicates of the same ecological type (table 2.16).

Table 2.13
Stepwise multiple regression analysis of surface soil laboratory N mineralization and soil chemical and microclimatic characteristics (without S sites)

n=45		In situ cumulative N mineralization R2
cumulative in situ N mineralization		
element concentrations		
N		
P		
K		
Ca		
Mg		
C		
lignin concentration		
extractable P		
exchangeable K+		
exchangeable Ca++	(-)	0.33
exchangeable Mg++		0.06
cumulative in situ soil temperature		
average water content		
Sum R2		0.39
F		14.38
pr>F		0.0001

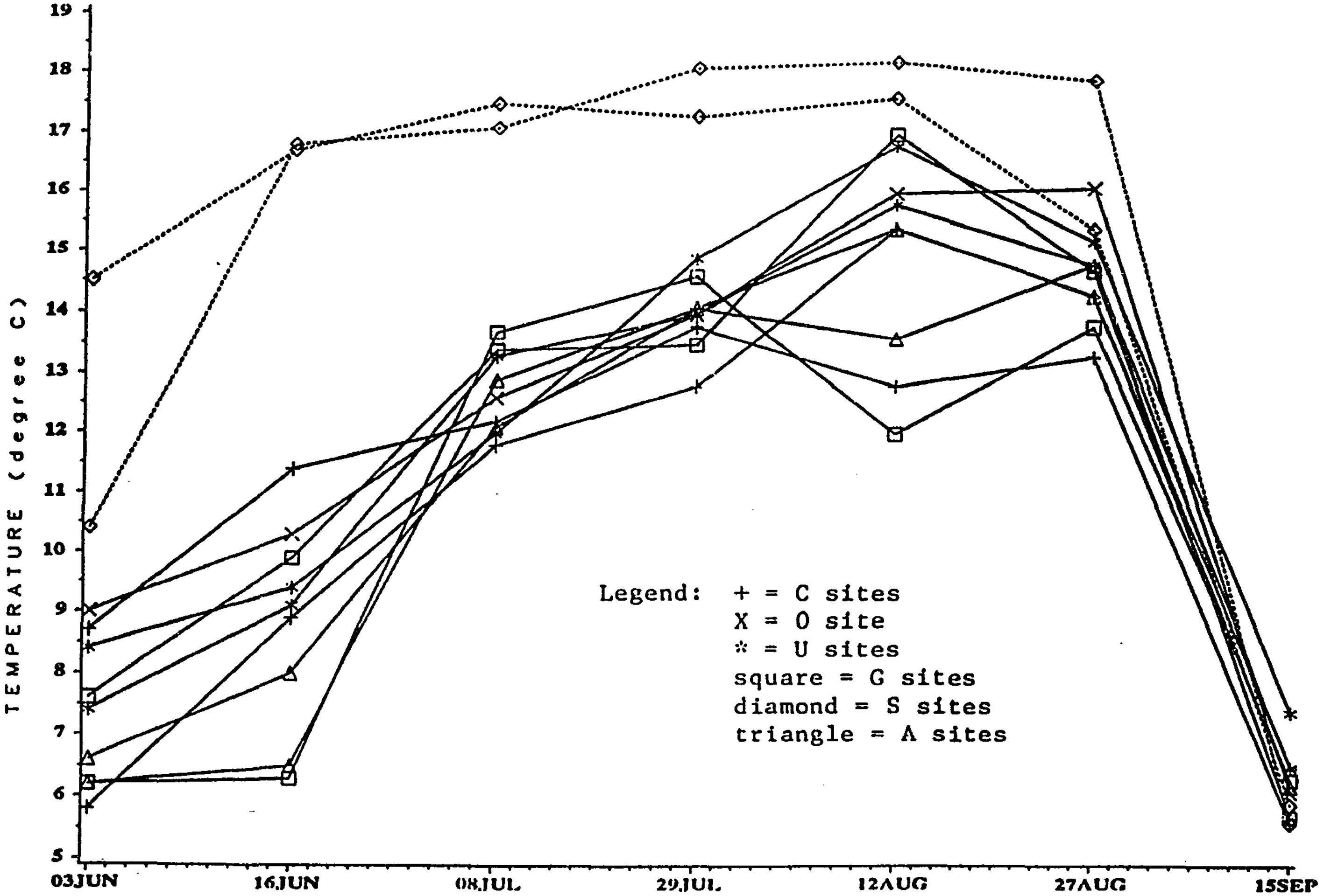


Figure 2.1 Soil temperature at a depth of 10 cm during the growing season of 1989

Table 2.14
Cumulative soil degree days at a depth of 10 cm over the course of the growing season in the six ecological types under study

Ecological types	(oC)
Pr>f	0.0001
Mature w.spruce	
(1)	1370±76 b
(2)	1431±109 ab
Harvested sites (year 1)	1535±54 ab
(year 14)	
Undisturbed	
(1)	1514±54 ab
(2)	1467±119 ab
Grass	
(1)	1484±92 ab
(2)	1317±72 b
Scraped	
(1)	1940±28 a
(2)	1943±51 a
Aspen	
(1)	1381±32 b
(2)	1324±38 b

Note: Estimates are means ± SE. In each column, values followed by the same letter are not significantly different ($p<0.05$).

Table 2.15
Water content of surface soil samples
(% dry weight)

Ecological types	September, 14 1988	May, 27 1989	July, 1 1989	August, 12 1989
p>f	0.0001	0.0001	0.0011	0.0001
Mature				
w.spruce	ab	ab	a	ab
(1)	108±25	127±54	168±45	124±20
	ab	ab	ab	ab
(2)	101±34	80±14	150±43	103±21
Harvested	a	ab	ab	a
sites	164±31	102±26	131±40	130±25
(year 1)				
(year 14)				
Undisturbed	ab	ab	ab	ab
(1)	117±36	140±28	142±46	120±56
	abc	a	a	ab
(2)	117±36	212±40	175±37	123±19
Grass	ab	a	a	ab
(1)	126±25	155±41	166±62	114±35
	a	ab	ab	ab
(2)	169±46	149±42	134±24	93±37
Scraped	b	b	b	b
(1)	29±6	22±5	28±3	19±2
	b	b	b	b
(2)	33±17	27±8	33±5	19±3
Aspen	a	ab	ab	a
(1)	151±18	136±35	145±24	190±21
	ab	b	ab	a
(2)	111±46	169±30	151±8	175±37

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 2.16
Tongue depressors weight loss in the surface soil of the 6 ecological types under study.

Ecological types	(%weight loss)
p>f	0.0002
Mature w.spruce	
(1)	4.05+7.97c
(2)	6.48+6.20c
Harvested sites (year 1)	12.38+9.18abc
(year 14)	
Undisturbed	
(1)	6.83+6.87c
(2)	11.73+10.77abc
Grass	
(1)	19.63+16.00a
(2)	10.68+10.34bc
Scraped	
(1)	5.17+5.93c
(2)	6.52+11.14c
Aspen	
(1)	16.84+10.58ab
(2)	18.38+8.73ab
(3)	6.97+4.92c

Note: Estimates are means ± SE. In each column, values followed by the same letter are not significantly different (p<0.05).

However, the decay rates found on one grass site and on two of the three aspen sites were significantly greater than rates encountered on the two mat8ure white spruce sites.

e) Greenhouse bioassay

Both aspen sites showed the greatest seedling yield and the greatest nutrient uptake for all sites (table 2.17 and 2.18). However, these values did not significantly differ from results obtained on most substrates. Biomass production and nutrient uptake of seedlings grown on surface soil materials from the recent clear-cut and from the scraped areas were much lower than on all other treatments (tables 2.17 and 2.18). Root to shoot ratio did not follow seedling yield nor seedling nutrient uptake patterns (table 2.17). Nutrient concentrations in various plant parts did not show any clear difference among treatments (tables 2.19, 2.20 and 2.21). Seedlings grown on surface soil from the grass type tended to show the lowest leaf (table 2.19) and root (table 2.21) N concentrations.

Results from linear regressions between soil properties and seedling growth and nutrient uptake are shown in table 2.22. No significant relationships were found when the recently

Table 2.17
Foliar, stem, root, and total dry weight and root/shoot ratio of birch (Betula papyrifera) seedlings grown on various surface soil material

Ecological types	foliar weight	stem weight (g/pot)	root weight	total weight	root/shoot (ratio)
Pr>f	0.0001	0.0002	0.0001	0.0001	0.0010
Mature					
w.spruce	ab	ab	ab	ab	b
(1)	0.765±0.239	0.307±0.099	0.744±0.225	1.816±0.513	0.70±0.12
	ab	ab	ab	ab	ab
(2)	0.867±0.164	0.313±0.086	1.326±0.486	2.506±0.703	1.11±0.28
Harvested	b	ab	ab	ab	ab
sites	0.163±0.094	0.086±0.048	0.432±0.227	0.682±0.355	1.82±0.91
(year 1)					
(year 14)					
Undisturbed	ab	ab	ab	ab	ab
(1)	0.587±0.226	0.200±0.101	1.449±1.010	2.236±1.242	1.88±0.91
	ab	ab	ab	ab	ab
(2)	0.581±0.222	0.239±0.068	0.876±0.266	1.697±0.543	1.09±0.11
Grass	ab	ab	ab	ab	ab
(1)	0.427±0.169	0.176±0.061	0.854±0.261	1.458±0.471	1.50±0.35
	ab	ab	ab	ab	ab
(2)	0.756±0.150	0.250±0.060	1.252±0.322	2.267±0.490	1.24±0.24
Scraped	b	b	b	b	b
(1)	0.222±0.042	0.037±0.010	0.169±0.027	0.429±0.059	0.67±0.16
	b	b	b	b	ab
(2)	0.245±0.028	0.057±0.011	0.258±0.030	0.561±0.047	0.86±0.16
Aspen	a	a	a	a	ab
(1)	1.051±0.154	0.383±0.074	2.165±0.686	3.600±0.897	1.48±0.29
	a	a	a	a	ab
(2)	1.239±0.308	0.459±0.161	2.370±0.823	4.068±1.276	1.37±0.20

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 2.18
Net nutrient uptake by birch (*Betula papyrifera*) seedlings grown on various surface soil materials

Ecological types	N	P	K	Ca	Mg
			(mg/pot)		
Pr>f	0.0001	0.0001	0.0001	0.0001	0.0001
Mature					
w.spruce	ab	ab	ab	ab	ab
(1)	19.03±5.37	5.04±0.56	17.44±4.93	21.10±5.03	3.88±0.73
	ab	ab	ab	ab	ab
(2)	28.10±8.45	6.37±1.50	22.66±5.25	27.42±5.99	4.89±1.04
Harvested	b	b	b	b	b
sites	6.73±3.43	1.74±1.00	4.31±2.16	8.31±4.47	1.30±0.81
(year 1)					
(year 14)					
Undisturbed	ab	ab	ab	ab	ab
(1)	23.70±9.36	3.79±0.82	16.48±6.28	24.24±9.74	4.29±1.35
	ab	ab	ab	ab	ab
(2)	17.75±6.89	4.19±1.52	14.77±6.17	21.29±7.52	3.18±0.96
Grass	ab	ab	ab	ab	ab
(1)	12.25±3.47	3.47±1.09	10.34±3.93	14.60±4.23	2.38±0.87
	ab	ab	ab	ab	ab
(2)	23.83±7.52	4.07±0.84	18.06±5.10	23.00±6.16	3.79±0.95
Scraped	b	b	b	b	b
(1)	6.05±0.63	0.99±0.21	4.10±0.54	3.10±0.42	1.16±0.18
	b	b	b	b	b
(2)	4.95±0.39	0.94±0.04	4.18±0.30	3.66±0.50	1.23±0.16
Aspen	a	a	a	a	a
(1)	38.54±11.40	8.48±1.79	26.75±6.08	38.81±9.34	6.04±1.68
	a	a	a	a	a
(2)	49.62±11.92	9.97±2.20	32.61±5.74	42.96±11.96	8.37±2.68

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$),

Table 2.19
Foliar nutrient concentrations of birch (*Betula papyrifera*) seedlings grown on surface soil materials

Ecological types	N	P	K	Ca	Mg
			(%)		
Pr>f	0.0015	0.0230	0.0706	0.0024	0.4042
Mature w.spruce (1)	abc 1.19±0.12	ab 0.40±0.18	a 1.22±0.11	bc 1.32±0.16	a 0.32±0.09
(2)	abc 1.17±0.21	ab 0.31±0.04	a 1.20±0.15	bc 1.24±0.13	a 0.27±0.04
Harvested sites (year 1)	abc 1.06±0.12	a 0.43±0.09	a 1.01±0.16	a 1.47±0.19	a 0.37±0.03
(year 14)					
Undisturbed (1)	abc 1.31±0.14	ab 0.30±0.11	a 1.21±0.06	ab 1.37±0.13	a 0.31±0.08
(2)	abc 1.19±0.19	ab 0.31±0.07	a 1.23±0.14	ab 1.39±0.14	a 0.31±0.12
Grass (1)	c 0.89±0.06	a 0.41±0.09	a 1.12±0.17	bc 1.27±5.60	a 0.34±0.07
(2)	abc 1.29±0.24	a 0.27±0.03	a 1.21±0.20	bc 1.27±0.07	a 0.26±0.05
Scraped (1)	a 1.70±0.27	ab 0.26±0.01	a 1.11±0.15	bc 0.95±0.06	a 0.32±0.03
(2)	bc 1.03±0.09	b 0.19±0.03	a 0.82±0.04	c 0.88±0.04	a 0.31±0.03
Aspen (1)	abc 1.18±0.03	ab 0.34±0.07	a 1.14±0.07	bc 1.27±0.10	a 0.28±0.04
(2)	ab 1.42±0.17	ab 0.36±0.06	a 1.30±0.16	bc 1.17±0.09	a 0.34±0.06

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 2.20
Stem nutrient concentrations of birch (<u>Betula papyrifera</u>) seedlings grown on various surface soil materials

