EFFECTS OF REPEATED FERTILIZATION AND A STRAW APPLICATION TO THE ORGANIC LAYERS UNDER JACK PINE AND SEEDLING RESPONSE

by

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We accept this thesis as conforming to the required standard

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ABSTRACT

In an optimum nutrition experiment, a 45-year old jack pine (Pinus banksiana Lamb.) stand in Quebec was repeatedly fertilized over a 10-year period with various levels of NPK fertilizers. In a separate experiment, a straw treatment was applied over snow to smother the ericaceous ground vegetation.

Nitrogen fertilizer additions for 10 years resulted in increased humus biomass in all treatments. The greatest gain was on plots receiving repeated low N doses. These organic layers also had the lowest decomposition rates. Heavier N applications increased humus decomposition substantially, but stand litter production was also increased. The straw-treated humus had decomposition rates approaching those found with high N additions.

Repeated low N additions immobilized fertilizer N within the humus. Most of the N applied at higher treatment levels appears to have been lost. Nitrogen mineralization rates were investigated in an aerobic incubation study. Nitrification occurred in spite of low pH (<4) on high N plots. The straw addition increased humus nitrogen mineralization rates.

The results of repeated additions of P and K were variable. Additions of P and K decreased nitrogen availability although decomposition rates were increased. It appeared that most of the P and K were lost from the organic layers due to leaching.

Large N additions had little effect on the humus C/N ratio. They increased the CEC and the pH but reduced the base saturation.
Straw additions lowered the humus C/N ratio but increased the CEC, pH and base saturation.

Dramatic changes in the ground vegetation occurred. With higher N additions the ericaceous vegetation was greatly reduced and increasingly replaced with Sambucus, Aster and other exotics. The straw application effectively smothered the ericaceous vegetation for 10 years.

Seedling bioassay studies showed that both the straw treated humus and the sustained low additions of N plus P and K resulted in the highest seedling biomass. This correlated well with stand growth response. Seedling N nutrition was adequate in all treatments and reflected the ability of mor humus to release immobilized N under improved environmental conditions in the greenhouse. Some possibilities why foliar N could not be correlated with seedling biomass are discussed.

It is concluded that in jack pine stands with thin mor humus layers, repeated light nitrogen additions plus phosphorus and potassium result in sufficient nutrient turnover rates to ensure the highest stand response.
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1.0 INTRODUCTION

Growth of many coniferous crops in northern boreal forests is often limited by the supply of nutrients, especially nitrogen. At the same time, the mor humus layers which commonly characterize these sites have large reserves of nitrogen unavailable for tree growth (Viro, 1963; Weetman and Webber, 1972). As an adaptation to these low levels of available nutrients, boreal tree species conserve what little nutrients they have by maintaining very 'tight' nutrient cycles from which losses are small (Tamm, 1979).

In order to improve tree growth on these sites, considerable research has been carried out to determine the growth response of boreal forests to nitrogen (N) fertilizers (Tamm, 1974; Krause et al., 1983). Research has also shown that chemical fertilizers have an effect on nutrient turnover rates of the humus (Roberge and Knowles, 1966; Mahendrappa, 1978). Added nutrients can stimulate microbial activity directly by adding nutrients in short supply or indirectly by ameliorating their environment (Williams, 1972). Increased mineralization can mobilize the organic nitrogen and other nutrient reserves contained within the humus and make them available for tree use. Rapid increases in humus decomposition rates can release nutrients in a short time which would normally be cycled over a much longer period (Kelly and Henderson, 1978). These nutrient releases may occur so rapidly that tree uptake cannot absorb them and they are effectively lost from the site.

In Canada, one of the earliest works in forest fertilization was the establishment of an optimum nutrition experiment in a jack pine
(Pinus banksiana Lamb.) stand in Quebec (Weetman and Algar, 1974). This experiment attempts to establish the possible upper limits of tree growth by manipulating nutrient concentrations and maintaining defined foliar nutrient regimes over an extended period of time with the application of N, P and K fertilizer. In the same stand, but unrelated to the optimum nutrition experiment, straw was used to smother the ground vegetation in order to reduce competition for available N and increase N uptake by the trees. The jack pine responded with substantial volume growth for both the sustained low nitrogen additions and the straw application (Weetman and Fournier, 1984).

Neither experiment was intended to be a fully integrated ecosystem study. However, both experiments presented the opportunity to investigate the effects repeated N, P and K applications had on the humus layers and ground vegetation under a coniferous stand. The substantial response of the trees to both the sustained low nitrogen additions and straw application obviously called for studies of changes in forest humus layer. The objective of the study was to test the hypothesis that the physical and chemical characteristics of the humus and the ground vegetation were significantly different from the untreated humus layers. Further, that these changes in the humus would significantly influence the nutrient supplying capacity of the humus to the jack pine seedlings in a bioassay experiment. Although no one can seriously imagine large-scale applications of straw to the forest floor, repeated applications of fertilizer on intensively managed forests will likely increase. Studies such as these can add awareness of the potential and magnitude of these changes to the humus capital of a forest ecosystem.
2.0 LITERATURE REVIEW

2.1 The Nitrogen "Problem"

Nitrogen is known to be one of the most important limiting factors affecting growth and yield of forests. Although it is a common element of the earth's atmosphere, only a small part of this nitrogen is contained in the active biogeochemical cycle. Here it plays a very important role, since most of the available nitrogen is obtained from transformation processes occurring in soil organic matter.

Within the boreal forest ecosystem, nitrogen release is slow, despite often large reserves held in the raw humus horizons. The German scientist Themlitz (1954) writes, "Although rich in nitrogen, mor humus actually hungers after nitrogen". This inadequate release of plant nutrients has been the object of much research since the early 1900's.

Much of the nitrogen present in mor humus occurs as organic nitrogen - nitrogen unavailable to plants until it is mineralized by soil microorganisms to inorganic forms. These organic nitrogen complexes are very resistant to decomposition in spite of the fact that 40% are in the form of easily mineralizable organo-nitrogen complexes (Bremner, 1965). Handley (1961) suggested that tannins present in the leaves of some plant species react with cytoplasmic proteins. These protect the mesophyll tissue from rapid decomposition and may be of fundamental importance in the formation of mor humus found under coniferous forests. Broadbent and Norman (1947) and Broadbent (1948) concluded that the stability of organic nitrogen complexes is more
apparent than real. Due to the absence of enough energy material, readily available for decomposition, a vigorous microbial population cannot be supported, with the result that decomposition is slow.

2.2 Mineral Nitrogen

Increasing use has been made of nitrogen fertilizers to augment nitrogen availability and thereby improve forest growth. Fertilizers can be applied to forests in either inorganic or organic forms. When nitrogen is applied to the moist forest floor in an inorganic form such as ammonium nitrate, the nitrogen is quickly incorporated into the soil solution or exchange complex. In this form it is immediately available to plants and soil organisms. In contrast urea, an organic nitrogen source, must first be converted to the inorganic ammonium (NH$_4^+$) form before it can be absorbed by plants.

Additions of ammonium salts to an alkaline aqueous solution, results in the escape of free ammonia according to the following reaction:

\[
\text{NH}_4^+ + \text{OH}^- \rightarrow \text{NH}_3 + \text{H}_2\text{O}
\]

Thus, if ammonium nitrogen fertilizers are added to alkaline soils, free ammonia may be lost. Under forests, the quantity of ammonia volatilized depends on soil conditions, such as temperature, moisture, pH and thickness of the humus layer. Since additions of urea can result in a rise in pH (Knowles, 1964; Roberge and Knowles, 1966; Overrein, 1968; Weetman et al., 1972; Foster, 1979), applying urea on
an acid humus can result in ammonia volatilization (Bernier et al., 1969; Overrein, 1969; and Bhure, 1970).

The use of ammonium nitrate, which does not raise the pH of the soil, will reduce volatilization losses often associated with urea additions. Overrein (1969) found volatilization losses from NH₄⁺ or NO₃⁻ treated podzol soils to be non-significant.

Leaching constitutes one of the main pathways whereby nitrogen is lost from soils. The quantity of nitrogen leached is dependent on many variables (Allison, 1965):

(a) form and amount of soluble and unadsorbed nitrogen present;
(b) amount and distribution of rainfall;
(c) infiltration and percolation rates, which are markedly affected by soil composition, texture, structure, profile depth and surface treatment;
(d) soil water-holding capacity and moisture content;
(e) cation exchange capacity as influenced by the amount of organic matter, clay content and pH;
(f) characteristics of the surface vegetation;
(g) evapotranspiration;
(h) rate of nitrogen uptake by plants.

Boreal forest ecosystems are able to completely or partially accumulate and retain nutrients added as fertilizer. Those nutrients not retained are leached out of the upper soil horizons and are effectively lost from the rooting zone. The leaching losses of nitrogen after addition of urea-N, NH₄-N and NO₃-N in a mixed Norway spruce - Scots
pine stand growing on a well-drained sandy soil was reported by Overrein (1968, 1969). Total leaching losses of nitrogen increased linearly with increasing rates of fertilizer applications. Leaching losses at 250 kg N/ha level were negligible with urea (1.6%), high for NH₄⁺ (21.5%) and very high for NO₃⁻ (91.8%). Studies on the retention of added ammonium and nitrate ions in the soil have shown that nitrate is not strongly retained in the soil (Nömmik and Popovic, 1971; Overrein, 1971). Not only may the added nitrogen be effectively moved below the rooting depth of forest trees (Tamm, 1973), but there is also the threat of nitrate contamination of ground water.

When nitrogenous fertilizers are added to the soil, the ammonium ion pool is directly increased. Part of this added nitrogen can be absorbed or "fixed" by organic matter (chiefly lignin) and clays (Allison, 1973). Ammonium can also be physically adsorbed to organic matter, but it is a very weak bond which can be readily removed when the ammonium concentration is lowered. Under certain conditions, the ammonia can react chemically with the organic matter to form insoluble compounds resistant to decomposition (Mortland and Wolcott, 1965; Nömmik, 1965). Conditions found in most raw humus layers however, restrict this process as reported by Knowles and Chu (1969) who found low fixation rates of ¹⁵NH₄⁺-N in black spruce raw humus. Nömmik (1970) also reported that the fixation of added ammonium was low in acid Norway spruce humus but increased rapidly as the pH was raised.

Nitrification is the reaction by which certain chemo-autotrophic organisms and some heterotrophs oxidize ammonium ions to nitrite and then to nitrate. Each stage is carried out by specific organisms, with
autotrophic bacteria responsible for most nitrate production. In coniferous forest ecosystems with typical acid humus layers, autotrophic nitrifiers can be ineffective or absent. Here, heterotrophic nitrifying fungi may be more important (Keeney and Gardner, 1970).

The first stage of the nitrification process is carried out by various bacteria: *Nitrosomonas*, *Nitrosococcus*, *Nitrosocystis*, *Nitrosospira* and *Nitrosogloea* (Alexander, 1965). The effects of inorganic N fertilizers on these species are limited to the ammonia they supply. Growth is generally speeded up since ammonia is their chief food (Allison, 1973). However, when fertilizer concentrations are high (immediately upon application, or around the pellet) some or most of the organisms can be killed.

The second stage of oxidation is carried on by *Nitrobacter* and *Nitrocystis* but due to the highly acidic conditions in boreal forest soils, *Nitrobacter* species are not numerous (Lutz and Chandler, 1959) and may explain the low level of nitrification in some forest soils. In eastern Canada, Roberge and Knowles (1966) detected only negligible amounts of nitrification in their incubation studies with an acid podzolic humus formed under a highly productive black spruce following fertilization with urea at 448 kg N/ha. Nitrification was detected only when the pH rose above 5.6 after an application of 3500 ppm urea-N in the laboratory to the humus previously fertilized in the field. Overrein (1967) made a similar observation. He found an accumulation of nitrate-N only after urea was applied to a Norway spruce mor humus.

Contrary to the above results, some investigators have reported significant nitrification in forest soils, but these have been
restricted mainly to Pacific West Coast soils (Bollen and Lu, 1968; Likens et al. 1969; Heilman, 1974). According to Heilman (1974), it has been shown that in applying urea on poor Douglas-fir sites, no nitrate was produced. On better sites, nitrate levels doubled after five months. Thus, limited nitrification may be due to the absence of ammonium on poor sites.

It has been reported (Tyler and Broadbent, 1960) that *Nitrobacter* is sensitive to even low ammonia concentrations. Considerable nitrite may be formed, but little nitrate. In acid soils, nitrites are unstable and some of the nitrogen may be lost (Allison, 1973).

Denitrification is the reduction of nitrite and nitrate to volatile gases, usually nitrous oxides and molecular nitrogen (Broadbent and Clark, 1965). In the wider sense, it refers to the gaseous loss of nitrogen either by biological or chemical means — exclusive of ammonia volatilization.

Denitrification as a biological process is accomplished by facultatively anaerobic bacteria which are capable of using nitrate or nitrite in place of oxygen as an electron acceptor in oxidizing various kinds of organic matter, including carbohydrates:

\[
C_6H_{12}O_6 + 4 NO_3^- \rightarrow 6 CO_2 + 6 H_2O + 2 N_2
\]

Denitrification is influenced by the soils pH, being very slow in acid soils and rapid in soils of high pH (Bremner and Shaw, 1958). Nömmik (1956) reported that denitrification rates are fairly constant.
at pH 6. Little denitrification occurs when the moisture content is less than 60% of the soil's water holding capacity (Bremner and Shaw, 1958).

Using lysimeter studies, Overrein (1968, 1969) noted that no denitrification occurred in mor humus. Soil receiving the higher rates of urea application, lost only small amounts of $N_2$. Weetman (1962) found in greenhouse studies, that half the nitrate applied as ammonium nitrate was lost. However, the artificial hot humid conditions of the greenhouse was credited in having stimulated nitrification and denitrification processes.

Chemo-denitrification, on the other hand, involves various chemical or non-enzymatic reactions which break down nitrates. Broadbent and Clark (1965), Nömmik and Thorin (1972) discussed some of the processes involved in chemo-denitrification.

1. Self-decomposition of nitrous acid under acid forest conditions to yield nitric oxide:

$$3 \text{HNO}_2 \longrightarrow 2 \text{NO} + \text{HNO}_3 + \text{H}_2\text{O}$$

The nitric oxide can in turn, be oxidized to nitrogen dioxide:

$$2 \text{NO} + \text{O}_2 \longrightarrow 2 \text{NO}_2$$

which, in turn, can react with water to form nitric acid:

$$3 \text{NO}_2 + \text{H}_2\text{O} \longrightarrow 2 \text{HNO}_3 + \text{NO}$$

$$2 \text{NO}_2 + \text{H}_2\text{O} \longrightarrow \text{HNO}_3 + \text{HNO}_2$$
Large losses of nitrogen from soils via this reaction are unlikely, although it is probably the only chemo-denitrification process occurring in acid forest soils since nitrite does not decompose above pH 6 (Nõmmik and Thorin, 1972).

2. Reaction of nitrous acid with α-amino acids in the Van Slyke reaction:

\[
RNH_2 + HNO_2 \rightarrow ROH + N_2 + H_2O
\]

This reaction probably does not result in much loss of nitrogen. It occurs at pH 5 or less—conditions where nitrite formation either by biological oxidation of ammonia or by enzymatic reduction of nitrate are not favourable. Therefore, even when nitrate is applied as fertilizer, little N\(_2\) will be formed (Bremner, 1965).

3. In a reaction similar to the Van Slyke reaction, ammonia may react with nitrous acid and form nitrogen:

\[
NH_3 + HNO_2 \rightarrow N_2 + 2 H_2O
\]

However, Bremner (1965) considers losses due to this reaction to be negligible.

4. Reaction of nitrate or nitrous acid with reducing material of the soil organic matter, which is probably of microbial origin. The phenolic components of the organic matter are believed to be important in fixation of nitrite and reduction to N\(_2\)O and N\(_2\).
2.3 **Organic Matter Decomposition**

The conditions which determine organic matter decomposition were studied extensively by Jansson (1958). The fundamental point in his theory of "continuous internal cycle" of nitrogen in the soil, is that mineralization and immobilization are going on continuously and simultaneously. The driving force behind this cycle is the heterotrophic soil population, whereas the energy sources required to keep this cycle going are the organic compounds returned to the soil in the form of litter.

When nitrogen is added to the forest floor, it may be immobilized by the heterotroph microbial population of the soil. This immobilization is biological in that the microorganisms assimilate the mineral nitrogen for their own biomass synthesis (Alexander, 1961).

Mineralization, which is the reverse of immobilization, occurs concurrently. In this process, the nitrogen incorporated into the organic structures is converted into ammonium by other microorganisms.