Ecological types	N	P	K	Ca	Mg
			(%)		
Pr>F	0.0031	0.4086	0.1138	0.0036	0.0091
Mature w.spruce (1)	ab 0.51±0.16	a 0.19±0.02	a 0.82±0.23	ab 1.10±0.25	ab 0.08±0.01
(2)	ab 0.55±0.09	a 0.16±0.02	a 0.75±0.07	ab 1.10±0.12	ab 0.09±0.01
Harvested sites (year 1)	b 0.46±0.04	a 0.20±0.05	a 0.72±0.16	a 1.50±0.14	ab 0.08±0.03
(year 14)					
Undisturbed (1)	ab 0.69±0.16	a 0.17±0.04	a 0.88±0.23	ab 1.34±0.15	ab 0.10±0.01
(2)	ab 0.57±0.08	a 0.18±0.02	a 0.77±0.14	a 1.41±0.11	ab 0.07±0.02
Grass (1)	b 0.41±0.04	a 0.18±0.01	a 0.62±0.05	ab 1.11±0.09	ab 0.10±0.03
(2)	ab 0.59±0.10	a 0.16±0.02	a 0.79±0.14	ab 1.08±0.17	ab 0.07±0.03
Scraped (1)	a 0.92±0.19	a 0.13±0.05	a 1.00±0.15	ab 1.11±0.25	a 0.12±0.01
(2)	ab 0.60±0.07	a 0.14±0.03	a 0.68±0.11	ab 1.02±0.12	ab 0.11±0.02
Aspen (1)	ab 0.57±0.07	a 0.19±0.04	a 0.82±0.20	ab 0.99±0.09	b 0.05±0.01
(2)	ab 0.58±0.08	a 0.17±0.02	a 0.80±0.10	b 0.80±0.20	ab 0.08±0.03

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 2.21
Root nutrient concentrations of birch (*Betula papyrifera*) seedlings grown on various surface soil materials

Ecological types	N	P	K	Ca	Mg
			(%)		
Pr>f	0.0181	0.0008	0.0630	0.0655	0.0090
Mature					
w.spruce	ab	ab	a	a	ab
(1)	1.12±0.18	0.23±0.05	0.78±0.21	1.06±0.11	0.18±0.02
	ab	a	a	a	ab
(2)	1.22±0.04	0.24±0.03	0.78±0.01	1.03±0.09	0.18±0.04
Harvested	ab	ab	a	a	ab
sites	1.07±0.12	0.19±0.03	0.48±0.06	1.04±0.08	0.14±0.05
(year 1)					
(year 14)					
Undisturbed	ab	ab	a	a	b
(1)	1.09±0.19	0.15±0.06	0.60±0.19	1.02±0.18	0.18±0.04
	ab	ab	a	a	ab
(2)	1.04±0.19	0.21±0.01	0.63±0.12	1.10±0.32	0.15±0.05
Grass	ab	ab	a	a	b
(1)	0.93±0.18	0.18±0.02	0.50±0.14	0.87±0.15	0.09±0.03
	ab	b	a	a	ab
(2)	0.97±0.15	0.12±0.02	0.54±0.10	0.84±0.17	0.13±0.04
Scraped	ab	ab	a	a	a
(1)	1.19±0.10	0.21±0.02	0.75±0.10	0.36±0.02	0.24±0.04
	b	ab	a	a	ab
(2)	0.81±0.11	0.15±0.03	0.70±0.11	0.35±0.03	0.15±0.02
Aspen	ab	ab	a	a	ab
(1)	1.09±0.11	0.20±0.04	0.55±0.11	1.01±0.04	0.13±0.82
	a	ab	a	a	ab
(2)	1.28±0.13	0.21±0.05	0.59±0.12	1.07±0.08	0.16±0.01

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 2.22
Linear regressions between total seedling yields in a greenhouse bioassay and certain soil characteristics

Soil Characteristics	All sites except site "O" (n=10)			All sites except sites "O" and "S" (n=8)		
	R2	P	slope	R2	P	slope
available N field	0.684	0.0031**	+	0.373	0.1079	+
laboratory	0.782	0.0007***	+	0.875	0.0006***	+
extractable P	0.587	0.0098**	+	0.176	0.3001	+
exchangeable K	0.521	0.0185*	+	0.074	0.5148	+
exchangeable Ca	0.221	0.1699	+	0.781	0.0036**	-
exchangeable Mg	0.386	0.0522	+	0.021	0.462	+
total N	0.597	0.0088**	+	0.183	0.2905	+
total P	0.69	0.0029**	+	0.391	0.0975	+
total K	N.D.			0.598	0.357	+
total Ca	N.D.			0.402	0.0915	+
total Mg	N.D.			0.842	0.0087**	+
C:N	0.011	0.7757	+	0.137	0.7357	+
C:P	0.253	0.1382	+	0.271	0.1857	+
lignin (%)	N.D.			0.0043	0.8236	+
lignin:N	N.D.			0.093	0.1469	+
Lignin:P	N.D.			0.0468	0.0613	-

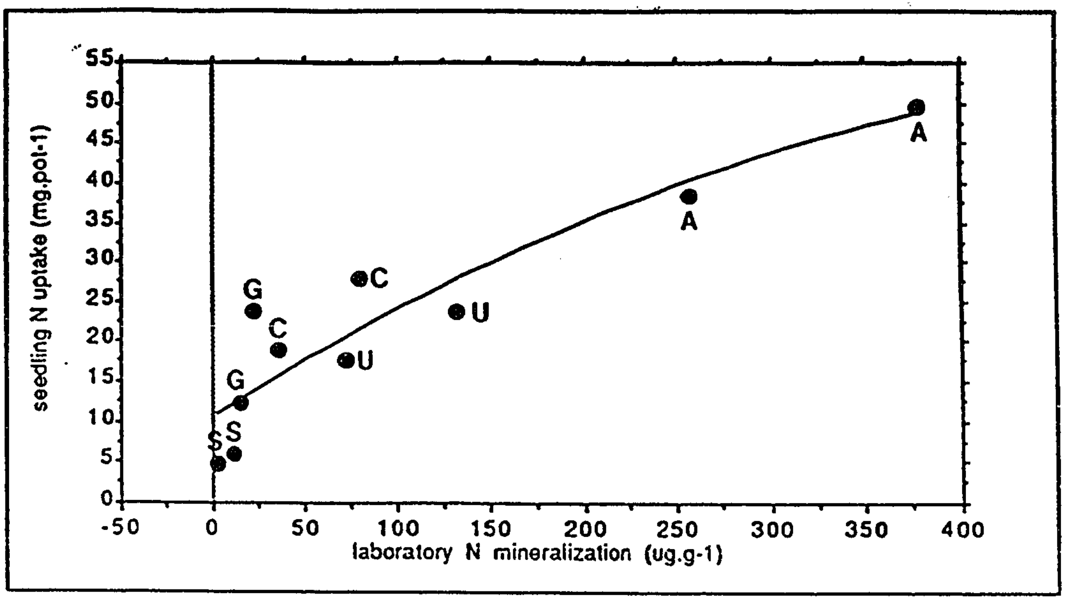
*, **, *** significant at $p<0.05$, $p<0.01$, $p<0.001$ respectively

N.D.: not determined

harvested site was included; these results are not presented. However when the recently harvested site was removed, seedling yield was significantly related to *in situ* N mineralization, laboratory N mineralization, extractable P, exchangeable K, and total N, P and Ca. The significance of these regressions was largely due to the contrasting properties of scraped sites surface soil and only laboratory N mineralization, exchangeable Ca and total Mg remained significantly related to seedlings yield when scraped sites were not included in the computations. Again, N and lignin concentrations were not related to seedling yield. The role of aspen sites in the relationship between bioassay N uptake and laboratory N mineralization rate is illustrated in figure 2.2.

2-Mineral soil characterization

No consistent differences in the concentrations of available nutrients in the mineral soil were seen among ecological types. However, one grass site showed high extractable P concentrations and one mature white spruce site showed high exchangeable Mg concentrations (table 2.23). Field N mineralization rates were higher on the recently clear-cut



Legend : A = Aspen
C = Mature white spruce
G = Grass
S = Scraped
U = Undisturbed

$y = 10.579 + 0.147x - 1.2308E\text{-}4x2$

$n = 10$; R-squared = 0.814; $pr > f = 0.0028$

Figure 2.2 Polynomial regression between bioassay seedling N uptake and laboratory N mineralization potential

Table 2.23
Extractable P and exchangeable bases in the mineral soil of the 6 ecological types under study.

Ecological types	Extractable P ug.g-1	K meq.100g-1	Ca meq.100g-1	Mg meq.100g-1
Pr>f	0.0001	0.5104	0.5244	0.0002
Mature				
w.spruce	b	a	a	a
(1)	19.60±8.68	0.23±0.11	6.26±2.66	3.38±1.29
	b	a	a	b
(2)	11.94±4.75	0.15±0.03	5.73±2.57	2.31±0.98
Harvested	b	a	a	b
sites	16.46±19.28	0.20±0.17	5.24±2.47	2.03±0.60
(year 1)				
(year 14)				
Undisturbed	b	a	a	b
(1)	15.04±18.54	0.35±0.33	6.99±2.70	1.86±0.53
	b	a	a	b
(2)	3.81±2.81	0.26±0.25	6.32±3.28	2.01±0.18
Grass	b	a	a	b
(1)	17.11±17.92	0.18±0.09	6.82±3.45	1.85±0.64
	a	a	a	b
(2)	51.96±7.37	0.27±0.16	7.74±2.63	1.96±0.72
Scraped	b	a	a	b
(1)	9.79±4.70	0.22±0.04	6.60±1.99	2.12±0.13
	b	a	a	b
(2)	8.73±4.74	0.20±0.06	8.07±2.48	2.45±0.57
Aspen	b	a	a	b
(1)	13.02±6.86	0.26±0.08	5.96±1.92	1.63±0.22
	b	a	a	b
(2)	12.91±7.64	0.15±0.08	6.45±0.98	1.73±0.92
	b	a	a	b
(3)	17.02±9.34	0.23±0.06	6.44±2.01	1.97±0.43

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

site than on all other sites (tables 2.24). No general trend in water content of mineral soil was seen among types (table 2.25).

DISCUSSION

The bioassay experiment showed that, compared to mature white spruce forest sites, the surface soil available nutrient supply: (1) declined on the recently harvested site and on the scraped sites, (2) was relatively equivalent on undisturbed and grass ecological types 14 years following harvesting, and (3) was improved on sites where aspen was regenerating.

The reduced seedling growth on scraped surfaces is supported by soil chemical analysis. Concentrations of available nutrients, as well as net nitrogen mineralization on these soils, were an order of magnitude lower than on all other soils. In boreal forests the forest floor provides major storage of organic matter and nutrients (Van Cleve and Alexander 1981). In mature white spruce forests (Van Cleve *et al.* 1983) reserves of N, P and K in the forest floor

Table 2.24
In situ net N mineralization in the top 10 cm of the mineral soil of the 6 ecological types under study (ug.g-1)

	Sampling periods *				Cumulative
Ecological types	1	2	3	4	one year
Pr>f	0.8352	0.0527	0.0642	0.0158	0.0015
Mature w.spruce					
(1)	a 0.40±0.51	a 0.72±1.18	a 3.76±3.30	ab 0.19±0.19	b 5.07±4.46
(2)	a 1.59±1.65	a 0.30±0.27	a 4.97±3.22	ab 0.20±0.34	b 7.06±4.47
Harvested sites (year 1)	a 4.09±4.10	a 1.71±1.78	a 5.89±3.34	a 3.85±7.23	a 15.54±8.03
(year 14)					
Undisturbed (1)	a 0.81±0.58	a 1.83±0.13	a 0.98±0.98	ab 0.31±0.39	a 3.93±0.83
(2)	a 1.04±1.17	a 0.42±0.73	a 3.34±3.46	b 0.02±0.05	b 4.83±4.54
Grass (1)	a 2.56±4.10	a 0.82±0.41	a 3.27±3.38	ab 0.45±0.31	b 7.10±4.00
(2)	a 0.80±0.93	a 2.44±3.23	a 1.62±1.81	ab 1.12±1.00	b 5.97±2.78
Scraped (1)	a 1.75±1.31	a 0.23±0.35	a 1.77±1.82	ab 0.28±0.12	b 4.03±2.90
(2)	a 2.33±3.48	a 1.22±1.59	a 1.17±0.88	ab 0.34±0.15	b 5.06±3.96
Aspen (1)	a 1.64±1.84	a 2.30±1.90	a 4.55±4.18	ab 0.51±0.52	b 8.99±6.12
(2)	a 1.04±1.34	a 1.61±1.37	a 6.17±3.17	a 1.18±2.07	ab 9.99±2.07

* period 1: September 15, 1988 - May 27, 1989
period 2: May 27, 1989 - July 1, 1989
period 3: July 1, 1989 - August 12, 1989
period 4: August 12, 1989 - September 15, 1989

Note: Estimates are means ± SE. values assigned to a same letter are not significantly different (p<0.05).

Table 2.25
Water content of mineral soil samples
(% dry weight)

Ecological types	September, 14 1988	May, 27 1989	July, 1 1989	August, 12 1989
p>f	0.0018	0.0007	0.0003	0.0001
Mature w.spruce	b	ab	abc	abc
(1)	17.1±7.4	37.8±5.6	35.7±3.5	21.8±6.2
	b	ab	abc	b
(2)	16.4±5.4	30.2±11.6	30.2±9.7	16.6±4.5
Harvested sites (year 1)	ab	ab	abc	ab
	33.9±4.9	30.7±3.3	33.0±6.2	31.0±7.5
(year 14)				
Undisturbed	ab	ab	abc	abc
(1)	26.0±2.2	35.6±7.3	38.9±3.3	23.1±3.0
	ab	a	a	ab
(2)	27.9±4.5	41.5±6.6	42.5±2.4	28.3±3.4
Grass	ab	ab	ab	ab
(1)	21.9±3.0	36.3±34	40.9±2.5	28.2±5.6
	ab	ab	abc	a
(2)	30.6±7.7	41.4±7.5	37.6±4.7	33.8±10.0
Scraped	ab	b	b	abc
(1)	28.0±8.1	21.4±0.8	29.7±6.5	20.0±3.0
	ab	ab	c	abc
(2)	28.2±13.7	34.1±12.1	27.3±2.0	22.1±1.8
Aspen	a	a	abc	c
(1)	35.3±6.0	41.9±5.2	37.7±6.0	13.9±2.3
	ab	a	ab	c
(2)	31.4±9.0	49.8±5.5	42.0±3.4	14.9±2.8

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

were respectively 129%, 100%, and 51% greater than the quantity found in living aboveground biomass.

The loss of nutrient may not be the only detrimental effect of removing the forest floor. Soil organic matter contributes greatly to soil cation exchange capacity, water retention (Brady 1974), and provides a source of C for microbial immobilization of nutrients. This latter mechanism has been observed as the most important factor preventing nutrient loss after a clear-cut in a loblolly pine plantation (Vitousek and Matson 1985).

Across a range of sites, in interior Alaska, temperature was shown to be the most important factor controlling N mineralization (Van Cleve and Yarie 1986). However, the positive effect of total or partial forest floor removal on soil temperature, which was also observed after forest floor burning (Dyrness *et al.* 1988), was not sufficient in the present study to compensate for the nutrient loss by forest floor removal and to provide an adequate supply of N.