Agronomic research has indicated that nitrogen additions increase the breakdown rate of organic matter (Brown and Dickey, 1970; Black and Reitz 1972). Under forest conditions, Salonius (1972) and Roberge (1976) observed increased respiration in black spruce forest floor samples shortly after urea was added. With a more favourable pH environment and readily available nitrogen for cell synthesis, more organic matter is metabolized.

That there is a correlation between the C/N ratio of the organic matter and nitrogen turnover rate is understandable. However, what
point nitrogen mineralization equals nitrogen immobilization is not clear. Harmsen and van Shreven (1955) reported values for equilibrium at C/N ratios = 20 to 25 and a nitrogen content of 1.5 to 2.0%. Bremner and Shaw (1957) showed that the critical C/N ratio of immobilization could exceed 30. Since immobilization is promoted when the C/N ratio is high, soils with a low C/N ratio will have more net mineralization occurring.

Additions of nitrogen fertilizers can reduce the C/N ratio. Roberge and Knowles (1966) reported a decrease in the C/N ratio from 58/1 to 42/1 in the L horizon of an acid black spruce humus. Popovic (1977) also reported a decreased C/N ratio in the humus ranging from 43/1 to 29-34/1 following fertilization.

Although application of nitrogen has been found to stimulate respiration and to decrease the C/N ratio, increased rates of decomposition have not always been reported. Zöttl (1960), Fessenden et al. (1971), Salonius, (1972) and Roberge (1976) all reported decreases in respiration following fertilization with ammonium salts. This would suggest that nitrogen was not limiting decomposition initially.

The availability of carbon may also limit decomposition. Studying the interactions between mineralization and immobilization, Knowles (1969) reported that additions of nitrogen to a black spruce humus did not immobilize the available nitrogen. By adding sugar as a readily available carbon source and an ample supply of other minerals in combination with an increase in pH, immobilization of the nitrogen was increased. Subsequently, Salonius (1972) showed that microbial activity was limited more by shortages of decomposable organic
substrate and the high acidic conditions than by nitrogen. Foster (1979) also found microbial respiration stimulated more by an increase in soil pH and available carbon than by additions of nitrogen.

It seems apparent then, that availability of nitrogen from organic matter, or from any nitrogen additions applied to the boreal forest floor, is not dependent on a single limiting factor. Instead, a number of factors such as acidity and readily available energy sources are important when evaluating immobilization-mineralization interaction.

2.4 Nitrogen Additions and Their Effect on Nitrogen Cycling Rate

Species growing under different site conditions can have marked differences in their use and cycling of nitrogen. Conifer species, especially, can respond to nitrogen availability by modifying various physiological processes (Miller et al., 1979). For example, trees can respond to decreased nitrogen availability by greater internal nitrogen cycling. This results in lower nitrogen concentrations in the needle litter. Unfortunately, decreased litter quality with high C/N ratios decompose slowly with a corresponding slow nitrogen mineralization rate. In turn, this lowers the available nitrogen even further and can aid in the formation of a mor humus (Figure 1). When the pool of available nitrogen is enlarged through the use of nitrogen fertilizer, the added nitrogen can directly affect the nitrogen transformations within the humus by increasing the rate of nitrogen cycling.

Many studies have shown that additions of nitrogen often result in increased nitrogen concentrations in needles (Morrison, 1974; van den Driessche, 1974), as well as in litter and throughfall (Mahendrappa
Figure 1. Influence of the interactions of several processes on nitrogen availability in low and high nitrogen sites (Gosz, 1981).
and Ogden, 1973). Berg and Staaf (1980) suggest that increased litter quality can result in a higher decomposition rate and a greater amount of nitrogen released per unit weight of organic matter. A lower percentage of nitrogen is immobilized leaving a larger amount of nitrogen available for tree growth (Gosz, 1981).

Increased nitrogen concentration can also affect the litter quality by reducing the amount of polyphenols and tannins present in the conifer needles. Davies et al. (1964) found that tree seedlings produced higher amounts of polyphenolic substances when nitrogen was in low supply. Since these protein-complexing substances are notoriously slow to decompose, any reduction in their concentration within the needles will ultimately increase the decomposition rate of the needle litter (Gosz, 1981).

Increased nitrogen supply also affects the internal redistribution of this nutrient and affects leaf persistence on the tree. Under conditions of low nitrogen supply, the tree has a high internal redistribution of nutrients before leaf fall (Lamb, 1975; 1976; Turner, 1977) thus resulting in lower nitrogen concentrations in needle litter. Furthermore, when the tree increases its leaf persistence on poorer sites (Gosz, 1981), the total amount of nitrogen utilized within the tree will be greater. By increasing nitrogen availability, the withdrawal of nitrogen from the needle will be low, resulting in higher nitrogen concentration in the needle litter. Decreased leaf persistence, of course, translates into greater litterfall. With more high quality energy material reaching the forest floor, higher decomposition and mineralization rates will occur.
Naturally, other factors than those encompassed by site quality have an effect on the nitrogen cycle by influencing the decomposition rates. The physical component plays as important a role as site quality. Such factors as temperature, moisture, aeration, oxygen and carbon dioxide supply all influence the decomposition processes by affecting decomposer organisms. However, their discussion lies beyond the scope of this investigation and they are presented here in order to complete the scheme of organic matter decomposition.

2.5 The Straw and Optimum Tree Nutrition Experiments

Within the boreal forest, the cycling of nutrients, especially nitrogen is slow and the biological competition for nitrogen is intense. The ground vegetation may be an important competitor with trees for the limited N available. Huikari and Paarlahti (1967) smothered the ericaceous vegetation in a Finnish pine swamp with straw and noticed an almost immediate response in tree growth. They attributed this response in part, to the decreased competition and the "green fertilization" by the decomposing vegetation. In order to test the hypothesis that smothering the ericaceous vegetation in a jack pine stand will increase N uptake by the trees, the straw experiment was initiated (Weetman and Algar, 1974).

Plants interact with fertilizer additions by assimilating nutrients through their roots, and, in return, add energy material and organic nitrogen back to the soil. In agricultural as well as forestry practice, the aim is generally to increase available nitrogen, raise
nutrient concentration to optimal levels in the plant and so increase yield.

Ebermayer (1876) made the first attempt to estimate the amount of nutrients required for optimal tree growth. Since then, there have been many studies to determine the optimum nutrient requirements of forest trees (Rennie, 1955; Swan, 1960, 1970; Ingestad, 1962, 1976, 1979; Tamm, 1968, 1974).

Most early research centred on the use of tree seedlings in pot cultures, to which additions of various amounts of nutrients were applied. But making predictions of forest tree response based on seedling growth has been difficult. The value of these trials in predicting growth response is dependent on a correlation between pot trials and field response. However, nutritional requirements of seedlings and adult trees may not be similar. Mead and Pritchett (1971) reported a generally low correlation between fertilizer response of Pinus elliotti in the field and those grown in pots. Added to these nutritional differences are other factors which can influence tree/seedling response. Artificial conditions in the greenhouse are more conducive to plant growth and could also increase/decrease certain chemical and physical processes in the soil and so alter nutrient availability. Even when pot trials are located under field conditions, marginal soil nutrient deficiencies may be overlooked because sufficient stress on the nutrient supplying powers of the soil has not occurred (Richards, 1968). Still, pot trials can provide an important diagnostic tool in assaying soil fertility because they can provide information on the nutrient supplying potential of the soil.
Conventional fertilization experiments have also not given the required information. In these experiments, a single application of fertilizer or applications repeated with long intervals are applied to forest stands. Closed forest stands have mechanisms to recycle nutrients. Additionally, the size of the nutrient pools and the rate of nutrient transformations is impossible to determine with any degree of accuracy. Therefore, little insight into the nutritional relations between forest stand, yield response and soil conditions can be made because of the highly variable nutrient status of the trees.

Optimum nutrition experiments are a newer type of factorial experiments (Tamm, 1968, 1974). Here, the nutrient uptake is controlled by annual leaf analysis. Annual or semi annual nutrient applications are adjusted in order to keep foliage levels of the main nutrients (N, P, K) as constant as possible over an extended period of time. The objective is to allow the forest stand to establish a form of 'steady state' with respect to internal concentration of nutrients and growth.

Generally, optimum nutrition experiments maintain three different constant elevated nutrient regimes. This allows direct correlations between stand growth response and nutrient levels. These experiments also permit a comparison of field and pot trials. In addition, field testing of 'deficient', 'satisfactory' and 'optimum' foliar nutrient levels is possible.