Exposure of the mineral soil facilitates white spruce seed germination and seedling survival (Nyland *et al.* 1979;

Putman and Zasada 1986). However, this practice greatly reduces soil nutritional quality and impairs tree growth. Practice such as root raking (Ballard 1978; Glass 1976), broadcast burning (Bisset and Parkinson 1980), or litter removal (Nyland *et al.* 1979) have been shown to alter soil nutritional quality to the detriment of tree growth. The recovery period of soil fertility from such an intense disturbance might be very long.

The poor performance obtained in the bioassay for seedlings growing on recently harvested surfaces is more difficult to explain. Soil chemical analysis and N incubation showed that the characteristics of this forest floor were at least equivalent to the quality of forest floor from mature white spruce sites and from most 14-year-old types. Since soils were not sterilized, it is possible that some biological factors were responsible for the poor seedling growth. Following disturbance, increased microbial competition for nutrients, due to increased available carbon, was observed by Vitousek and Matson (1985). The increased NO_3^- production on these sites, typical of recently disturbed forest floor (Likens *et al.* 1969; Vitousek *et al.* 1982), suggested that microbial activity is undergoing intense modifications in response to altered site conditions. Berg and Ekbohm (1983) observed that N was immobilized in the forest floor of a recently clear-cut site at a C:N ratio much lower than in adjacent uncut forests. They concluded that microbial populations as well as mechanisms regulating nutrient mineralization are different when the ecosystem is severely disturbed.

These early changes in nutrient dynamics may not be of great consequence for the productivity of future stands as indicated by seedling performance on all 14-year-old unscraped sites.

The good performance of birch seedlings growing on aspen forest floor seems to be related to improved N mineralization rates as suggested by laboratory N mineralization estimates and, to a lesser degree, by field N mineralization estimates. However, some discrepancies were seen between these two estimates. Nitrogen mineralization estimates were higher on aspen sites than on the recently harvested site as determined by the laboratory incubation estimates while the opposite was observed with field incubation estimates. Also, grass site N mineralization estimates were very low in the laboratory incubation but were not different from most sites for field estimates.

The buried bag technique should give a more accurate estimate of actual field N mineralization because this method is sensitive to temperature fluctuation in the field (Raison et *al*. 1987). However, *in situ* soil temperature and water content were not selected in a stepwise regression analysis of field N incubation in relation to soil chemistry, laboratory N mineralization estimates, and soil field temperature and water content (table 2.11). Therefore, the discrepancy between estimates of N mineralization in the field and under laboratory conditions may be caused by factors unrelated to microclimatic variables. For example, in the laboratory experiment, the soil was sieved and roots were, in a large measure, discarded. While in the field estimate soil cores were disturbed as little as possible. Sieving reduces the input of labile N from freshly broken roots and may have reduced the estimate of N mineralization from grass sites where the forest floor is heavily rooted. Another factor, the non-homogenization of the material for field incubations may have caused a greater variability which prevented the observation of significant differences among most types.

The availability of N is strongly linked to soil microbial activity (McGill and Cole 1981), which can be affected by vegetation through energy and nutrient supply (Clarholm 1985). The increased N mineralization rates from undisturbed to grass to aspen forest floor types is closely linked to the vegetation biomass production of these regenerating types (chapter 3). This lends support to the claim that there is a continuum between plant root production, microbial activity, and N availability (Baath 1980; Clarholm 1985; Lungren 1982; Sundman *et al.* 1978). A greater root production increases the energy input to the soil which consequently, increases soil microbial biomass and N mineralization.

Plants can also modify soil nutrient availability by the influence of their litter. Ratios of element to carbon and lignin content of litter are important factors by which species can influence nutrient cycling rates (Aber and Mellilo 1982).

The species composition of a plant community has been shown to alter soil properties (Howard and Howard 1980). It is generally believed that conifers promote slower nutrient turnover because of higher lignin and other polyphenol content and lower nutrient content (Perry *et al.* 1987). Conifers have been shown to increase N immobilization and decrease nutrient supply to the detriment of tree growth (Stone and Will 1965). It has been speculated that cycling of nutrients might be accelerated by the presence of a deciduous component (Assman 1977; Perry 1978; Tappeiner and Alm 1975).

Damman (1971) stated that soil changes through species influence take at least a few decades. In the present study the improvement of soil fertility after only 14 years of aspen growth indicates that these changes can be even more significant in the future when aspen litter will not be as diluted with the forest floor originating from the white spruce forest. In the natural successional pattern the forest floor, which was formed during the development of the white spruce stand, would be totally or partially altered by fire. However, on post-harvested sites the material originating from the spruce stand constitutes a large portion of the total forest floor material in which litter from successional species is diluted.

This dilution factor could explain why N concentrations, C:N ratios or lignin:N ratios of the total forest floor were not related to N mineralization estimates as they were in more mature ecosystems (Van Cleve *et al*. 1986). The litter from early successional species may be decaying rapidly, supplying nutrient at a fast rate, while N mineralization in the bulk of the forest floor, which originated from the previous white spruce forest is slow. This view supports the hypothesis of a slow, and a fast concomitant N cycles in soil (Broadbent 1980). This phenomenon might be even more significant in a successional context where fast decaying species replace slow decaying ones. Fyles and McGill (1987) found that the properties of the LFH horizons of some forest sites in central Alberta reflected the age and species composition of the existing vegetation while characteristics of A horizons were related to conditions in previous, as well as present, stands.

Rapid decay of early successional species leaf litter may increase forest floor decomposition and decrease storage of organic matter and nutrients in the forest floor. This pattern of forest floor evolution after a clear cut was observed in deciduous forests (Covington 1981; Federer 1984; Johnson *et al.* 1985), in a mixed forest (Bird and Chatarpaul 1988), and in a hemlock dominated ecosystem (Hix and Barnes 1984), but not in a hardwood stand in Nova Scotia (Wallace and Freedman 1985) nor in the present study. The absence of a change in forest floor weight may indicate that there is no significant increase in organic matter decomposition rates after a clear cut as suggested by the absence of an increase in the mass loss of tongue depressors. The absence of observable change in forest floor weight after harvesting may however be due to the high variability of this measurement; the great disturbances to the site during the harvesting operations and site preparation treatments have created a high variability in forest floor thickness and may have prevented the observation of a decrease in the biomass of the forest floor.

Species can also modify the soil resource by immobilizing nutrients in perennial tissues. Studies have demonstrated that some deciduous tree species, aspen in particular, accumulate Ca and sometimes Mg at a much faster rate than coniferous species and may deplete soil-available stores (Alban 1982, Alban et *al.* 1978; Cromack and Monk 1975, Ruark and Bockheim 1987; Yount 1975). This phenomenon could explain the decrease in soil exchangeable Ca, observed in the present study, in the forest floor of aspen regenerating sites. However, this decrease may not alter site productivity, at least for a few rotations, because exchangeable Ca is found in large quantities on these sites (Van Cleve et *al.* 1983). Nevertheless, some studies suggest that if aspen is to be harvested on a short rotation basis, Ca depletion of the site could become a problem due to low atmospheric inputs (Boyle and Erk 1972; Boyle et *al.* 1973; Johnson et *al.* 1982; Weetman and Weber 1972).

Van Cleve and Yarie (1986) showed across a range of vegetation types, that temperature was the most important variable explaining organic matter decomposition, N mineralization and forest productivity. This is a different picture from the one obtained from work in temperate latitude forests where organic chemistry and/or moisture appears to play dominant roles in mineralization rates and element supply among forest types and soil temperature appeared to play a secondary role (Van Cleve et *al.* 1986).

The importance of temperature as a controlling factor of plant production in interior Alaska is due to the relationship between micro-climate and aspect and to the great range of temperatures encountered over short distances at these high latitudes because of low sun angle.

The results of the present study suggest that, on regenerating upland south-facing sites, species influence through litter effect (chemistry and structure), more than temperature, controls nutrient availability. This is illustrated by the lack of a relationship between temperature and N mineralization or other indices of element availability and by the high yields of seedlings growing on the aspen forest floor in the greenhouse bioassay. Relationships between litter quality and soil properties will be addressed in chapter 5.

The removal of the forest did not seem to promote a major increase in soil temperature unless the forest floor was severely disturbed as in the scraped treatment. On a floodplain site in interior Alaska, Dyrness *et al.* (1988) observed a slight increase in temperature after forest harvesting. This increase was much more significant when the forest floor had been burned.

The results of the present study suggest that soil fertility can be altered by species composition. The decline in soil fertility associated with the development of a spruce forest (Pastor *et al.* 1987) may be compensated for, during natural succession, by the positive influence of a deciduous component.

More research is needed in this area to test whether or not a deciduous tree component increases the productivity of spruce stands. This could lead to new management possibilities that would substain soil fertility following harvesting.

CHAPTER 3

NUTRIENT CONTENT AND BIOMASS OF ABOVEGROUND ANNUAL PRODUCTION, TOTAL ABOVEGROUND BIOMASS AND LEAF LITTERFALL OF REGENERATING VEGETATION ON POST-HARVESTED WHITE SPRUCE SITES

ABSTRACT

Nutrient content and biomass of annual production, total aboveground biomass, and leaf litter production of 14-year-old plant communities evolving from harvested white spruce sites were estimated by biomass sampling. The annual biomass production of regenerating aspen clumps was equivalent to the annual production of mature white spruce sites. However, the productivity of other regenerating communities was lower. The aboveground nutrient requirement was greater in each of the regenerating communities than in mature white spruce sites except on sites were the forest floor had been scraped. The aboveground N, P, and K requirements of aspen clumps were, on an area basis, close to five times greater than in mature white spruce forest. This fact, together with the large input of nutrients to the

soil by a litter with high nutrient concentrations, suggest that the development of an aspen clump after a clear-cut contributes to accelerated cycles of nutrients. The development of a grass community during the same period after clear-cutting is acompanied by much lower rates of nutrient uptake and return in litterfall.

INTRODUCTION

The rapid recovery of vegetation following forest harvesting is an important factor limiting nutrient losses. Element accumulation in biomass by species of low nutrient use efficiency (NUE), recovery of evapotranspiration, modification of soil temperature, and reduction of nitrification are known processes by which plant regeneration contributes to the regulation of nutrient cycling following disturbance (Marks and Bormann 1972; Vitousek 1977, 1981). In a forest management context early successional colonizing plants are often considered as competitors of commercial species for space, light, water, and nutrients (Brand and Janas 1987; Flint and Childs 1987; Warren et al. 1987). Another role of colonizers, not as frequently mentioned, is their mid- or long-term effect on soil nutrient availability. Nutrient storage in biomass and the production of litter of different quality (chemistry and structure) are mechanisms by which species composition can modify rates of nutrient cycling in an ecosystem.

The objective of this study was to describe the utilization of nutrients by different plant communities found on post-harvested white spruce sites. Nutrient uptake, storage in biomass, and return in litterfall in the different communities control nutrient loss following disturbance, competition for nutrients between commercial and non-commercial species in the newly establishing forest, and consequently, fertility for future stands.

MATERIALS AND METHODS

Field sites

Three fourteen year old post-harvested white spruce sites were selected for this study. All were located on gentle, upland south-facing slopes and showed similar soil development. The vegetation growing on these sites was classified into four ecological types: (1) undisturbed forest floor; (2) dense grass; (3) scraped forest floor; (4) aspen regeneration. Undisturbed, grass, and scraped types were found on two of the three sites while the aspen type was found on all three sites. From 15 to 20 sampling units were randomly selected within each ecological type, with the number of replicates per site (5-10) proportional to the area. A more complete description of sampling design and of community composition is presented in Chapter 1.

Vegetation sampling and chemical analysis

Vegetation sampling took place in early August. This period, late in the growing season but before visible autumn senescence, should provide best estimation of maximum pools of mobile nutrients for communities containing both evergreen and deciduous species (Chapin and Van Cleve 1989). Vegetation was destructively sampled on a randomly located square meter area at every sampling unit of undisturbed, grass and scraped types. The understory of aspen sites was sampled in the same manner. Tree biomass of the aspen regeneration was not assessed with a unit area destructive procedure. Basal diameters were recorded on areas of 4 m^2

in every sampling units. Thereafter, five, five and ten trees were harvested in early August from aspen sites 1, 2, and 3, respectively. Basal diameters of harvested trees ranged from 1 to 6.10 cm. Age, which was determined by counting annual rings, ranged from 8 to 13. Biomass was separated into leaf, current twig, branch, and bole compartments. Ovendry weight of each of these fractions were regressed against their respective diameters using the log-log transformation. Line intercept were adjusted for bias (Baskerville 1972). Regression equations were constructed for every site (3) and for every plant component (4) for a total of twelve equations (table 3.1). The r^2 ranged from .94 to .99 for foliar biomass, from .97 to .98 for current twig biomass, from .88 to .99 for branch biomass, and from .96 to .99 for bole biomass. It was necessary to construct equations for every site because at a given basal diameter trees were dominant on a given site while they were being suppressed on another.

Regression equations were used in conjunction with the record of basal diameter distribution of every sampling

Table 3.1
Biomass equations for young aspen stands

type: ln biomass = a + b*ln (diameter)
-biomass in g
-diameter at soil surface in cm

	a	b	MSE	R2
Site 1				
foliage	-0.052	1.509	0.0545	0.943
twigs	-0.087	1.136	0.2083	0.979
branch	-0.024	0.772	0.0249	0.995
bole	-0.262	1.080	0.7254	0.964
Site 2				
foliage	-0.083	1.545	0.0691	0.955
twigs	-0.105	1.176	0.1357	0.983
branch	-0.125	0.755	0.2080	0.939
bole	-0.279	1.190	0.6427	0.999
Site 3				
foliage	-0.195	1.527	0.1444	0.985
twigs	-0.203	1.203	0.1536	0.975
branch	-0.383	0.835	0.3672	0.885
bole	-0.551	1.249	0.7508	0.989

unit to estimate the biomass of the four comptartements (leaf, twig, branch and bole) on a weight per area basis.

Plant material was oven dried to constant weight at 60°C, then ground to 2 mm in a Wiley mill and analyzed as described in Van Cleve and Viereck (1972). Nutrient content of vegetation on aspen sites was obtained by multiplying average nutrient concentrations per site and per biomass compartment with the estimated biomass.

Aboveground annual biomass production and nutrient requirement of herbaceous species were estimated as being the total mass and nutrient content at the period of sample harvesting. Those of *Populus balsamifera* and *Picea glauca* seedlings of S sites were estimated as being the total mass and nutrient content of current twig and current foliage. In the aspen stands the annual biomass production and the aboveground nutrient requirement of aspen trees were estimated with two different approaches: (1)- as being the sum of current twig and leaf compartements (Van Cleve and Oliver 1982) (2)- using the equations of Ruark and Bockheim (1987) for *Populus tremuloides* in Wisconsin to assess the proportion of bole wood that can be considered as current growth for this age class and adding this value to the first estimate.