The ultimate aim of fertilization research is to enable the forest manager to predict stand response by using simulation models of forest ecosystems. The use of fertilizers manipulates site conditions by the addition of an external influence. How this can affect nutrient
cycling, nutrient availability and ultimately, primary productivity, is still little known. Only by understanding the various regulatory mechanisms forest systems have at their disposal and how to alter or maximize their function, will the models be able to assess and reflect true conditions.

2.6 Definitions

Liberal use of the terms forest floor and humus layers are employed. The forest floor refers to all organic materials resting on but not mixed with the mineral soil surface. Humus, or humus layer, is defined as the whole of the dead organic matter present in or on the soil and undergoing continuous decay, transfer and synthesis. Although current North American literature characterizes the humus layer as all decomposing organic remains beneath the litter layer as well as the Al soil horizon (Pritchett, 1979), within the confines of this thesis, forest floor and humus layers are used interchangeably. Likewise, the litter layer, consisting of unaltered dead organic matter, is considered part of the humus.
3.0 MATERIALS AND METHODS

3.1 Site Description

The research plots are located in Mont Tremblant Parc, Quebec. Situated in the southern extremity of the boreal forest (Forest Section B-7, Rowe 1972), this even-aged jack pine stand was 45 years old at the time the plots were established in 1970. Classified as a Site Class I (Plonski, 1974), the stand had a density of 2125 trees/ha, a dominant height of 14.3 m, a mean diameter of 14.7 cm (DBH) and contained a total volume of 161 m³/ha (Weetman and Algar, 1974).

The forest floor consisted of a typical thin raw humus layer commonly found under boreal pine stands (Figure 2). This mor was 5.5 cm in depth, weighed 43,000 kg/ha oven dry and covered a deep, sandy Ortho Humo-Ferric Podzol (Canada Department of Agriculture, 1970). Ground vegetation as shown in Figure 3 consisted of an upper stratum of *Kalmia angustifolia* (L.) and *Vaccinium angustifolium* Ait. with a lower moss layer of *Pleurozium schreberi* (B.S.G.) and *Cladonia rangiferina* (L.) Web.

3.2 Treatments

The optimum nutrition experiment was set up as a completely randomized 2 x 4 factorial with four levels of nitrogen and two levels of phosphorus and potassium (Table 1). Each treatment was replicated twice and the fertilizers applied to 0.02 ha circular plots. The fertilizer was applied early in June with an hand cyclone seeder, and over the 10 year period there were six applications. The first
Soil profile showing the humo-ferric podzol formed on deep outwash sand and covered with a thin mor humus layer.

Figure 2. Soil profile showing the humo-ferric podzol formed on deep outwash sand and covered with a thin mor humus layer.
Figure 3. Vegetation consists of jack pine with a sparse understory of black spruce. The shrub layer is composed of *Kalmia* and *Vaccinium*. 
TABLE 1. Design and treatments applied to the forest floor of an immature jack pine stand.

**Optimum Nutrition Experiment**

<table>
<thead>
<tr>
<th>N Level</th>
<th>PK Regime</th>
<th>+ PK</th>
<th>- PK</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_0 = 0$ kg N/ha</td>
<td>2 plots</td>
<td>2 plots</td>
<td></td>
</tr>
<tr>
<td>$N_1 = 56$ kg N/ha</td>
<td>2 plots</td>
<td>2 plots</td>
<td></td>
</tr>
<tr>
<td>$N_2 = 112$ kg N/ha</td>
<td>2 plots</td>
<td>2 plots</td>
<td></td>
</tr>
<tr>
<td>$N_3 = 224$ kg N/ha</td>
<td>2 plots</td>
<td>2 plots</td>
<td></td>
</tr>
</tbody>
</table>

$P = 56$ kg P/ha as triple superphosphate.  
$K = 56$ kg K/ha as muriate of potash.

**Straw Experiment**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>2 plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td></td>
</tr>
<tr>
<td>Straw treated</td>
<td></td>
</tr>
</tbody>
</table>
nitrogen addition was as urea; all subsequent additions were in the form of ammonium nitrate. Since the aim was to keep nitrogen concentrations within a narrow targeted range, the decision to apply fertilizer was based on foliar nutrient concentrations from the previous year. Table 2 lists the total amount of nitrogen applied each year in an attempt to maintain foliar N concentrations at 1.4% N = N₁; 1.8% N = N₂ and 2.2% N = N₃ (Weetman and Algar, 1974).

The straw treatment was established on 0.25 ha square plots. These plots received approximately 3.6 metric tons of straw which was applied to a depth of 60 cm on top of the snow in March, 1970 (Figure 4). In the following years, these plots received no further treatments.

3.3 Sample Preparation and Laboratory Methods

For the laboratory and greenhouse studies, 5 humus samples, 30 x 30 cm, were collected randomly from each plot in late August, 1979. Placed in polyethylene bags and shipped to the laboratory, they were air dried and stored at 1-2°C until processed. Litter was collected at the same time from seven plastic trays 25.5 cm x 52.5 cm which had been located randomly on each of the treated sites early in June, 1979. The litter was transported in paper bags and stored at 1-2°C.

Humus samples destined for chemical analysis were air-dried, sieved through a 6 mm sieve and the resulting organic mixtures of L, F and H horizons ground in a Wiley Mill to pass through a 20 mesh screen. Humus samples were then oven-dried at 70°C for 48 hours. Analysis was completed on 10 humus samples per plot. Humus used in the incubation
TABLE 2. Amount and time of fertilizer applied to a jack pine stand during the 10-year period.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Fertilizer applied/year (kg/ha)</th>
<th>Total (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N0</td>
<td>-      -      -      -      -      -      -</td>
<td>336</td>
</tr>
<tr>
<td>P</td>
<td>56     56     56     56     56     56     -      336</td>
<td>336</td>
</tr>
<tr>
<td>K</td>
<td>56     56     56     56     56     56     -      336</td>
<td>336</td>
</tr>
<tr>
<td>N1</td>
<td>56     56     56     56     56     56     56     336</td>
<td>336</td>
</tr>
<tr>
<td>P</td>
<td>56     56     56     56     56     56     56     336</td>
<td>336</td>
</tr>
<tr>
<td>K</td>
<td>56     56     56     56     56     56     56     336</td>
<td>336</td>
</tr>
<tr>
<td>N2</td>
<td>112    112    112    112    112    112    112    672</td>
<td>336</td>
</tr>
<tr>
<td>P</td>
<td>56     56     56     56     56     56     56     336</td>
<td>336</td>
</tr>
<tr>
<td>K</td>
<td>56     56     56     56     56     56     56     336</td>
<td>336</td>
</tr>
<tr>
<td>N3</td>
<td>224    224    224    224    224    224    224    1344</td>
<td>336</td>
</tr>
<tr>
<td>P</td>
<td>56     56     56     56     56     56     56     336</td>
<td>336</td>
</tr>
<tr>
<td>K</td>
<td>56     56     56     56     56     56     56     336</td>
<td>336</td>
</tr>
</tbody>
</table>
Figure 4. Straw application on top of snow in early March, 1970.
study was not ground after sieving but was bulked for each plot.

A vegetation survey was undertaken at the time the samples were collected in the field. For each plot, 5 subplots of 1 m² diameter were randomly laid out and the percent presence, abundance and sociability estimated using the Braun-Blanquet (1932) method of analysis.

Total depth of the L, F and H layers was measured in the field on the original large humus squares dug out of the forest floor. Measurements were taken at opposite corners and the average for each pair calculated. This gives two values for each sample block and 10 values for each plot.

In order to determine humus weight, 100 cm² subsamples were cut from each of the larger humus squares, giving a total of 10 samples per plot. Green mosses were removed and roots larger than 1 cm in diameter and not in a recognizable state of decomposition were removed. Samples were oven-dried at 105°C for 48 hours before weighing. Litter weights for each tray were determined after oven drying at 70°C for 48 hours.

Humus samples were redried prior to nutrient analysis. For total nitrogen and phosphorus determinations, a modified Kjeldahl digestion (Twine and Williams, 1971) was used. For each sample, 0.2 g of humus was weighed and digested for 12 hours in 5 mL of digestion solution (100 g potassium sulphate and 1 g selenium in 1 L concentrated H₂SO₄) at about 300°C, the samples were diluted to 100 mL with distilled water and analysed on the Technicon Autoanalyser.
Nitrogen was determined using an ammonia cartridge of a Technicon Auto-Analyser which makes use of the Berthelot reaction (reaction of ammonia with sodium phenate and sodium hypochlorite to yield a blue indophenol complex which is quantified in a colorimeter). Phosphorus was determined using an ortho-phosphate cartridge of a Technicon Auto-Analyser and involves formation of a reduced phospho-molybdate complex, which is quantified in a colorimeter. Results are given as percent of the original dry weight.

To determine potassium, magnesium and calcium concentrations, 1.0 g of humus sample was ashed at 400°C for three hours. The ash was then dissolved in 7.5 mL of 20% HCL by heating gently on a hotplate. Distilled water was added to make 100 mL and the sample analysed on a Varian Techtron Atomic Absorption Spectrophotometer using an air-acetylene flame. Following the addition of La2O3, calcium concentrations were analysed with a nitrous oxide-acetylene flame. Results are expressed as percent of the original sample dry weight.

The pH of 10 humus samples from each plot was measured using one gram of air dried humus, finer than 2 mm. The humus was weighed into 50 mL beakers and 8.0 mL of distilled water added. The pH was measured to the nearest 0.1 unit. To lessen the salt effect, 0.5 mL of 0.165 M CaCl2 was added to each sample beaker and the pH remeasured. This method gives an approximate 1:8 dilution in water and 0.01 M CaCl2.

Exchangeable cations and total exchange capacity of the humus was analysed using the sodium chloride method. For exchangeable cations, 2.0 g of sample was weighed into tubes and 30 mL of 1.0 M
NaCl solution added. The tubes were then shaken for one hour and the contents transferred to Buchner vacuum suction funnels fitted with Whatman No. 5 filter paper. The humus was washed with 70 mL NaCl, the leachate transferred to 250 mL volumetric flasks and diluted to volume with distilled water. The extract was mixed well and analysed on the Atomic Absorption Spectrophotometer for K, Ca and Mg.

To determine cation exchange capacity (C.E.C.), the funnels containing the saturated humus sample were replaced onto the filtering flasks, washed with 100 mL of isopropanol and the leachate discarded. The humus was then washed with 100 mL 1.0 N KCl and the leachate transferred to 250 mL volumetric flasks. The flasks were diluted to volume with distilled water, mixed well and analysed for Na on the Atomic Absorption Spectrophotometer.

Soil organic matter was determined titrimetrically using the Walkley-Black method. Air dried soil was ground with an agate mortar and pestle to pass through a 35 mesh screen. Because of the very high organic matter content, 0.1 g of humus was weighed into 250 mL Erlenmeyer flasks. Exactly 15 mLs of 1 N K₂Cr₂O₇ was added and the flasks swirled to disperse the humus in the solution. Then 30 mLs of concentration H₂SO₄ was added and the flasks immediately swirled for 1 minute and left digesting for a total of 30 minutes. The solution was diluted with 150 mL of distilled water and several drops of Ferroin indicator added. The solution was then titrated with 0.5 N FeSO₄. Results were calculated and reported as % C.

To examine the pattern of release of NH₄⁺-N and NO₃⁻-N during decomposition, incubation studies were carried out. Air dried humus,
finer than 6 mm, was bulked for each treatment and 5.0 g equivalent dry weight of humus weighed into 4 oz plastic jars with screw caps. The samples were moistened with 15 mL distilled H₂O to approximate 65% of the water holding capacity of the humus and this moisture content was maintained throughout the incubation study by periodically adding distilled water to restore the samples to their original weights. The caps were placed loosely on top and the jars placed in a thermostatically controlled incubator and maintained at 20°C under aerobic conditions. At regular intervals (0, 2, 4 and 8 weeks) three jars were removed. The available nitrogen was extracted by shaking the contents of the jar with 50 mL KCL for one hour. The supernatant was filtered through a Whatman No. 42 filter paper and analysed for NH₄⁺ and NO₃⁻-N (Keeney and Nelson (1982) on a Technicon Autoanalyser.

The bioassay experiments were carried out in the greenhouse at the University of British Columbia. Ten intact humus samples (L,F,H) from each treated plot were trimmed to fit 20 cm diameter pots. The pots were filled with enough sand so that the surface of the humus layer was kept about 3 cm below the top of the pot. In the greenhouse, the pots were placed in a completely random design under phosphorescent grow lights and the pots location changed periodically.

The pots were sown in October 1979 with jack pine seed collected from a tree adjacent to the experimental plots. Enough seed was sown to ensure 12-15 germinants in each pot (Figure 5). The grow lights were set for one month at 12 hours, one month at 14 hours, two months at 16 hours and then back to one month at each of 14 and 12 hours.
Figure 5. Jack pine seedlings growing on treated humus in the greenhouse.
This gave a total of six active growing months. The soil in the pots was kept moist.

In early May, 1980, the seedlings were harvested. They were carefully removed from the humus in order to preserve as much of the root system as possible. Roots were washed clean and shoot and root weights determined after oven drying for 48 hours at 70°C.

Nutrient analysis was completed on the foliage and followed the procedure as outlined above for the humus. Results are given as percent of the original dry weight.

3.4 Statistical Analysis

In order to compute the analysis of variance for the individual parameters, the optimum nutrition experiment was treated as a completely randomized block design. The factor ±PK was analysed as the block effect, the factor N as treatment level and the sample observations were nested within the replications. The analysis was based on the following linear model:

\[ Y_{ijkl} = \mu + \alpha_i + \gamma_j + \omega_{ij} + \lambda_{(ij)l} + \varepsilon_{(ijl)k} \]

Where:

- \( Y_{ijkl} \) = measurement of the \( k \)th observation in the \( l \)th replication in the \( j \)th treatment in the \( i \)th block,
- \( \mu \) = mean of all observations,
- \( \alpha \) = effect of the \( i \)th block (±PK),
- \( \gamma \) = effect of the \( j \)th treatment (\( N_0, N_1, N_2, N_3 \)),
- \( \omega \) = effect of the \( ij \)th interaction,
- \( \lambda \) = effect of the \( (ij)l \)th interaction,
- \( \varepsilon \) = random error.
\[ \omega \ ij = \text{effect of the interaction between the } i^{th} \text{ block, and } j^{th} \text{ treatment (N x PK)}, \]

\[ \lambda (ij)l = \text{effect of the } l^{th} \text{ replication in the interaction between the } i^{th} \text{ block and } j^{th} \text{ treatment}, \]

\[ \epsilon (ijl)k = \text{experimental error}. \]

Sources of variation, degrees of freedom and expected mean squares for the analysis of variance are given in Table 3. The interaction between the variability within treatments and the variability within observations was tested for significance. If found significant, no further data analysis was performed. If the interaction was not significant, the two sources of variation were pooled to create a new, larger, source of variation. The analysis of variance was performed using this experimental error. Duncan's Multiple Range Test (Steel and Torrie, 1980) was used to compare treatment means with \( P = 0.05 \). Because some of the measured characteristics are commonly expressed as a percentage, an arc sine transformation (Gilbert, 1973) was used to normalize the data distribution.
TABLE 3. Analysis of variance table.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>Expected mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>PK</td>
<td>b-1</td>
<td>SS_I</td>
<td>MS_I</td>
<td>$\sigma^2_e + K_1\sigma^2_r + K_3\sigma^2_{PK}$</td>
</tr>
<tr>
<td>N</td>
<td>t-1</td>
<td>SS_Ii</td>
<td>MS_Ii</td>
<td>$\sigma^2_e + K_1\sigma^2_r + K_2\sigma^2_N$</td>
</tr>
<tr>
<td>PK x N</td>
<td>(b-1)(t-1)</td>
<td>SS_III</td>
<td>MS_III</td>
<td>$\sigma^2_e + K_1\sigma^2_r + K_4\sigma^2_{PK*N}$</td>
</tr>
<tr>
<td>Variability within treatments</td>
<td>bt(r-1)</td>
<td>SS_IV</td>
<td>MS_IV</td>
<td>$\sigma^2_e + K_1\sigma^2_r$</td>
</tr>
<tr>
<td>Variability within observations</td>
<td>btr(m-1)</td>
<td>SS_V</td>
<td>MS_V</td>
<td>$\sigma^2_e$</td>
</tr>
</tbody>
</table>

Where:

- $b$ = no. of blocks (PK) = 2
- $t$ = no. of treatments (N) = 4
- $r$ = no. of replications (R) = 2
- $m$ = no. of observations = 10
- $\sigma^2_e$ = residual variance
- $\sigma^2_r$ = variance between replications
- $\sigma^2_{PK*N}$ = variance due to interaction between PK and N
- $\sigma^2_N$ = variance due to N
- $\sigma^2_{PK}$ = variance due to PK
- $K_1 - K_4$ = coefficients of the variance components.
4.0 RESULTS AND DISCUSSION

4(a) SOME PHYSICAL-CHEMICAL CHANGES IN THE GROUND VEGETATION, LITTER AND HUMUS

Following 10 years of sustained nitrogen additions or a single heavy straw application, both visual physical and chemical changes were evident in the organic matter and ground vegetation. This chapter will deal with some of these changes revealed by field and laboratory analyses.