Leaf litter production and nutrient content

Leaf litter was collected from every site. Litter from major species of herbaceous plant was collected on standing plants after senescence while tree leaves were collected in litter trays. Three samples per species and per site-type were collected. Only nutrient concentrations were obtained from these samples. Estimates of litter production were made by multiplying these concentrations with the estimated foliar mass of each type of vegetation at maximum standing biomass. This calculation assumes no loss of mass during senescence and may overestimate flux of nutrient by this pathway (Prescott *et al.* 1989).

Statistical analysis

Because of the variety of methods used to determine plant biomass production, element requirement, and leaf litter production, means for vegetation types were not compared statistically. However, tissue nutrient concentrations were compared among species using analysis of variance and Tukey multiple range test (SAS 1985). When necessary, a logarythmic transformation of the data was performed to ensure homogeneity of variance.

Results obtained in this study are compared with the estimations of productivity and nutrient requirements of mature white spruce forests reported by Van Cleve *et al.* (1983) on sites adjacent to the ones used in the present study.

RESULTS

Annual aboveground biomass production and nutrient requirement

Aspen regeneration showed the greatest biomass production and nutrient requirement among the 14-year-old regenerating systems (Table 3.2). This vegetation type is followed by grass, undisturbed, and then the scraped type for biomass production and N, P and K requirements. Ca and Mg

Table 3.2
Aboveground annual biomass production and selected elements requirements in the 6 ecological types under study (g.m-2)

Ecological types	Biomass	N	P	K	Ca	Mg
Mature w.spruce (n=4)*	366±63	1.56±0.43	0.20±0.03	1.41±0.41	1.37±0.17	0.24±0.03
Harvested sites (year 1)	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
(year 14)						
Undisturbed						
(1)	154±33	1.67±0.45	0.29±0.12	1.75±0.47	2.36±0.54	0.44±0.13
(2)	162±42	1.72±0.37	0.33±0.07	2.13±0.75	2.24±0.54	0.25±0.03
Grass						
(1)	233±37	2.31±0.41	0.36±0.08	2.60±0.37	1.32±0.25	0.16±0.07
(2)	325±104	2.93±0.95	0.43±0.17	2.97±1.57	2.23±1.09	0.26±0.18
Scraped						
(1)	101±52	0.99±0.44	0.15±0.08	0.69±0.29	0.87±0.40	0.14±0.07
(2)	175±43	1.39±0.42	0.25±0.07	1.27±0.42	1.46±0.35	0.20±0.07
Aspen **						
(1)	308±36 870±85	5.51±0.76 6.80±0.87	0.86±0.11 1.21±0.14	3.60±0.41 4.86±0.51	3.54±0.40 6.00±0.60	0.74±0.08 0.86±0.08
(2)	454±72 1236±174	8.88±1.30 10.21±1.4	1.13±0.16 1.59±0.22	5.71±0.87 7.33±1.08	5.39±0.91 8.07±1.25	0.99±0.17 1.19±0.20
(3)	439±93 1320±415	7.86±1.71 9.46±2.22	0.96±0.22 1.37±0.34	5.40±1.18 7.22±1.76	5.12±1.05 6.08±1.18	1.07±0.22 1.26±0.28
Mature quaking aspen (n=2)*	565±199	6.14±2.12	0.74±0.27	3.17±0.79	3.95±1.59	0.77±0.44

* : From Van Cleve et al. (1983)

-wood production not included

** : First line : estimate #1
Second line: estimate #2

Note: Estimates are means ± SE.

requirement were relatively equivalent in all regenerating systems except on aspen sites were they were much greater. The 14 year old regenerating vegetation types showed a lower production of biomass than in mature white spruce except in the case of aspen sites and one grass site where the aboveground biomass production was roughly equivalent to the production of a mature white spruce forest (Van Cleve 1983). Nevertheless, the nutrient requirement of regenerating vegetation types was generally higher than in the mature forest except on sites where the forest floor had been scraped.

The N, P and K aboveground requirements were lower on the scraped sites, equivalent on undisturbed sites, twice as high in the regenerating grasses, and nearly five times greater in the aspen regeneration (using the most conservative estimate) than in the mature white spruce stands. Calcium and Mg aboveground requirements were, however, roughly equivalent on regenerating sites as compared to mature white spruce sites with the exception of the aspen sites, where they were from two to five times greater than on all other sites.

Proportions of biomass production and of total standing biomass per species and site is presented in table 3.3. The herbaceous layer of scraped sites, composed mostly of *Calamagrostis canadensis*, represented a large portion of the total biomass production. The understory of aspen sites, on the other hand, contributed only for 5 % of the total stand production.

The estimates of nutrient uptake per species and site are shown in table 3.4. The large variability of these values, attributed to the non-homogeneous composition of communities, makes it difficult to discern differences between species nutrient requirements on a given site. However, it is apparent that the uptake of nutrients by *Calamagrostis canadensis* represent a large portion of the total nutrient uptake in scraped and grass types.

Biomass and storage of nutrients in aboveground biomass

Aboveground plant biomass on aspen sites was from 10 to 40 times greater than on other 14-year-old regenerating sites (table 3.5). The storage of nutrients in aspen aboveground biomass was roughly equivalent to 10 times the amounts found

Table 3.3
Biomass production and total standing biomass per species on regenerating sites

Ecological types and species	Production		Biomass	
	(g.m-2)	% of total	(g.m-2)	% of total
Undisturbed				
(1)				
Epilobium angustifolium	104±41	68	104±41	68
Equisetum spp.	45±17	29	45±17	29
miscellaneous	4±6	3	4±6	3
(2)				
Epilobium angustifolium	104±30	64	104±30	64
Equisetum spp.	53±23	32	53±23	32
miscellaneous	5±4	3	5±4	3
Grass				
(1)				
Calamagrostis canadensis	165±54	70	165±54	70
Epilobium angustifolium	68±27	29	68±27	29
(2)				
Calamagrostis canadensis	196±49	60	196±49	60
Epilobium angustifolium	129±118	40	129±118	40
Scraped				
(1)				
Populus balsamifera	25±22	25	53±50	35
Picea glauca	18±31	18	39±43	26
Calamagrostis canadensis	55±15	55	55±15	37
micellaneous	3±5	3	3±5	2
(2)				
Populus balsamifera	15±17	9	45±53	14
Picea glauca	56±49	32	171±127	53
Calamagrostis canadensis	97±37	55	97±37	30
micellaneous	7±10	4	7±10	2
Aspen				
(1)				
Populus tremuloides *	827±80	95	3635±303	99
understory	43±10	5	43±10	1
(2)				
Populus tremuloides *	1201±144	97	5109±595	99
understory	36±16	3	36±16	1
(3)				
Populus tremuloides *	1273±412	96	5677±204	99
understory	47±25	4	47±25	1

Note: Estimates are means ± SE.
* : estimate 2 (see methods)

Table 3.4
Nutrient requirements per species on regenerating sites (g.m-2)

Ecological types and species	N	P	K	Ca	Mg
Undisturbed					
(1)					
Epi.	1.16±0.28	0.23±0.05	1.14±0.45	1.51±0.32	0.31±0.03
Equi.	0.43±0.25	0.05±0.04	0.52±0.54	0.63±0.40	0.12±0.03
mis.	0.08±0.07	0.01±0.01	0.09±0.06	0.22±0.12	0.01±0.03
(2)					
Epi.	1.14±0.28	0.24±0.05	1.25±0.45	1.31±0.32	0.15±0.03
Equi.	0.51±0.25	0.07±0.04	0.73±0.54	0.77±0.40	0.08±0.03
mis.	0.07±0.05	0.02±0.02	0.15±0.22	0.16±0.12	0.02±0.03
Grass					
(1)					
Cal.	1.45±0.30	0.19±0.04	1.53±0.25	0.57±0.24	0.02±0.03
Epi.	0.86±1.12	0.16±0.19	1.07±1.60	0.75±1.04	0.14±0.14
(2)					
Cal.	1.60±0.30	0.18±0.04	1.29±0.25	0.82±0.24	0.04±0.03
Epi.	1.33±1.12	0.25±0.19	1.69±1.60	1.41±1.04	0.22±0.14
Scraped					
(1)					
Pop. b.	0.43±0.27	0.07±0.04	0.23±0.13	0.39±0.31	0.09±0.07
Pi.	0.12±0.19	0.03±0.07	0.10±0.17	0.12±0.21	0.00±0.00
Cal.	0.40±0.11	0.05±0.01	0.33±0.09	0.34±0.10	0.05±0.01
mis.	0.04±0.05	0.00±0.00	0.03±0.05	0.02±0.01	0.00±0.00
(2)					
Pop. b.	0.16±0.20	0.02±0.03	0.11±0.13	0.15±0.20	0.02±0.03
Pi.	0.39±0.32	0.08±0.07	0.29±0.26	0.33±0.31	0.02±0.02
Cal.	0.81±0.32	0.15±0.06	0.85±0.42	0.95±0.34	0.15±0.07
mis.	0.04±0.03	0.00±0.00	0.03±0.03	0.03±0.02	0.00±0.00
Aspen					
(1)					
Pop. t.*	6.24±0.80	1.09±0.13	4.07±0.49	5.30±0.57	0.68±0.09
und.	0.57±0.03	0.12±0.02	0.79±0.10	0.70±0.10	0.18±0.05
(2)					
Pop. t.*	9.83±1.24	1.49±0.19	6.85±0.86	7.43±0.91	1.04±0.13
und.	0.38±0.11	0.09±0.03	0.47±0.16	0.66±0.31	0.15±0.06
(3)					
Pop. t.*	8.69±2.12	1.18±0.31	6.32±1.63	5.34±1.11	1.08±0.26
und.	0.79±0.54	0.18±0.15	0.90±0.60	0.72±0.40	0.17±0.11

Note: Estimates are means ± SE.

Legend:
Cal. : *Calamagrostis canadensis*
Epi. : *Epilobium angustifolium*
Equi. : *Equisetum spp.*
mis. : miscellaneous species
pi. : *Picea glauca*
Pop.b.: *Populus balsamifera*
Pop.t.: *Populus tremuloides*
und. : understory

* : estimate 2 (see methods)

Table 3.5
Standing crop of biomass and mass of selected elements in aboveground living vegetation of the 6 ecological types under study

Ecological types	biomass (kg.m-2)	N	P	K (g.m-2)	Ca	Mg
Mature w.spruce (n=4)*	17.4±4.3	25.0±5.5	3.10±0.98	23.05±3.10	67.2±13.4	4.51±1.50
Harvested sites (year 1)	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
(year 14)						
Undisturbed						
(1)	0.15±0.03	1.67±0.45	0.29±0.12	1.75±0.47	2.36±0.54	0.44±0.13
(2)	0.16±0.04	1.72±0.37	0.33±0.07	2.13±0.75	2.24±0.54	0.25±0.03
Grass						
(1)	0.23±0.04	2.31±0.41	0.36±0.08	2.60±0.37	1.32±0.25	0.16±0.07
(2)	0.32±0.10	2.93±0.95	0.43±0.17	2.97±1.57	2.23±1.09	0.26±0.18
Scraped						
(1)	0.15±0.10	1.21±0.60	0.20±0.12	0.89±0.49	1.20±0.63	0.15±0.07
(2)	0.32±0.14	2.03±0.79	0.36±0.12	1.89±0.64	2.34±0.77	0.22±0.06
Aspen						
(1)	3.68±0.30	13.2±1.2	2.94±0.26	11.2±0.9	18.3±1.5	1.47±0.11
(2)	5.14±0.61	16.9±2.1	3.87±0.45	15.5±1.9	21.5±2.62	2.19±0.28
(3)	5.72±2.05	17.6±4.9	3.37±1.02	16.3±4.9	21.6±6.4	2.14±0.55
Mature quaking aspen (n=2)*	11.02±6.4	25.9±12.3	2.71±1.04	18.1±8.1	65.3±26.9	5.14±3.32

* : From Van Cleve et al. (1983)
Note: Estimates are means ± SE.

in the other types. However, storage of N, K, Ca and Mg in mature white spruce aboveground biomass was from 50 to 200% greater than the amounts found in 14-year-old aspen sites. The stores of P in aboveground vegetation were roughly equivalent in mature white spruce and in 14-year-old aspen regeneration.

Foliar nutrient concentrations

No difference among sites was found in foliar nutrient concentrations within a given species. Therefore, replicates of each species were grouped and their elemental concentrations were compared (table 3.6). *Calamagrostis canadensis* leaves and *Picea glauca* current needles showed the lowest nutrient concentrations of all plant species and for all nutrients. The foliar Mg concentration of these two species was exceptionally low. Both *Populus* species, as well as the understory of aspen stands, showed high concentrations of major nutrients, especially N and P. *Epilobium angustifolium* showed relatively high concentrations of all nutrients except N. *Equisetum* species showed low concentrations of N and P but relatively high concentrations of K, Ca, and Mg.

Table 3.6
Concentrations of selected elements in foliar tissues of major species found on post-harvested sites
n = 9-30

Species	Percent dry mass				
	N	P	K	Ca	Mg
Pr>f	0.0001	0.0001	0.0001	0.0001	0.0001
Populus tremuloides	a 2.06±0.31	a 0.24±0.05	b 1.24±0.19	b 1.14±0.08	ab 0.23±0.05
balsamea	b 1.66±0.19	a 0.27±0.06	c 0.93±0.19	ab 1.39±0.35	ab 0.32±0.05
Understory-aspen	c 1.40±0.31	a 0.30±0.09	a 1.71±0.33	a 1.67±0.24	a 0.39±0.05
Epilobium angustifolium	d 1.17±0.15	a 0.23±0.05	b 1.33±0.33	b 1.29±0.22	b 0.23±0.08
Equisetum spp.	e 1.01±0.11	b 0.13±0.04	bc 1.27±0.47	a 1.66±0.28	b 0.23±0.08
Calamagrostis canadensis	ef 0.88±0.14	b 0.11±0.03	c 0.85±0.18	d 0.37±0.07	c 0.02±0.01
Picea glauca	f 0.75±0.11	b 0.14±0.01	d 0.41±0.06	c 0.62±0.08	c 0.02±0.01

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Leaf litter production and nutrient concentration

As with nutrient concentrations of fresh leaves, no difference was seen in the leaf litter nutrient concentrations of the same species among different sites. Consequently, samples from the same species were grouped to compare elemental concentrations between species (table 3.7). Nitrogen concentrations of leaf litter paralleled N concentrations of fresh foliar tissues. Both *Populus* species showed the highest concentrations of N in their leaf litter. Nevertheless, these species showed the greatest reabsorption of N (calculated as being the difference between green leaf concentrations and litter concentrations). *Populus* species were followed by *Epilobium*, and then by *Equisetum*, *Calamagrostis*, and *Picea* for N concentration. The same order of species was maintained for the comparison of P concentrations. However, differences in P concentrations were much larger. *Picea* and *Calamagrostis*, had leaf litter P concentrations 3 to 5 times lower than *Populus* species. Potassium concentrations were higher in *Epilobium* and both *Populus* species than in *Picea*, *Equisetum*, or *Calamagrostis*. *Picea* and *Calamagrostis* leaf litter showed low concentrations of Mg and Ca.