4.1 Ground Vegetation

The moss, herb and shrub layers were examined to ascertain the effects of the various treatments. As a secondary component of the forest ecosystem, this lesser vegetation is affected by the chemical and physical characteristics of the forest floor and soil.

A summary of the ground vegetation survey is given in Table 4. The control plots exhibited the typical Kalmia-Vaccinium association as seen in Figure 3. These shrubs cover much of the forest floor whereas the moss and lichen layer appear in somewhat smaller patches. As the nitrogen levels are increased (Figure 6), both the abundance and sociability of the shrub layer is decreased until at the N₃ level Kalmia covers under 5% of the plots and occurs singly rather than covering the ground. Vaccinium covers less than 25% but still grows in clumps. Large nitrogen additions also effectively reduces the moss layer and eliminates Cladonia rangiferina entirely. Instead,
TABLE 4. Ground vegetation analysis of the optimum nutrition and straw experiments.

<table>
<thead>
<tr>
<th>Vegetation Treatments</th>
<th>Kalmia angustifolia</th>
<th>Vaccinium angustifolium</th>
<th>Pleurozium schreberi</th>
<th>Polytrichum spp.</th>
<th>Other species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>*</td>
<td>+</td>
<td>*</td>
<td>+</td>
<td>*</td>
</tr>
<tr>
<td>-PK N₀</td>
<td>100 3.3</td>
<td>100 5.4</td>
<td>100 3.3</td>
<td>100 3.3</td>
<td>2.2 Cladonia rangiferina</td>
</tr>
<tr>
<td>N₁</td>
<td>100 3.2</td>
<td>100 2.2</td>
<td>100 4.4</td>
<td>10 +</td>
<td>1.1 Cladonia rangiferina</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ Hypnum crista-cristensis</td>
</tr>
<tr>
<td>N₂</td>
<td>90 2.2</td>
<td>90 2.3</td>
<td>80 2.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N₃</td>
<td>90 1.1</td>
<td>100 2.2</td>
<td>10 +</td>
<td>10 +</td>
<td>+ Sambucus canadensis</td>
</tr>
<tr>
<td>+PK N₀</td>
<td>100 2.2</td>
<td>90 2.2</td>
<td>80 3.4</td>
<td>10 +</td>
<td>1.1 Cladonia rangiferina</td>
</tr>
<tr>
<td>N₁</td>
<td>90 3.3</td>
<td>90 3.3</td>
<td>100 2.3</td>
<td></td>
<td>+ Solidago macrophylla</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.1 Carex spp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ Sambucus canadensis</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ Hieracium pratense</td>
</tr>
<tr>
<td>N₂</td>
<td>100 2.2</td>
<td>10 +</td>
<td>50 1.2</td>
<td>10 +</td>
<td>+ Viburnum cassinoides</td>
</tr>
<tr>
<td>N₃</td>
<td>20 1.1</td>
<td>30 2.2</td>
<td>10 +</td>
<td>40 1.2</td>
<td>2.2 Carex and Calamagrostis spp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ Solidago macrophylla</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.1 Solidago macrophylla</td>
</tr>
<tr>
<td>Straw treatment</td>
<td>100 2.1</td>
<td>100 2.1</td>
<td>100 2.2</td>
<td>100 1.2</td>
<td>+ Sambucus canadensis</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.2 Aster spp.</td>
</tr>
</tbody>
</table>

* Frequency of occurrence (%).
+ Degree of abundance. Scale: + = rare; 1 = <5%; 2 = 5-25%; 3 = 25-50%; 4 = 50-75%; 5 = >75%.
° Degree of sociability. Scale: 1 = isolated; 2 = troup; 3 = patches; 4 = colonies; 5 = complete coverage.
Figure 6. Reduction of the Kalmia-Vaccinium shrub layer in a jack pine stand following $N_2$ treatments.
other species such as *Carex trisperma* and *Sambucus* cover the forest floor (Figure 7).

On plots receiving additions of phosphorus and potassium as well as nitrogen, results mirror those found on plots not receiving these additional nutrients. On plots receiving only P and K, the shrub layer was much reduced when compared to the controls. Additions of nitrogen raised the percent presence somewhat at the N₁ PK level, but as nitrogen additions increase, there is a marked drop in frequency and abundance. *Pleurozium* is reduced until at the N₃PK level it occurs only sparsely on 10% of the sample plots. However, the occurrence of exotic species such as *Solidago macrophylla*, *Viburnum cassinoides*, *Viola*, *Aster*, *Sambucus* and *Carex* species is more frequent than on plots not receiving P and K additions.

As seen in Figure 8 the straw addition was very effective in smothering the ground vegetation. Now, 10 years later, the original ground vegetation seems ready to re-dominate the site. The moss and shrub layer all exhibited 100% frequency in the sample plots, but the abundance rating is still low. It is highly likely that many more years will be required to eliminate the effects of the straw.

It is known that the existing ground vegetation is a very active competitor for added nutrients. Their roots are much closer to the surface than tree roots, enabling them to absorb greater quantities of nutrients than trees per unit weight. However, plant species have varying capabilities in reacting to changes in the nutrient status. In this case, the *Kalmia* and *Vaccinium* species were not particularly effective in utilizing the available nitrogen since they decreased in
Figure 7. Appearance of exotic species in a jack pine stand following $N_3$ treatments.
Figure 8. A straw application effectively reduced the Kalmia - Vaccinium shrub layer for almost 10 years in a jack pine stand.
both frequency and abundance with increasing nitrogen additions. Damman (1971) studying a Kalmia heath in Newfoundland, found total soil nitrogen to be very high, but it was not in an available form to the plant. Kalmia appears capable of dominating a site and maintaining itself indefinitely on substrates with low decomposition and mineralization rates and a corresponding immobilization of nutrients. The increased nutrient availability, especially of nitrogen, was obviously detrimental to the ericaceous vegetation growing on plots receiving high nitrogen additions.

Other investigators have reported similar results. Following fertilization with nitrogen, phosphorus and lime, Viro (1965) noted that on a Scots pine site in Finland, over 50% of the Vaccinium had died. He attributed this phenomenon to frost. Because of the extra nutrients available, growth continued later than normal. This resulted in the cellular tissue being unable to lignify before winter. Thus, although Vaccinium is hardy in its resistance to climate, on poor soils it seems sensitive to variations in fertility (Schroeter, 1923).

Whether frost accounts for the dramatic reduction of the ericaceous vegetation in this case is doubtful. However, since no observations were made on possible frost damage, it may have been a contributing factor. Interestingly, there was increased tree mortality on higher nitrogen plots which possibly may have been caused by frost. In a similar experiment in Sweden, Tamm (1974) noted climate injuries such as "winter drought" increased markedly with nitrogen fertilization.
Other researchers have noted that fertilizer application can cause a "burning" effect on lesser vegetation— including mosses and lichens. Roberge et al. (1968) noted the toxic effects to feather mosses following fertilization with 450 kg urea-N/ha, with the moss flora turning brown and dying. Studying the effect of N, P and K fertilization on the ground vegetation in Norway spruce stands in Finland, Mäkkenen et al. (1980) noted that the moss coverage declined immediately following fertilization. Even after eight years, the moss had not completely recovered. Similarly in this study, *Pleurozium schreberi* decreased with additions of more nitrogen but there is no definite trend evident with *Polytrichum*, as its occurrence is sporadic in most cases. *Cladonia* however, disappeared at the N₂ level. These high nitrogen amounts were most likely toxic, not only to the moss and lichen layer but to the ericaceous vegetation as well.

Although the existing vegetation did not respond favourably to the changed environment, other species did. For example, grasses and herbs became more abundant with higher nitrogen additions. Mäkkenen et al. (1980) also noted that grasses and herbs benefited from nitrogen fertilization. Jeglum (1971) investigated the relationship between the vegetational community and the pH of the upper soil horizon. He found the abundance of *Carex* and *Calamagrostis* sp. greater at a higher pH range of 4.0-4.9. These grasses first appear on the N₁PK plots which were found to have a pH of about 3.8 (see Figure 13). They increased in abundance on the N₂PK (pH 4.0) but declined somewhat at the N₃PK treatment level. This treatment recorded a drop in the hydrogen ion concentration to a pH of 3.8. On plots not receiving PK
additions, the grasses did not appear until the N₃ treatment level, which had an average pH of 3.9. All other plots had much lower pH values.