Table 3.7
Concentrations of selected elements in foliar litter of major species found on post-harvested sites
n = 6-12

Species	Percent dry mass				
	N	P	K	Ca	Mg
Pr>f	0.0001	0.0001	0.0001	0.0001	0.0001
Populus tremuloides	a 0.84±0.08	a 0.19±0.02	a 0.85±0.10	d 1.18±0.12	a 0.23±0.05
balsamifera	b 0.67±0.04	a 0.18±0.02	b 0.75±0.13	bc 1.47±0.16	a 0.21±0.04
Epilobium angustifolium	c 0.61±0.05	b 0.11±0.02	ab 0.78±0.14	c 1.38±0.19	a 0.28±0.07
Equisetum spp.	cd 0.58±0.04	d 0.03±0.01	c 0.36±0.10	b 1.56±0.17	a 0.21±0.03
Calamagrostis canadensis	de 0.54±0.05	d 0.04±0.01	d 0.176±0.06	e 0.50±0.09	c 0.02±0.01
Picea glauca	e 0.51±0.04	c 0.07±0.01	d 0.22±0.06	a 1.74±0.13	c 0.02±0.01

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

The total amount of nutrient returned in litterfall (table 3.8) in all 14-year-old regenerating systems, except for the three aspen sites and one grass site, approached the values found in mature white spruce with the exception of K which was returned in much greater amounts on regenerating sites. However, because of unequal leaching periods between senescence and sample collection dates, it is difficult to draw conclusions about K content of litterfall. On aspen sites, amounts of nutrients returned by litterfall were, on the average, twice as important as amount estimated for other regenerating systems and in mature white spruce. The single exception was P which was returned on aspen sites in quantities ranging from 5 to 7 times the amounts estimated for other systems.

Table 3.8
Foliar litter nutrient content on regenerating sites (g.m-2)

Ecological types	MASS	N	P	K	Ca	Mg
UNDISTURBED						
(1)	149±32	0.89±0.19	0.13±0.03	0.97±0.20	2.14±0.45	0.39±0.21
(2)	157±40	0.94±0.24	0.13±0.03	1.00±0.25	2.26±0.57	0.40±0.25
GRASS						
(1)	233±37	1.31±0.21	0.14±0.02	0.81±0.13	1.76±0.28	0.22±0.04
(2)	325±104	1.84±0.59	0.22±0.02	1.34±0.43	2.76±0.88	0.40±0.13
SCRAPED						
(1)	94±46	0.54±0.25	0.08±0.04	0.31±0.15	0.98±0.44	0.07±0.03
(2)	149±42	0.80±0.22	0.08±0.02	0.32±0.09	1.37±0.38	0.04±0.01
ASPEN						
(1)	231±34	1.94±0.29	0.44±0.07	1.96±0.29	2.78±0.42	0.53±0.08
(2)	370±48	3.11±0.40	0.70±0.09	3.14±0.41	4.37±0.57	0.85±0.11
(3)	340±77	2.86±0.66	0.65±0.15	2.89±0.23	4.01±0.92	0.78±0.18
Mature white spruce site*	155±77	0.93±0.28	0.10 ±0.0	0.33±0.08	2.56±0.77	0.19±0.06

* from VanCleve et al. (1983)

Note: Estimates are means ± SE.

DISCUSSION

1-Elemental concentrations in leaf tissue and nutrient use efficiency of regenerating species

Herbaceous species as well as *Populus* had higher foliar element concentrations than white spruce and perennial grass. This factor, together with a high production of foliage compared to woody tissue, make these species efficient in preventing nutrient losses.

In other forest ecosystems herbaceous species have been found to be efficient for the retention of K because they have higher K foliar concentrations than woody species (Boring et al. 1981; Siccama and Bormann 1970). In the present study there was no clear difference between foliar K concentrations of herbaceous plants and deciduous trees. However, on aspen sites the understory showed higher foliar K concentrations than the overstory.

The calculations of N and P growth efficiency (calculated as being the amount of aboveground biomass (table 3.2) produced per amount of element lost in leaf litterfall (table 3.8), NUE) showed 14-year-old aspen stands to be the most efficient regenerating type (table 3.9). This phenomenon is surprising since herbaceous species usually have higher photosynthetic rates than woody species (Bazzaz 1979). However, the high foliar N concentrations found in aspen could promote a high photosynthetic NUE because in the leaf more N is diverted to photosynthetic components than to structural components (Field and Mooney 1986). An increase in foliar N concentration both within and among species promotes a higher photosynthetic NUE (Chapin 1989).

2- Immobilization of elements in biomass

Storage of nutrients in aboveground living biomass was greater in aspen than in all other regenerating types because of greater production of perennial tissues. However, storage of nutrients in the grass community might have been underestimated in this study because belowground biomass was not measured. Other studies have shown that considerable amounts of N are recycled through

Table 3.9
Nitrogen and phosphorus growth efficiency on regenerating sites (g wood + leaves + twigs produced g-1 nutrient lost in litterfall)

Ecological types	N	P
UNDISTURBED		
(1)	173	1185
(2)	172	1246
GRASS		
(1)	178	1664
(2)	177	1477
SCRAPED		
(1)	111	777
(2)	155	1113
ASPEN		
(1)	448	1977
(2)	397	1766
(3)	462	2031

belowground transfer in perennial grass communities (Clark 1977).

Nutrients that are stored in living biomass are preserved from ecosystem loss through leaching. However, they are also made unavailable to other, sometime more desirable, plant species. The large proportion of nutrients stored in *Calamagrostis canadensis* on grass and scraped sites may be detrimental to the growth of commercial tree species.

The living vegetation is often a major storage compartment of K in forest ecosystems (Pearson et al. 1987; Van Cleve et al. 1983). A rapid recovery of the storage of K in biomass might prevent its loss through leaching. On the other hand, high storage of an element in vegetation may reduce the quantity of this element in available form in the soil. A few studies have shown that accumulation of Ca in aspen stands reduces the quantity of this element in available form in the soil (Alban 1982; Alban et al. 1978; Cromack and Monk 1975; Ruark and Bockheim 1988, Yount 1975). However, the large reserves of Ca in local soils probably forestalls this potential problem.

3-Strategy for colonization

On post-harvested sites soil conditions determine, in a large measure, the success of a strategy of plant colonization. Low density colonization by annual plants is seen on undisturbed surfaces; disturbance of the forest floor seems to favor grass invasion; given that vegetative propagules of aspen are present in the soil and not destroyed by scarification, an aspen clump may develop by sprouting; while scraping the forest floor allows the site to be sparsely colonized by a variety of plants. These observations are consistent with results reported by Zasada (1986). The rapid development of an aspen stand by vegetative expansion appears to be the most successful strategy for the recovery of plant production, nutrient storage in biomass and nutrient cycling rates. This sprouting strategy has been reported to be the most successful mechanism of colonization in other post-harvested forest ecosystems (e.g. Boring *et al.* 1981).

4-Recovery of nutrient cycling

Fourteen years after clear-cutting rates of nutrient cycling approached values found in mature white spruce forest except on sites colonized by aspen where they were much greater. Aspen colonization provides: (1)- greater carbon fixation both per unit area and per unit weight of N or P, (2)- greater accumulation of nutrients in biomass, (3)- greater uptake of nutrients from the soil, but also, (4)- greater return of nutrients in litterfall. The quantity of nutrients returned to the soil in litterfall and the decomposability of litter (which was not addressed in this study) from early successional species may promote faster nutrient cycling rates (Vitousek and Walker 1987).

The 14-year-old regenerating sites represent the aggradation phase of vegetation development after disturbance (Bormann and Likens 1979). During this phase there is an accumulation of biomass and nutrients in living biomass. The different rates of biomass production, nutrient accumulation in biomass, nutrient uptake, and nutrient return in litterfall among the 14-year-old ecological types of the present study, suggest that these processes are not evolving at the same rates among communities or that some vegetation types may have reached a plateau in their aggradation phase. Grass communities are fully stocked; without a replacement by species of greater stature, these communities may exhibit the fullest potential of their biomass production. If, on these sites, invasion by woody species is inhibited, as it has been observed in other perennial grass communities (Horsley 1977; Rice 1972), the aggradation phase of ecosystem development could be periodically suppressed. On the other hand, the aggradation phase of an aspen stand may last up to 70 years (Ruark and Bockheim 1988). Manipulation of site conditions to favor colonization by specific early successional species may allow the manager control of ecosystem development and nutrient dynamics.

CHAPTER 4

MEASUREMENT OF NUTRIENT AVAILABILITY ON HARVESTED SITES WITH ION EXCHANGE RESIN BAGS

ABSTRACT

Ion exchange resin (IER) bags were used to measure ion leaching in soils on undisturbed white spruce sites, on a recently harvested site, and on 14-year-old regenerating sites colonized by different plant communities. A pulse of nitrate, phosphate, and sulfate was seen, during the spring, on the recently harvested site. No other differences were observed between sites. Poor correlations were obtained between conventional soil nutrient availability indices and ion exchange resin bag measurements.

INTRODUCTION

The assessment of soil nutrient availability by standard laboratory chemical extraction methods causes several conceptual problems. The supply of nutrient to plant roots can be described as a flux which varies through time (Krause and Ramlal 1987; Ingestad 1987). Therefore, the instantaneous measurement of nutrient availability may generate an unreliable estimate of the nutrient supply to plant roots over the course of a growing season. Furthermore, chemical extraction methods are usually not sensitive to site variables such as soil pH, soil temperature, moisture availability, and plant and microbial competition for inorganic nutrients, factors which greatly affect nutrient availability to plants. The ion exchange resin (IER) bag technique, introduced by Binkley and Matson (1983), has in theory, the advantage of measuring nutrient availability *in situ* with minimal disturbance to the soil. It also has the advantage, in contrast to the use of lysimeters, of permitting the measurement of ion fluxes during periods of low moisture availability, which are frequent in the semi-arid climate of interior Alaska. The IER bag technique was successfully used in an arid environment by Lajhta (1988).

The IER bag technique is not without problems. As mentioned by Krause and Ramlal (1987), there are a number of unknowns concerning the mechanisms of ion sorption by resin bags in the soil environment that do not permit a quantitative assessment of nutrient fluxes.

The objectives of this study were: (1)- to assess, using the IER bag technique, the seasonal fluxes of elements in the soil profile of mature white spruce sites as well as post-harvested sites of different ages and vegetation composition,and (2)- to compare these values with conventional nutrient availability measurements. Since IER bags have been shown to be poor competitors with plant roots and microbes (Binkley 1984b), the amount of ion sorbed by resin bags may also be used as an index of the leakiness of the ecosystem to nutrient fluxes.

MATERIALS AND METHODS

Cation and anion exchange resin bags were prepared, in general, as described in Krause and Ramlal (1987). The single change was that an amount providing 5 *u* mol(-) of anion exchange resin was inserted in each anion resin bag instead of 10 to reduce the thickness of the bag and thus minimize the textural discontinuity between soil particles and the resin beads. The charge of the resin placed in cation exchange resin bags was of 10 u mol (+) per bag. Bio-rad AG3-X4A cation exchange resin and Biorex 70 anion exchange resin (both marketed by Bio-rad Laboratories Ltd.) were selected for this study because of their efficiency to remove common nutrient ions from solution as tested by Krause and Ramlal (1987). The cation exchange resin was used in the Na+ form which is the form in which the product is supplied. The anion resin was converted from the chloride to the bicarbonate form as described by Sibbesen (1978).

A set of IER bags was placed in the field in early June 1988. A description of the sites and of the sampling design is provided in chapter 1. At every sampling unit a hole was dug with a 15 cm diameter corer and 4 resin bags were installed. A cation and an anion exchange resin bag was inserted at mid-depth in the forest floor and another cation and anion exchange resin bag was inserted at a depth of 5 cm in the mineral soil. Cation and anion exchange resin bags were placed on opposite sides of the core hole and the core was placed back in the hole. Six weeks later, in mid-July, the first set was retrieved from the field and replaced by a fresh set which was left in the field for six weeks. When retrieved from the soil, in mid-September, the last set of bags was installed and left over-winter to be removed in late May, 1989. When removed from the soil, resin bags were placed in individual plastic bags and then frozen until washed and analyzed.

At the time of analysis bags were thawed, thoroughly washed with dionized water, and then eluted as described by Krause and Ramlal (1987). Anion bags were eluted with 50 ml of 0.05 M $NaHCO_3$ and cation bags with 50 ml of 0.1 M HCl. The eluant from anion exchange resin bags was analyzed for NO_3^-, $H_2PO_4^-$, and SO_4^{2-} on an ion chromatograph (Dionnex series 4000i). The eluant from cation exchange resin bags was analyzed for NH_4^+ on an autoanalyser (Technicon 1976), for Ca^{2+} and Mg^{2+} on a Beckman direct current plasma spectrophotometer, and for K^+ on a Perkin Eklmer atomic absorption spectrometer.

Other methods of nutrient availability assessment are described in chapter 2.

Cation and anion data were subjected to an analysis of variance per soil horizon with site-type and season as fixed variables. Analysis of variance were also performed for each element per season and soil horizon to test differences among site-type. The Waller-Duncan test was used for mean separation (Waller and Duncan 1969). When necessary, analysis of variance were performed on a logarithmic transformation of the data to ensure homogeneity of variance. Finally, correlations between resin bag estimates and conventional soil nutrient availability indices were performed per soil horizon and season. All statistical analysis were performed on SAS (1985).

RESULTS AND DISCUSSION

The effect of season and site-type was significant for all anions and cations sorbed by the resins, both in the forest floor and in the mineral soil (table 4.1). The effect of season was always more important than the effect of site-type. The large number of significant interactions between season and site-type complicates the interpretation of the results.