4.2 Humus Weight and Litterfall

4.2.1 Results

4.2.1.1 Humus mass and depth

Estimates of average total humus weight (kg/ha) for each treatment as well as the average depth (cm) are presented in Figures 9 and 10. Additionally, photographs taken in the field show the differences between the N₁ (Figure 11) and N₃ (Figure 12) treated humus layers. The results for both variables can be summarized as follows:

1. The addition of nitrogen significantly affected both the weight and depth of the humus.

2. Additions of PK did not significantly affect these two variables.

3. The largest increase in both weight and depth occurs at the N₁ level. Humus weight increases by more than 65% compared to the control and the depth increases by more than 2 cm.

4. Further additions of nitrogen decreased the weight compared to the N₁ level, but weights still remained higher than the control.

5. Increased nitrogen additions had a similar effect on the depth. However, the shrinking of the humus layer was more dramatic than the weight loss with the average for the N₃ level being 2 cm lower than the control.
Figure 9. Estimates of the average weight (kg/ha) of the combined L, F, H humus layers (± standard deviation) of the optimum nutrition experiment and straw treatment plots.
Figure 10. Average forest floor depth (cm) of the optimum nutrition experiment and straw treatment plots (± standard deviation).
Figure 11. Humus weight and depth increased dramatically following $N_1$ treatments.
Figure 12. With increased nitrogen additions, humus layers decreased in weight and depth as shown here on N$_3$ treated humus.
6. Results for the humus receiving the PK additions generally reflect those trends found on the plots receiving nitrogen alone. Still, the PK treatments appeared to reduce some of the dramatic changes as both Figures 9 and 10 show.

7. The addition of the straw significantly affected the weight of the humus but its effect on the depth was not significant.

4.2.1.2 Litter

Estimated three month litter weights for each treatment, separated into the components foliage, bark and total weights, are presented in Table 5. To provide a better interpretive tool in explaining decomposition rates, the decomposition rate factor \( (k) \) (Olsen, 1963) was calculated using the equation \( (k = \frac{L}{X_{ss}}) \). Here, \( L = \) annual litterfall (3 month litter data calculated on a yearly basis by multiplying the 3 month litter data by 4) and \( X = \) weight of the forest floor. The \( k \) values for each treatment are also given in Table 5.

Although the field data did not show statistical differences between the nitrogen levels nor the PK additions, the trend shows that fertilizer applications increased the total amount of litterfall. Foliage litter weights increased slightly with larger nitrogen additions and were also higher on PK plots. No trends are discernible for the bark litter so that total litter weights reflect the foliage litter pattern. Litter weights for the straw treatment were much higher than the control for each of the litter components.
TABLE 5. Estimated three month litter weights (kg/ha) in the treated jack pine stand and their corresponding above ground decomposition rate factor $k$, calculated on an annual basis.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Foliage</th>
<th>Bark</th>
<th>Total</th>
<th>$k \times 10$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_0$</td>
<td>151.5</td>
<td>101.9</td>
<td>253.5</td>
<td>.237</td>
</tr>
<tr>
<td>$N_1$</td>
<td>182.5</td>
<td>92.8</td>
<td>275.1</td>
<td>.155</td>
</tr>
<tr>
<td>$N_2$</td>
<td>248.5</td>
<td>77.5</td>
<td>326.0</td>
<td>.228</td>
</tr>
<tr>
<td>$N_3$</td>
<td>228.8</td>
<td>104.9</td>
<td>333.6</td>
<td>.263</td>
</tr>
<tr>
<td>$N_0PK$</td>
<td>170.4</td>
<td>55.5</td>
<td>223.9</td>
<td>.164</td>
</tr>
<tr>
<td>$N_1PK$</td>
<td>267.2</td>
<td>107.6</td>
<td>374.7</td>
<td>.233</td>
</tr>
<tr>
<td>$N_2PK$</td>
<td>205.5</td>
<td>200.9</td>
<td>406.5</td>
<td>.313</td>
</tr>
<tr>
<td>$N_3PK$</td>
<td>291.3</td>
<td>78.0</td>
<td>368.9</td>
<td>.268</td>
</tr>
<tr>
<td>Straw</td>
<td>241.1</td>
<td>133.6</td>
<td>374.5</td>
<td>.258</td>
</tr>
</tbody>
</table>
4.2.2 Discussion

The results show that the lowest level of nitrogen addition resulted in the largest accumulation of organic matter. Since the litter weights for N1 were only slightly higher than the controls, the majority of the organic matter buildup must be due to a slower rate of decomposition. In fact, the calculated k value was found to be the lowest of all treatments. The periodic small doses of nitrogen seemed not to have stimulated the microorganisms into increased mineralization rates as other investigators have reported (Mahendrappa, 1978).

Addition of 1,344 kg N/ha did increase the decomposition over the 10 year period. The k value was calculated at 0.0263 and the total humus depth on the N3 plots had shrunk considerably in spite of the increased litter input. Total humus weight was still somewhat higher than the controls however, suggesting that the most of the cellulose and hemicellulose had decomposed, leaving more decay resistant phenols, waxes and other materials behind. Investigating the decay curves for individual substrate fractions and their reflection on the total weight loss, Minderman (1968) found annual loss rates varying from 10%, 25% and 50% for phenols, waxes and lignin respectively. Indeed, the humus on these high nitrogen plots felt 'greasy' to the touch, which may have been caused by the relatively high concentrations of these waxes and possibly the phenol components.

Addition of PK and nitrogen increased decomposition rates even more, with humus on the N2PK plots having the highest decomposition
rate factor of all treatments. Average humus weight was still higher than the control, but this was likely due to the larger amounts of litter which fell on the N\textsubscript{2}PK plots (Table 5).

The influence of the PK additions to increasing the organic matter decomposition is probably due more to the addition of phosphorus than potassium. Phosphorus was found to increase decomposition rates when coupled with nitrogen additions (Kelly and Henderson, 1978; Mahendrappa, 1978). The application of PK alone however, decreased the k factor ($k = 0.0164$) considerably suggesting that nitrogen was a limiting factor in controlling the decomposition rate. Kelley and Henderson (1978) reported similar results. In their litter decomposition study, additions of P alone decreased the microflora populations and significantly retarded decomposition.

The straw application consisted of 3.7 metric tons of straw applied on top of the forest floor. Almost 10 years later, this straw is still visible as a distinct layer within the humus formation. Total humus weight has increased by more than 15,000 kg/ha over the controls and is partly the result of over 1,500 kg/ha litter falling on the forest floor.

Still, decomposition rates are high, illustrating that nitrogen is not limiting microorganism activity in spite of the high C/N ratio normally attributed to straw. Indications that smothering the ground vegetation was so successful that substantially more nitrogen was available for tree growth. The increased litterfall and straw is now supporting an active microbial population as reflected in the high decomposition rate factor.
4.3 **Humus pH**

4.3.1 **Results**

The results of the pH determinations recorded in H₂O and CaCl₂ solutions are presented in Figure 13. Although a significant interaction between N and PK was found to occur at the N₃, N₃PK level, Figure 13 does show the following trends:

1. Additions of PK significantly raised the pH on all but the N₃ PK plot which recorded a slightly lower value than N₃.
2. Increased nitrogen application also increased the pH in most instances. However, this increase was not found to be significant.
3. The straw treated plots had significantly higher hydrogen ion concentrations compared to the control plots.

4.3.2 **Discussion**

The pH has important influences on the nitrogen transformation processes which occur in the organic layers. Therefore, it was one of the first humus characteristics measured.

Generally, the pH of the control plots was low, as can be expected from a humus formed under a jack pine stand. The pH was significantly raised however, when PK was added. Much of this increase was due to the calcium content of the phosphorus fertilizer. Triplesuperphosphate was used as the P source and in this form it can contain 12-16% calcium (Jones, 1979). In fact, the calcium content of the humus was found to be significantly higher on those plots which
Figure 13. Average pH of the humus (± standard deviation) measured in 1:8 dilution distilled H₂O and 0.01 M CaCl₂.
received PK additions. The cause for the pH decline at the N3PK treatment level relative to N2PK, is uncertain. A measurement error cannot be discounted but other variables investigated seem to indicate that the pH drop may be real.