Table 4.1
Effect of site-type and season on ion sorption by resin bags (F-ratio)

resin bag determination	site-type		season		type*season	
surface soil horizon						
NO3-N	7.30	***	30.25	***	8.71	***
H2PO4-P	8.50	***	44.23	***	8.23	***
SO42-S	5.61	***	34.40	***	7.08	***
NH4+N	3.38	***	9.90	***	1.27	
K+	5.11	***	111.43	***	1.20	
CA2+	1.84	*	47.47	***	2.85	***
Mg2+	1.87	*	41.02	***	2.75	***
mineral soil						
NO3-N	2.19	*	13.16	***	1.73	
H2PO4-P	3.05	***	8.03	***	3.43	***
SO42-S	5.27	***	16.84	***	0.90	
NH4+N	7.80	***	21.01	***	2.19	**
K+	3.75	***	48.44	***	1.00	
CA2+	3.23	***	26.88	***	1.22	
Mg2+	3.65	***	31.44	***	1.65	*

*,**,*** significant at $p<0.05$, $p<0.01$, $p<0.001$ respectively

When an analysis of variance was performed per season and soil horizon (tables 4.2-4.8), clear differences among ecological types were only seen during the spring, the period of maximum water availability. At this period, the forest floor of the recently harvested site showed significantly higher concentrations of the three anions measured (NO_3^-, $H_2PO_4^-$, SO_4^{2-}) than on any other site. The analysis of variance was performed on a logarithmic transformation of the data to insure homogeneity of variance. No differences among sites were seen with any other ions measured, regardless of season. Van Cleve and Dyrness (1983), using lysimeters, found that the fluxes of Ca and Mg were increased after disturbance in a black spruce forest within the same region. They found no difference in the fluxes of phosphorus and potassium. The differences in these observations may however be due to the sensitivity of the procedure used.

Increased nitrate leaching after disturbance is a commonly observed phenomenon in forest ecosystems (Vitousek *et al.* 1979, 1982) and can account for substantial N losses if plant growth is retarded (Bormann and Likens 1979). The increased amount of nitrate sorbed by the resins on recently

Table 4.2
Nitrate sorption by ion exchange resin bags
(ug.bag-1)

Ecological types	surface soil			mineral soil		
	spring	summer	fall	spring	summer	fall
Pr>F	0.0001	0.0005	0.3522	0.2069	0.7079	0.1006
Mature w.spruce (1)	b 6±3	cd 4±4	a 10±2	a 9±10	a 10±3	a 10±4
(2)	b 5±1	bcd 6±4	a 8±2	a 6±4	a 13±9	a 9±5
Harvested sites (year 1)	a 784±617	bcd 6±4	a 65±130	a 626±946	a 19±25	a 71±120
(year 14)						
Undisturbed (1)	b 138±123	bcd 6±7	a 20±20	a 175±127	a 11±14	a 23±22
(2)	b 131±111	abcd 7±4	a 12±13	a 172±124	a 6±4	a 10±8
Grass (1)	b 41±49	abcd 7±4	a 16±13	a 220±163	a 9±4	a 13±10
(2)	b 56±56	abc 8±4	a 10±7	a 182±140	a 13±6	a 9±3
Scraped (1)	b 2±2	abcd 7±4	a 8±1	a 10±8	a 13±7	a 12±4
(2)	b 3±2	a 11±3	a 13±5	a 6±5	a 10±4	a 8±2
Aspen (1)	b 36±22	ab 10±5	a 9±8	a 248±162	a 13±3	a 13±4
(2)	b 47±60	ab 10±3	a 6±2	a 220±142	a 12±2	a 10±2
(3)	b 10±8	ab 10±5	a 15±16	a 164±80	a 10±5	a 10±4

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 4.3
Phosphate sorption by ion exchange resin bags
(ug.bag-1)

Ecological	surface soil			mineral soil		
types	spring	summer	fall	spring	summer	fall
Pr>f	0.0001	0.0036	0.0001	0.0417	0.0001	0.0001
Mature						
w.spruce	c	b	b	b	c	b
(1)	160±171	3±7	195±152	81±139	5±4	36±86
	c	b	b	b	c	b
(2)	100±114	7±9	98±53	36±21	20±30	9±11
Harvested	a	b	a	b	c	a
sites	4188±3006	100±71	551±350	68±60	18±19	107±62
(year 1)						
(year 14)						
Undisturbed	bc	b	b	b	c	b
(1)	719±980	31±29	93±124	56±102	5±8	37±49
	bc	b	b	b	c	b
(2)	886±1279	43±20	65±70	98±87	6±8	51±35
Grass	c	b	b	a	c	b
(1)	157±87	56±51	273±393	151±4	24±26	23±27
	c	b	b	b	bc	b
(2)	265±169	83±80	101±106	146±385	42±19	7±12
Scraped	c	b	b	b	c	b
(1)	197±246	19±20	25±40	6±8	24±47	4±7
	c	b	b	b	c	b
(2)	106±141	10±15	32±60	57±127	7±14	6±7
Aspen	ab	b	b	b	ab	b
(1)	1600±1350	96±61	120±137	59±99	68±64	13±9
	bc	b	b	b	c	b
(2)	404±190	16±14	258±312	51±95	15±23	29±20
	ab	a	b	b	a	b
(3)	1500±900	255±358	218±177	53±69	89±75	10±3

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 4.4
Sulfate sorption by ion exchange resin bags

Ecological types	surface soil spring	surface soil summer	surface soil fall	mineral soil spring	mineral soil summer	mineral soil fall
Pr>f	0.0001	0.0730	0.0001	0.3266	0.0001	0.0001
Mature w.spruce	b	a	ab	a	b	c
(1)	105±24	35±18	102±30	128±64	63±14	53±21
	b	a	cd	a	b	ab
(2)	89±84	58±16	60±25	103±46	73±16	150±166
Harvested	a	a	a	a	a	a
sites (year 1)	1923±1610	78±64	116±64	131±102	209±129	185±88
(year 14)						
Undisturbed	b	a	cd	a	b	c
(1)	234±318	41±7	36±10	187±95	47±14	52±23
	b	a	cd	a	b	c
(2)	360±409	38±10	40±14	103±96	45±11	50±7
Grass	b	a	d	a	b	c
(1)	60±26	47±13	28±10	110±68	49±6	39±12
	b	a	d	a	b	c
(2)	130±117	46±12	33±9	160±94	59±12	41±3
Scraped	b	a	cd	a	b	b
(1)	555±645	60±21	61±14	109±120	71±15	73±25
	b	a	cd	a	b	b
(2)	226±77	52±7	55±2	76±22	56±12	85±99
Aspen	b	a	cd	a	b	b
(1)	187±153	55±15	56±10	210±175	58±7	86±32
	b	a	bc	a	b	b
(2)	87±35	44±6	74±26	161±89	64±18	92±12
	b	a	cd	a	b	b
(3)	125±100	46±15	61±14	195±155	76±33	74±42

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 4.5
Ammonium sorption by ion exchange resin bags (ug.bag-1)

Ecological types	surface soil spring	surface soil summer	surface soil fall	mineral soil spring	mineral soil summer	mineral soil fall
Pr>f	0.0390	0.0227	0.0259	0.0059	0.0087	0.0001
Mature						
w.spruce	ab	b	bc	b	ab	c
(1)	13±7	19±8	31±46	8±7	14±6	10±3
	a	b	bc	b	ab	c
(2)	22±28	22±14	34±29	5±2	15±7	14±3
Harvested	a	ab	ab	a	ab	a
sites	23±18	51±69	155±181	22±20	18±9	56±46
(year 1)						
(year 14)						
Undisturbed	ab	b	bc	ab	ab	c
(1)	10±8	34±25	37±35	11±7	14±6	13±7
	ab	b	bc	ab	b	c
(2)	20±11	30±11	29±7	10±4	10±2	9±3
Grass	a	a	abc	ab	a	ab
(1)	25±16	91±90	97±146	12±9	24±19	44±29
	ab	b	abc	ab	ab	bc
(2)	19±9	22±16	67±69	10±4	14±5	30±15
Scraped	b	b	c	b	b	c
(1)	3±1	13±5	11±4	2±1	9±3	12±6
	b	b	c	b	b	c
(2)	3±1	17±12	13±3	3±3	8±3	16±10
Aspen	a	b	a	b	b	bc
(1)	25±14	19±6	188±251	4±4	12±3	18±3
	ab	b	abc	b	ab	bc
(2)	13±2	23±9	71±50	6±4	14±7	23±12
	ab	ab	abc	b	ab	bc
(3)	23±10	54±54	67±36	5±4	17±2	20±7

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 4.6
Potassium sorption by ion exchange resin bags (ug.bag-1)

Ecological types	surface soil spring	summer	fall	mineral soil spring	summer	fall
Pr>f	0.0812	0.0001	0.0909	0.3197	0.1429	0.0414
Mature						
w.spruce	a	cd	a	a	a	abc
(1)	929±243	503±297	2046±434	141±111	298±144	661±448
	a	a	a	a	a	bc
(2)	867±507	1645±992	2090±200	100±51	550±293	600±50
Harvested	a	abc	a	a	a	abc
sites	843±470	1094±551	1969±533	235±130	480±442	1053±493
(year 1)						
(year 14)						
Undisturbed	a	bcd	a	a	a	abc
(1)	668±609	862±324	1799±642	387±287	235±151	921±711
	a	bcd	a	a	a	bc
(2)	828±422	841±498	1631±731	381±311	129±111	617±315
Grass	a	ab	a	a	a	ab
(1)	1591±998	1251±416	1922±615	194±109	593±578	1140±709
	a	abc	a	a	a	bc
(2)	829±460	1095±687	2001±330	312±169	406±392	639±311
Scraped	a	d	a	a	a	abc
(1)	223±103	295±114	1280±453	110±63	258±138	723±460
	a	d	a	a	a	c
(2)	340±168	332±178	1655±654	72±66	126±52	465±164
Aspen	a	bcd	a	a	a	a
(1)	597±479	745±804	1898±742	213±75	606±673	1253±661
	a	bcd	a	a	a	c
(2)	392±131	589±177	2086±136	188±174	433±481	513±343
	a	cd	a	a	a	abc
(3)	412±144	514±310	1954±435	206±93	434±232	665±238

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different ($p<0.05$).

Table 4.7
Calcium sorption by ion exchange resin bags
(mg.bag-1)

Ecological types	surface soil			mineral soil		
	spring	summer	fall	spring	summer	fall
Pr>f	0.0875	0.0367	0.8653	0.0543	0.0001	0.3702
Mature						
w.spruce	a	b	a	a	b	a
(1)	2.6±2.1	1.3±0.6	3.3±2.4	1.6±0.6	2.5±0.8	4.1±1.5
	a	ab	a	a	b	a
(2)	1.3±0.5	2.5±1.7	4.1±1.9	2.0±0.5	2.2±0.7	3.2±1.8
Harvested	a	a	a	a	b	a
sites	10.2±5.7	2.7±1.4	4.6±2.1	3.6±1.8	2.7±1.1	4.6±1.8
(year 1)						
(year 14)						
Undisturbed	a	ab	a	a	b	a
(1)	16.8±14.1	1.7±0.7	3.9±2.0	5.5±1.6	2.0±0.8	5.5±3.5
	a	ab	a	a	b	a
(2)	5.3±7.1	2.5±1.2	4.1±2.5	1.9±4.7	2.9±1.0	6.8±0.6
Grass	a	ab	a	a	b	a
(1)	11.1±13.3	2.0±0.8	4.6±3.7	4.3±0.7	2.2±1.0	4.5±3.6
	a	ab	a	a	b	a
(2)	4.5±4.4	2.0±1.6	3.3±2.3	3.3±1.9	2.3±0.3	4.8±3.9
Scraped	a	ab	a	a	a	a
(1)	5.6±2.6	2.0±1.0	4.9±1.7	3.5±2.6	5.1±2.4	5.8±1.8
	a	ab	a	a	b	a
(2)	5.6±2.0	1.8±0.8	4.5±1.3	4.7±0.9	3.1±0.9	5.0±2.6
Aspen	a	b	a	a	b	a
(1)	9.5±7.1	1.3±0.8	4.4±1.8	4.7±0.6	1.8±0.9	4.8±1.1
	a	ab	a	a	b	a
(2)	10.0±3.2	1.6±0.7	3.4±1.5	3.7±0.9	2.7±1.3	3.9±1.2
	a	b	a	a	b	a
(3)	8.0±2.6	1.3±0.5	3.4±1.4	4.1±1.1	3.1±0.7	4.0±1.6

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different (p<0.05).

Table 4.8
Magnesium sorption by ion exchange resin bags
(ug.bag-1)

Ecological types	surface soil			mineral soil		
	spring	summer	fall	spring	summer	fall
Pr>f	0.0864	0.0223	0.0008	0.1007	0.0012	0.0148
Mature						
w.spruce	a	ab	bc	a	b	abc
(1)	380±348	210±58	665±315	500±253	1013±490	1760±849
	a	ab	c	a	b	abc
(2)	280±104	336±224	511±261	770±131	926±220	1251±613
Harvested	a	ab	bc	a	b	bc
sites	1355±731	374±162	738±388	805±330	734±314	1178±537
(year 1)						
(year 14)						
Undisturbed	a	ab	c	a	b	abc
(1)	1580±1844	224±111	523±273	730±157	524±268	1326±733
	a	ab	c	a	b	ab
(2)	790±876	310±123	455±228	940±532	685±266	2061±556
Grass	a	ab	bc	a	b	bc
(1)	1880±2302	287±100	718±561	670±349	618±390	1186±805
	a	ab	c	a	b	c
(2)	690±567	327±211	531±282	820±454	728±596	926±736
Scraped	a	a	a	a	a	a
(1)	850±281	491±267	1306±612	500±141	1621±1117	2103±110
	a	ab	ab	a	b	abc
(2)	590±376	419±184	1149±298	634±161	703±239	1408±762
Aspen	a	ab	abc	a	b	abc
(1)	1830±1048	305±274	955±456	940±164	488±252	1219±453
	a	b	c	a	b	c
(2)	1740±373	266±178	615±402	890±205	830±600	1006±568
	a	b	bc	a	b	c
(3)	1770±440	249±94	687±254	825±174	812±286	994±466

Note: Estimates are means ± SE. In each column, values assigned to a same letter are not significantly different (p<0.05).

disturbed sites is also consistent with the results from buried bag incubations (Chapter 2). Fahey *et al.* (1985) observed, in a climate of similar summer precipitation, that N transfer to the mineral soil was restricted to the snowmelt period.

Increased phosphate leaching after forest harvesting has been seen in other studies (Krause and Ramlal 1987). The seasonal pattern of P availability, showing a pulse at the beginning of the growing season was also observed in a tundra ecosystem (Chapin *et al.* 1978) and in a grassland on a podzolic soil (Gutpa and Rorison 1974). This seasonal pattern was attributed, in the tundra ecosystem, to a crash in microbial populations during the spring (Chapin *et al.* 1978). Other factors could explain this pattern in the present study. For example, high water availability during snowmelt may permit ionic movements through the soil profile as well as in the resin bags. These movements should be greatly restricted during the rest of the growing season due to low amounts of rainfall and drier soils.

The coarser texture of resin beads, compared to soil particles, may also restrict the flow of water and nutrients to resin bags during periods when the soil is not saturated. Therefore, actual transfer of nutrients and water in the soil when it is moist but not wet may not be detected with IER bag measurement.

The increased leaching of sulfate on recently disturbed sites was not, to the knowledge of the author, seen in other studies. No increase in sulfate leaching was measured in a harvested coniferous forest (Krause and Ramlal, 1987), nor in a logged Douglas-fir stand in Oregon (Martin and Harr 1988). Mitchell *et al.* (1989) even measured a decline in sulfate concentrations following harvesting due to a reduction of soil pH and a greater sulfate adsorption.

Leaching of anions appears to return to previous levels rapidly after disturbance, since amounts of anions sorbed by the resins were not different in 14-year-old sites than in mature forests. The increased availability of anions observed on recently disturbed sites may not be of great consequence for ecosystem nutrient budgets since little flow reaches even as deep as one meter in these soils due to the low precipitation regime (Van Cleve and Dyrness 1985).

IER bag measurements were poorly correlated with other nutrient availability assessments (table 4.9). Only nitrate sorbed by IER bags seems to correlate at a highly significant level (even when scraped sites were not included in the calculation), with laboratory or field incubation measurements. The high mobility of nitrate in soil may facilitate its transfer to resin bags. The lack of agreement between methods for other elements may be caused, as explained previously, by the restricted movement of water to the resin bags due to textural discontinuity and low soil moisture content. It could also be caused, as suggested by a laboratory experiment (appendix 1), by the limited *in situ* capacity of resin bags to accumulate nutrients over a period of time.

Table 4.9
Correlation coefficients between resin bag determinations and other soil nutrient availability assessments
R(p) N=85

a) soil surface horizon

resin bag measurement	other soil nutrient availability assessments			
season-1			laboratory incubation	
NO3-	buried bag NO3-	0.01(0.94)	NO3	0.18 (0.18)
NH4+	bur. bag total N	0.07(0.61)	total N	0.22 (0.10)
NO3 + NH4	bur. bag total N	0.07(0.58)	total N	0.24 (0.06)
H2PO4-	extractable P	0.22(0.04)*		
K+	exchangeable K	0.04(0.71)		
Ca++	exchangeable Ca	0.15(0.15)		
Mg++	exchangeable Mg	-0.20(0.05)		
season-2			laboratory incubation	
NO3-	buried bag NO3-	0.52(0.0001)***	NO3	0.23(0.08)
NH4+	bur. bag total N	0.32(0.013)*	total N	0.47(0.0002)***
NO3 + NH4	bur. bag total N	0.53(0.0001)***	total N	0.43(0.0008)***
H2PO4-	extractable P	0.21(0.0386)*		
K+	exchangeable K	0.29(0.004)**		
Ca++	exchangeable Ca	-0.007(0.95)		
Mg++	exchangeable Mg	-0.27(0.008)**		
season-3			laboratory incubation	
NO3-	buried bag NO3-	0.57(0.0001)***	NO3	0.35(0.007)**
NH4+	bur. bag total N	0.22(0.09)	total N	-0.01(0.99)
NO3 + NH4	bur. bag total N	0.50(0.0001)***	total N	0.22(0.10)
H2PO4-	extractable P	0.27(0.034)*		
K+	exchangeable K	0.09(0.45)		
Ca++	exchangeable Ca	0.13(0.33)		
Mg++	exchangeable Mg	-0.02(0.89)		

*, **, *** **significant** at $p<0.05$, $p<0.01$, p,0.001 respectively

Table 4.9
Correlation coefficients between resin bag determinations and other soil nutrient availability assessments
R(p) N=85

b) mineral soil

resin bag measurement	other soil nutrient availability assessments	
season-1		
NO3-	buried bag NO3-	0.06 (0.65)
NH4+	bur. bag total N	0.12 (0.35)
NO3 + NH4	bur. bag total N	0.12 (0.36)
H2PO4-	extractable P	0.07 (0.50)
K+	exchangeable K	-0.06 (0.58)
Ca++	exchangeable Ca	0.05 (0.59)
Mg++	exchangeable Mg	0.29 (0.004)**
season-2		
NO3-	buried bag NO3-	0.32 (0.014)*
NH4+	bur. bag total N	0.19 (0.14)
NO3 + NH4	bur. bag total N	0.26 (0.044)*
H2PO4-	extractable P	-0.06 (0.56)
K+	exchangeable K	0.13 (0.22)
Ca++	exchangeable Ca	-0.02 (0.81)
Mg++	exchangeable Mg	0.31 (0.002)**
season-3		
NO3-	buried bag NO3-	0.25 (0.054)
NH4+	bur. bag total N	0.30 (0.02)*
NO3 + NH4	bur. bag total N	0.30 (0.02)*
H2PO4-	extractable P	0.03 (0.82)
K+	exchangeable K	0.27 (0.03)*
Ca++	exchangeable Ca	-0.06 (0.65)
Mg++	exchangeable Mg	-0.01 (0.93)

*, **, *** significant at $p<0.05$, $p<0.01$, p,0.001 respectively

CHAPTER 5

SOIL-PLANT INTERACTIONS

INTRODUCTION

Differences in N mineralization rates were found among 14-year-old post-harvested sites colonized by different plant communities as determined by laboratory and field soil testing (chapter 2). The estimation of nutrient uptake on regenerating sites (chapter 3) also showed major differences among ecological types.

This chapter contains a discussion about the interactions between the various methods used in the present study to estimate nutrient fluxes.

1-Comparison between indices of N cycling rates

No reference method is known to accurately measure N mineralization rates *in situ* (Raison *et al.* 1987). Five different methods were used to describe N dynamics in the present study. Each method has its own perspective and assumptions:

1-Estimation of aboveground requirement for N by plants growing in the field This method generates no disturbance to the soil. Soil microbial populations, plant-microbe interactions in the rhizosphere, as well as the soil microclimate are not altered. Also, this method requires no assumption concerning the definition of plant-available nutrient as chemical extraction methods do (An element absorbed by vegetation is available). However, the non-estimation of belowground N requirements, especially if across sites these quantities are not proportional to aboveground requirements, could give unreliable estimates of soil N mineralization rates (Chapin and Van Cleve, 1989). Also, the non-estimation of internal N cycling within the plant could have a similar effect. However, these quantities should be very low for young plant communities. Another factor, the different composition of plant communities across sites, could provide an unreliable estimate of the estimation of soil N mineralization rate. It is possible that differences among sites could be caused by the different ability of species to acquire nutrient and not to the supplying capacity of the soil.

2-Greenhouse bioassay With the use of this method nutrients are extracted from a soil sample by an indicator plant. Thus, the plant's ability to extract nutrient from the soil is constant among treatments. This method is also sensitive to biological factors such as mycorrhizal formation (Perry *et al.* 1982). Moreover, since all nutrients are present the growth of planted seedlings represent an integration of the nutritional quality of the substrate. As used in the present study this procedure could, however, generate unreliable estimates of field N mineralization rates because of disturbance to the substrate and because field microclimatic conditions are not maintained. By the use of climate control facilities, this limitation could be partially overcome. Raison *et al.* (1987) have shown that disturbance to the soil can either increase or decrease soil N mineralization rates.

3-Laboratory N mineralization estimates As used in the present study, this method has the same disadvantages of the previous method of not representing field microclimatic conditions (although temperature-moisture response surfaces can be developed) and of creating disturbance to the soil. The separation of the substrate from living plants may also cause a bias in the estimation of soil N mineralization rate.

4-Buried bag incubation This method is sensitive to field soil temperature and, to some extent, soil water content fluctuations in the field. However, root severing during installation might inflate N mineralization estimates in heavily rooted soils. Also, the separation of the root system from aboveground parts might disturb conditions in the rhizosphere and prevent an accurate estimation of actual soil N mineralization rates in the field.

5-Field resin bag: This method causes low disturbance to the soil and is faithful to soil microclimatic conditions. However, the dependence of ion capture upon water fluxes, the poor competitive ability of resin bags with plant roots and microbes (Binkley 1984b), and the tendency of resin to equilibrate with changing nutrient soil solution ammonium concentrations rather than to accumulate ammonium ions

(Appendix 1) make this method doubtful for the estimation of N mineralization.

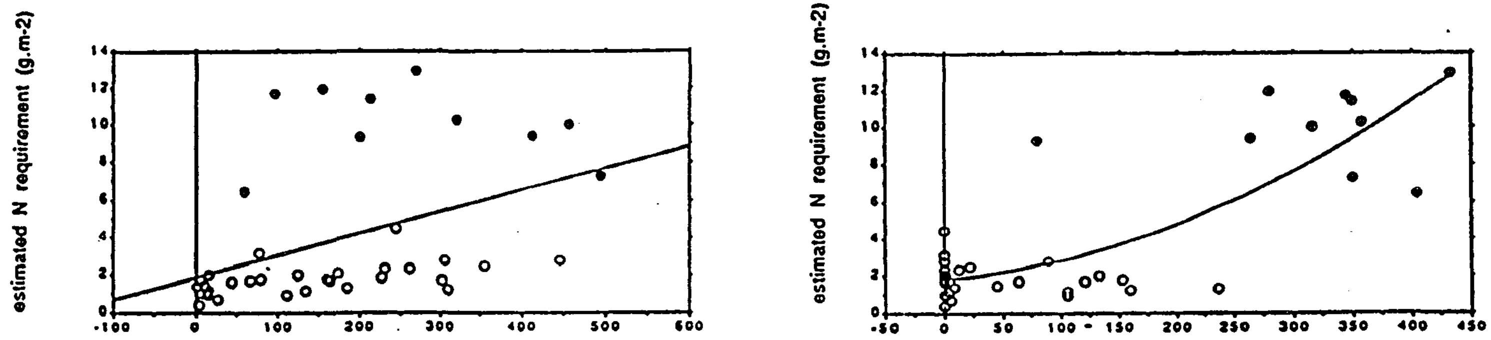
The following table summarizes the assumptions made with each method. Resin bags are not included in these comparisons since interactions of this technique with other methods have been discussed in chapter 4.

Methods	species	microclimate	disturbance
Estimation of N uptake by plant harvesting	-	-	-
Greenhouse bioassay	+	+	+
Laboratory incubation	+	+	+
Buried bag incubation	+	+-	+

Legend +: fixed

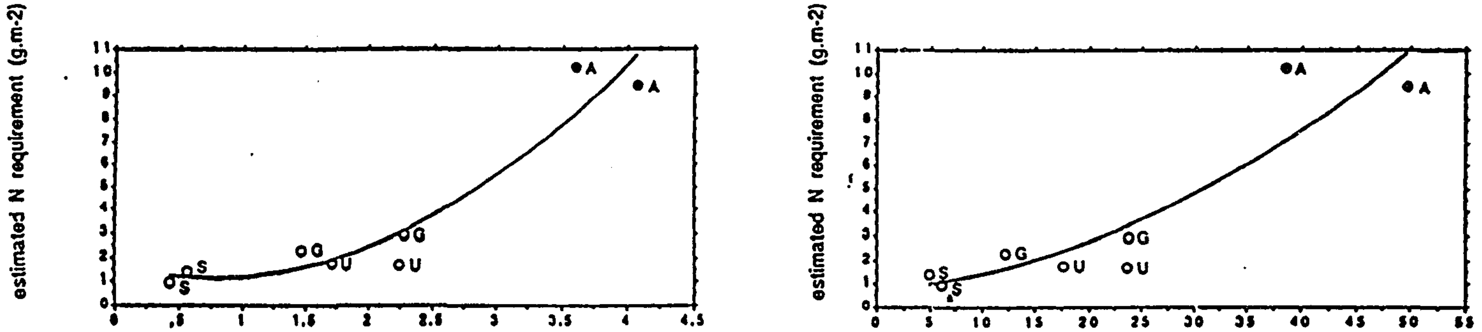
-: field conditions

Linear regressions between methods estimating N mineralization rates are shown in figure 5.1 . The general agreement between estimates of plant N requirement *in situ* and other field or laboratory methods tends to indicate that the divergent factors to which each method is sensitive



a) cumulative field net N mineralization (ug.g-1)
$y = 0.012x + 1.828$
n=40; r-squared = 0.189 pr>f = 0.005

b) laboratory net N mineralization (ug.g-1)
$y = 1.744 + 5.786E\text{-}3x + 4.535\text{-}5x2$
n = 40; r-squared = 0.684; pr>f = 0.0001



c) yield of bioassay seedlings (g.pot-1)
$y = 1.652 - 1.386x + 0.887x2$
n = 8; R-squared = 0.916; pr>f = 0.0021

d) N uptake of bioassay seedlings (mg.pot-1)
$y = 0.705 + 0.032x + 3.450E\text{-}3x2$
n = 8; R-squared = 0.838; pr>f = 0.0106

Figure 5.1 Regressions between estimated N uptake of 14-year-old post-harvested communities and surface soil N mineralization indices

Legend: closed circles: Aspen sites; Open circles: Other sites (ability of species to acquire nutrient, soil *in situ* temperature or moisture content, disturbance to the substrate), are not important in explaining differences between treatments.

The significance of the relationships in figure 5.1 is largely due to the slow N cycling rates of scraped sites and to the enhanced N cycling rates of 14-year-old aspen sites.

The agreement between methods estimating N availability suggests that the high N cycling rates of aspen sites are, at least in part, the result of organic matter quality (chemistry or structure). Soil microclimatic conditions or the fast growth of aspen appear to play a secondary role. Moreover, the significance of linear regressions between pooled litter N concentrations and surface soil N mineralization estimates suggest a role of litter quality in the enhanced N cycling rates of aspen stands:

	leaf litter N concentration		
Laboratory N mineralization rates (ug.g1)	R2: 0.899	P: 0.0003	n=8
Field N mineralization rates (ug.g-1)	R2: 0.505	P: 0.0362	n=8

2-Balance between nutrient supply and demand

Comparisons between parameters of soil nutrient availability (chapter 2) and estimates of nutrient requirement by plant communities (chapter 3) generate insight on the balance between nutrient supply and demand in these ecosystems. Table 5.1 shows that cycles of N, P and K are much tighter on aspen sites than in any other sites including mature white spruce stands. This observation is consistent with Vitousek and Reiners (1975) who have hypothesized that nutrient retention in an ecosystems is proportional to the net increment of biomass and therefore should be higher in young plant communities than in more mature ones.

Table 5.1
Differences between estimated pools of available nutrient in the surface soil and estimated nutrient uptake by vegetation (g.m-2)

Ecological types	N	P	K	Ca	Mg
Mature w.spruce (1)	-0.75	+0.21	+4.30	+63	+7.27
(2)	-0.66	+0.31	+3.28	+75	+6.47
Harvested sites (year 1)	+4.42	+0.63	+9.38	+102	+10.00
(year 14) Undisturbed (1)	-0.16	+0.11	+4.51	+99	+8.71
(2)	-0.77	+0.23	+6.08	+141	+11.58
Grass (1)	-0.05	+0.29	+4.83	+131	+9.48
(2)	+2.69	+0.69	+8.37	+155	+16.70
Scraped (1)	-0.73	+0.12	+3.02	+8	+6.20
(2)	-1.13	+0.03	+1.82	+8	+8.22
Aspen (1)	--	-0.69	+2.18	+67	+8.66
(2)	-6.92	-0.98	-0.94	+56	+6.86
(3)	-7.35	-0.94	-1.36	+52	+6.50

Notes: __ not determined

Nutrient requirement determined as described in chapter 3 available N: calculated as being the total amount of N mineralized over the course of a full year as measured with buried bags.
Extractable P: total extractable P in the surface soil
K, Ca, Mg: total exchangeable bases in surface soil horizon

+: supply greater than demand
-: demand greater than supply

CONCLUSION

The central hypothesis of the present work was that changes are occurring in the dynamics of nutrient cycling following the harvest of white spruce stands, and that the evolution of nutrient dynamics on post-harvested sites varied with the type of vegetation colonizing the site.

Estimates of nutrient utilization by regenerating plant communities (chapter 3) showed that regenerating aspen clumps have greater nutrient uptake rates, nutrient return in litterfall rates, as well as a greater biomass production than any other 14-year-old communities. This observation indicates that species composition of post-harvested communities controls, to a certain extent, the dynamics of nutrient cycling on regenerating sites.

Aspen currently is not a commercial species in Alaska. It would be interesting for forest managers to know if changes are occurring in the soil as a result of colonization by different communities and if so, can these changes be beneficial to the growth of commercial species? These concerns were addressed in chapter 2 where nutrient availability was estimated using several techniques.

Results indicated no changes in the pools of soil nutrients on harvested sites except where the forest floor was scraped. The absence of observable changes may be due to the great variability of the soil thickness caused by the mechanical disturbance to the soil during and after the harvesting operations. Changes in the availability of nutrients, especially N, were observed between sites of different ages after clear-cutting and sites of different vegetation composition. Sites regenerating to aspen tended to show the highest rates of N availability.

The general agreements between N mineralization estimates and the estimates of N uptake in the field by plant communities (chapter 5) further indicates that changes are occurring in the soil as a result of plant colonization.

More research is needed to identify the exact mechanism by which the species composition of regenerating communities affects the availability of soil nutrients. The influence of aboveground and belowground litter quality (both chemistry and structure) of colonizing species may be an important mechanism by which species modify the soil resource. The use of the litter bag technique could help to elucidate the role of litter composition in nutrient dynamics on post-harvested sites.

Applied research is also needed. The growth of planted white spruce seedlings in association with natural regenerating communities should be observed in a broad context where competition for nutrients and water as well as allelopathic and herbivore interactions are present.

From the limited observations of this study, some general forest management recommendations can be made:
-Scraping the forest floor greatly impairs site fertility.
-Pools of nutrients appear to be resistant to the disturbance created by forest harvesting. However, the dynamics of nutrient cycling appears to be influenced by the type of vegetation colonizing the site.
-The highest rates of nutrient cycling, the highest plant productivity and the tightest nutrient cycles (limiting the possibility of nutrient loss by leaching) were seen on sites

regenerating to aspen. These factors together with the compatibility of aspen and spruce in the natural forests make aspen an interesting species to consider for a mixed species reforestation strategy.

The maximum nutrient requirement of a forest plantation will be achieved at canopy closure (Miller 1984). Following this event, mechanisms of translocation will account substantially for nutrient requirements. Colonization by a fast growing successional species may insure optimum nutrient availability at a time which will be most critical for the growth of a commercial stand.

The forest floor of harvested sites contains large reserves of N. However, rates of N mineralization are likely to limit forest growth. On the regenerating sites under study, colonization by aspen seems to promote an increase in N mineralization rate. There is thus a possibility that the management of species composition on regenerating sites would aid in maintenance or improvement of site fertility.

Ecological classification of forest land is usually based upon permanent, physical and geological site characteristics. The results from the present study suggest that the biotic component of ecosystems, may control to a certain extent site productivity. The fact that this component can be manipulated by forest managers opens possibilities for improving forest productivity.

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APPENDIX

INTERPRETATION OF THE MEASUREMENT OF SOIL AMMONIUM PRODUCTION WITH ION-EXCHANGE RESIN BAGS

ABSTRACT

A simple experiment was designed to test whether ammonium ions captured by an ion exchange resin bag is cumulative or if resin bags equilibrate with every new increment of solution flowing through them. The experiment showed that, the capture of ammonium ions was cumulative in pure solutions. However, in typical soil solutions (containing a variety of ions), a new equilibrium was attained with every increment of solution flowing through the resin bag. Therefore, ion exchange resin bag measurements are representative of the last concentration of ammonium ion that was in contact with the resin and do not accurately represent the cumulation of ammonium ions that were made available in the soil over a period of time.

INTRODUCTION

No universal method is currently being used for the determination of soil N availability. Methods most commomly used to assess *in situ* mineral-N fluxes include the "burried-bag" method developed by Eno (1960) and modification from this procedure (Raison *et al.* 1987). A more recent technique, the use of *in situ* ion-exchange resin (IER) bags, is being more and more frequently used for the estimation of soil N availability in ecological studies (Binkley 1984a; Binkley et al. 1986; Gibson 1986; Hart and Binkley 1985; Krause and Ramlal 1987; Lajtha 1988). One of the main attributes of this method is that IER bags absorb available nutrient *in situ*, with a minimum of disturbance to the soil. However, this method remains largely qualitative since the mechanisms of ion sorption from the soil solution to the resin are not fully understood (Krause and Ramlal 1987). Some of the questions still remaining concern the following aspects:

1-How is water circulation and ion flux, affected by the textural discontinuity between soil particles and resin beads (Schnabel, 1983)?

2-Are the different ion species sorbed by the resin in the same relative proportions that are found in the soil solution? Binkley (1984b) had already shown that nitrate was sorbed 30 times more rapidly than ammonium by IER bags when present in the same concentration in the soil solution.

3-Do ions reach IER bags by diffusing fluxes or only by convective fluxes?

4-Does the IER ability to sorb ion decrease with time by organic fouling?

5-What is the volume of soil from which ions are absorbed?

6-Finally, do IER bags act as a sink for ions in the soil solution or do they act like soil exchange sites, responding to ion concentration in the soil solution as changes in ionic concentration occur.

The objective of this study was to investigate the latter concern. IER bags have been compared to lysimeters (Schnabel 1983) or to plant roots (Gibson 1986). But these comparisons may not be appropriate if IER bags, instead of acting as a sink (sorbing ions as they are released to the soil solution over a period of time), act like soil exchange sites: sorbing or desorbing ions as changes in the soil solution are occurring. In the latter case, the results from IER bags would have to be considered as an index of the last ionic concentration of the soil solution; while in the former case these results would have to be considered as a index of the release of ions to the soil solution during a certain period of time and therefore related to the burried bag technique. These considerations need to be investigated to realistically interpret results from the IER bag technique.

MATERIALS AND METHODS

Cation exchange resin bags were prepared by placing 10 *u* mol(+) of cation exchange resin (Biorex 70) in nylon stocking. The bags were washed with dilute HCl and regenerated with M NaCl as described by Krause and Ramlal (1987). Elution was performed by placing individual bags in flasks containing 50 ml of 0.1 M HCL and shaking fo 30 minutes. Ammonium concentrations were determined using an autoanalyzer and the method outlined by Whitledge *et al.* (1981).

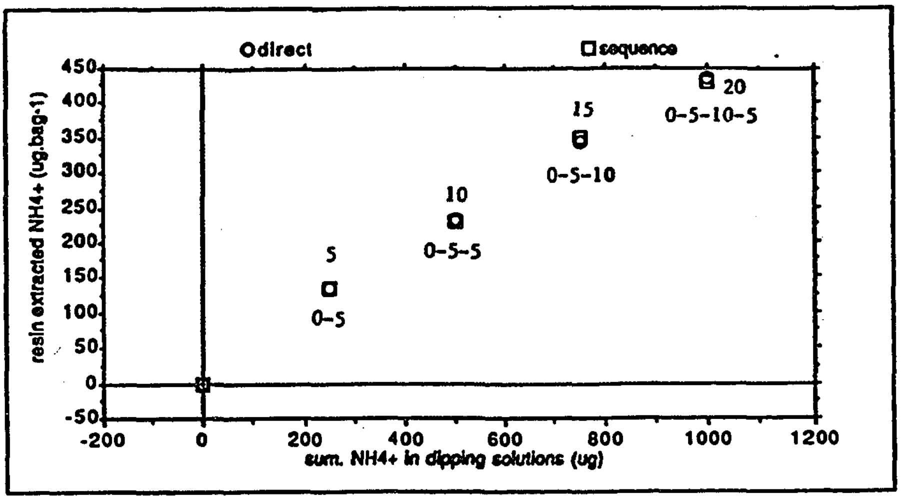
IER bags were agitated for 30 minutes in 50 ml of either 0, 5, 10, 15 or 20 (ug.g-1) NH4+ solutions made with (NH4)2 SO4. They were then eluted to determine the amount of ammonium ions sorbed by the IER bags. Another set of resin bags was placed in a sequence of solutions of different ammonium concentrations designed to simulate changes in soil solution NH4+ concentration. They were only eluted at the end of the sequence. They were agitated during 30 minutes in every solution and then rinsed twice with dionized water before being dipped in the next solution. The treatments were the following (ug.g-1 NH4+): a) 0-5 b) 0-5-5 c) 0-5-10 d) 0-5-10-5.

Each treatment was repeated three times. This experiment was then repeated but this time the solutions were made from one composite sample of soil solution made from saturation extracts in which ammonium concentrations were adjusted by addition of (NH4)2 SO4. The saturation extract solution was made by combining saturation extracts of 10 forest floor samples coming from a single mature white spruce site. The extraction of the solution was performed as describe by Rhoades (1982). The initial saturation extract solution contained concentrations of NH_4^+, K^+, Ca^{2+} and Mg^{2+} of 0.2, 54, 77, 21 ($ug.g^{-1}$) respectively and had a pH of 5.42.

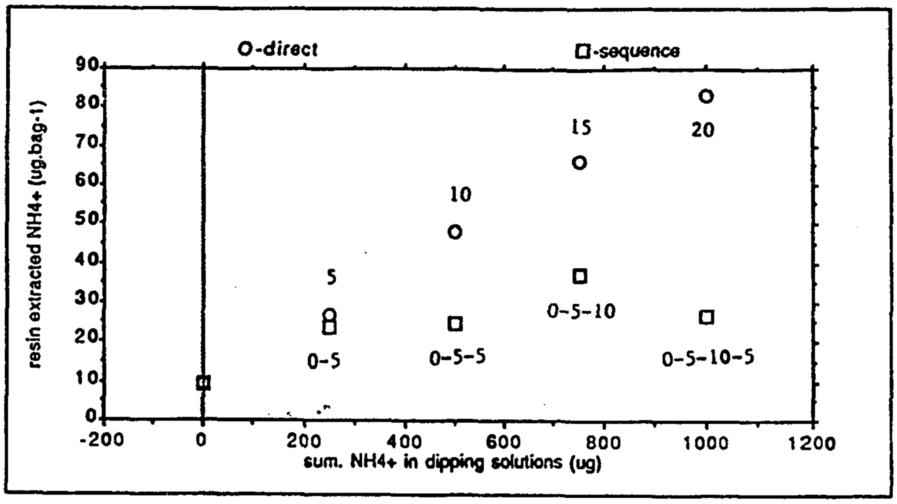
RESULTS

In the pure ammonium solutions IER bags acted as a sink for NH_4^+ ions (fig. 1a). Equivalent amounts of ammonium ions were sorbed when the bags were dipped in a sequence of solutions containing low concentration of ammonium as when dipped in a single solution containing the total amount of ammonium ions contained in the sequence.

The sorption curves of ammonium ions in soil solution showed a totally different pattern (fig. 1b). The amount of ammonium ions sorbed by the resin is more related to the last ammonium concentration of the sequence than to the total amount of ammonium ions that had been in contact with the resin bag. It is also noteworthy that, for the same ammonium concentration in the initial solutions, the amount of ammonium ion sorbed by the resin in the saturation extract solution was much lower than the amount sorbed in pure solutions (note different scale for the two graphs).



a) Pure solutions



b) Soil saturation extracts

Figure 1. Relationships between NH4+ extracted by resin bags and the summation of NH4+ ions in dipping solutions

Note: Each symbol represents an average of 3 values. Standard errors are contained within the height of symbols. The numbers on the graphs represent the concentrations of NH4+ in dipping solutions (ug.g-1).

DISCUSSION

The pattern of sorption of ammonium by IER bags could have been predicted with a knowledge of the ionic composition of the soil solution and by the knowledge of the resin preference for the different ionic species present in the solution. However, soil solution is a complex mixture of organic and inorganic substances for which the selectivity sequence of commercial resin is not known. According to Helffreich (1962), for the general-purpose cation exchangers the selectivity sequence of the most common cations is: $Ca^{++} > Mg^{++}$ for bivalent cations and $K^+ > NH4^+ > Na^+$ for univalent cations. Several factors can account for preference by an ion-exchanger: the ion-exchanger tends to prefer (1) the counter ion of higher valence, (2) the ion with the smaller (solvated) equivalent volume, (3) the ion with the greater polarizability, (4) the ion which interacts more strongly with fixed ionic groups or with the matrix, and finally (5) the counter ion which participates least in complex formation with the co-ion (Helfferich 1962).

The resin was in Na+ form prior to the interaction with NH4+ solutions. The smaller volume of NH_4^+ ions compared to the volume of Na^+ ions can explain the preference of the resin for the former and the behavior observed in pure solutions where only Na^+ and NH_4^+ cations are interacting. In the soil solution experiment, the presence of high concentration of Ca^{++} could have easily washed out the NH_4^+ ions retained on the resin.

As calcium ions are almost always found in larger quantities than ammonium ions in the soil solution of natural soils, it is likely that the IER bag method will give an index of net ammonium availability rather than an index of total N mineralization over a period of time.

Binkley et al. (1986) observed a significant correlation between the estimation of N mineralization with the buried-bag technique and resin bag accumulated ammonium + nitrate over 17 forest sites in Wisconsin. On the other hand, Hart and Firestone (1989) found that values of N availability measured with IER bags and buried bags were not always correlated. According to the finding of the present study, it is likely that *in situ* indices of N availability will correlate with IER bag measurements because it is likely that instantaneous concentrations of mineral-N will correlate with the total release of N over a period of time. However, the resin bag technique may not correctly estimate fluxes of N if resin bags are left in the field for a substantial period of time and if changes in the N concentrations of soil solution are occuring during that period.