Effect of the nitrogen additions on the pH can be seen on those plots not receiving PK additions. This increase is in contrast to most investigators, who have found no increase in humus pH values following fertilization with ammonium nitrate. In fact, slight decreases are generally reported when using this inorganic nitrogen form (Overrein, 1967; Weetman et al. 1972). Because nitrogen salts are readily ionized in the soil solution, the \( \text{NO}_3^- \) is moved easily out of the soil system. At the same time, increased leaching of bases occurs as the \( \text{Ca}^{++} \), \( \text{Mg}^{++} \) and \( \text{K}^+ \) move down with the nitrate.

Results of the optimum nutrition experiment show a slight decline at the N1 level. But, as larger doses of ammonium nitrate are applied, the pH increases. Possibly, the organic exchange sites have become so saturated with the ammonium ion, that they accept \( \text{OH}^- \) groups and form ammonium hydroxide.

The interaction between the N and PK levels was mentioned above. This interaction chiefly occurred at the N3PK level. Whereas the pH increases as more nitrogen is added, the addition of PK adversely affected the highest nitrogen level by decreasing the pH somewhat. This interaction however, was found significant for the pH recorded in \( \text{H}_2\text{O} \) only. The pH values measured in \( \text{CaCl}_2 \) (± 0.225) were less variable than those recorded in \( \text{H}_2\text{O} \) (± 0.244) and this may explain why the interaction was not significant in \( \text{CaCl}_2 \).
The pH of the straw treated plots was substantially higher than the controls. The straw came from a local farm and it seems reasonable to assume that the original pH of the straw was higher than the acid humus on which it was placed. During the past 10 years, however, this straw layer has undergone considerable decay. Since the products of decomposition are predominantly acid, a continuous decrease in the pH of this substrate has likely occurred.

The dispersion of organic matter has been related to increases in the pH (Hubert and Gonzales, 1970; Ogner, 1972; Salonius, 1972). With the solubilization of organic matter, the availability of carbon is increased. Salonius (1972) and Foster (1979) found microbial activity not limited initially by the nitrogen but rather by unavailable organic substrate. With the increase in humus pH following heavy fertilizer application, heretofore unavailable carbon sources may have become available for microbial use, resulting in increased decomposition rates as discussed above.

The pH of the humus also has very important influences on the nitrogen transformation processes which occur in the humus. For example, ammonia volatilization losses are greater when the pH is increased (Bernier et al., 1969; Weetman and Algar, 1974). At higher pH values, the phenolic hydroxyl and carboxyl groups of organic matter tend to dissociate and become more reactive. Ammonium ions may then be subjected to non-biological immobilization by reacting with the lignin or other organic constituents (Nömmik, 1970; Allison, 1973). The highly acid conditions in raw humus can explain the low level of nitrification in boreal forests. Roberge and Knowles (1966) detected
nitrification only when the pH rose above 5.6 after repeated fertilization with urea. Some nitrification is always occurring however, and a rise in the pH should result in an increase in nitrification.

4.4 Nitrogen

4.4.1 Results

4.4.1.1 Total Nitrogen

Concentrations of total nitrogen in the treated humus are given in Figure 14 and Table 6. The analysis again showed a weak interaction between PK additions and nitrogen levels. Using the estimated humus weight and the nitrogen concentration, the total amount of nitrogen in kg/ha for each treatment was calculated and the results presented in Table 6. Inspection of the data illustrates the following points:

Total nitrogen (%)

1. Average total nitrogen on the control plots was 1.15% N, with no significant increase until the N$_2$ level (1.31% N).

2. Nitrogen concentrations of the N$_3$ treated humus was down (1.24% N) in spite of the large nitrogen additions these plots received (1,344 kg N/ha).

3. The additions of P and K as a whole had no significant influence on the nitrogen concentration of the humus. However, means for the PK treatments were higher (1.25% N) than for treatments not receiving PK (1.21% N).

4. The lowest nitrogen concentration was measured on plots receiving PK only (1.11% N).
Figure 14. Average nitrogen concentration (± standard deviation) of the treated humus.
TABLE 6: Average nitrogen concentration, total nitrogen and available nitrogen ($\text{NH}_4^+ - N + \text{NO}_3^- - N$) in the treated humus (kg/ha)*.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>N-concentration (%)</th>
<th>Total-N (kg/ha)</th>
<th>Available-N (kg/ha) weeks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>N0</td>
<td>1.15ab</td>
<td>491</td>
<td>5.1</td>
</tr>
<tr>
<td>Ni</td>
<td>1.16ab</td>
<td>814</td>
<td>12.1</td>
</tr>
<tr>
<td>N2</td>
<td>1.31ef</td>
<td>749</td>
<td>30.0</td>
</tr>
<tr>
<td>N3</td>
<td>1.24de</td>
<td>628</td>
<td>27.2</td>
</tr>
<tr>
<td>N0PK</td>
<td>1.11a</td>
<td>605</td>
<td>11.7</td>
</tr>
<tr>
<td>N1PK</td>
<td>1.20bc</td>
<td>772</td>
<td>11.8</td>
</tr>
<tr>
<td>N2PK</td>
<td>1.31ef</td>
<td>680</td>
<td>16.0</td>
</tr>
<tr>
<td>N3PK</td>
<td>1.38f</td>
<td>760</td>
<td>27.6</td>
</tr>
</tbody>
</table>

* Values in the same vertical column followed by the same letter are not significantly different (P < 0.05).

**One plot only.

| N0         | 1.15a               | 441             | 5.1 | 16.2 | 17.9 | 19.5 |
| Straw      | 1.38b               | 800             | 13.4 | 45.8 | 45.9 | 46.50 |

* Values in the same vertical column followed by the same letter are not significantly different (P = <0.05).
5. The highest % N was recorded on the N3PK (1.38% N) which had received the largest nitrogen additions and the PK treatments.

6. The straw plots also recorded high concentrations (1.38% N) although these plots had received no nitrogen additions.

Total nitrogen (kg/ha)

1. All treated plots recorded higher total nitrogen amounts compared to the control.

2. The N1 level contained the largest amount of nitrogen with substantial declines at the N2 and N3 level.

3. Additions of PK alone increased the nitrogen by more than 100 kg N/ha.

4. Subsequent nitrogen and PK additions raised total nitrogen, but the results were not uniform.

5. The straw plots recorded very high amounts, second only to the N1 level.

4.4.1.2 Available Nitrogen

The available NH4\(^+\)-N and NO3\(^-\)-N concentrations of the humus determined during the incubation study are listed in Table 7. In order to better evaluate the magnitude of the processes involved, some of the data were graphed and are presented in Figures 15 to 18. The available nitrogen content for each treatment was calculated by using estimated humus weight and the available nitrogen concentration. The results are listed in Table 6.
TABLE 7. Available nitrogen (ppm) in the humus layer following eight weeks of incubation at 20°C and 60% WHC*.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>NH$_4^+$-N</th>
<th>Time (weeks)</th>
<th>NO$_3^-$-N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>$N_0$</td>
<td>105a</td>
<td>364ab</td>
<td>401b</td>
</tr>
<tr>
<td>$N_1$</td>
<td>160b</td>
<td>433c</td>
<td>453c</td>
</tr>
<tr>
<td>$N_2$</td>
<td>509g</td>
<td>811e</td>
<td>864f</td>
</tr>
<tr>
<td>$N_3$</td>
<td>500g</td>
<td>653d</td>
<td>808e</td>
</tr>
<tr>
<td>$N_0PK$</td>
<td>200d</td>
<td>319a</td>
<td>317a</td>
</tr>
<tr>
<td>$N_1PK$</td>
<td>176c</td>
<td>390bc</td>
<td>397b</td>
</tr>
<tr>
<td>$N_2PK$</td>
<td>280e</td>
<td>425c</td>
<td>470c</td>
</tr>
<tr>
<td>$N_3PK$</td>
<td>374f</td>
<td>606d</td>
<td>597d</td>
</tr>
</tbody>
</table>

*Values in the same vertical column followed by the same letter are not significantly different (P < 0.05).
Figure 15. Total available nitrogen (NH$_4^+$-N and NO$_3^-$-N) in the humus of the control, and N$_2$ treated plots following 0, 2, 4 and 8 weeks incubation at 20°C and a water content of 60% WHC.
Figure 16. Total available nitrogen (NH$_4^+$-N and NO$_3^-$-N) in the humus of the N$_3$ treated plots following 0, 2, 4 and 8 weeks incubation at 20°C and a water content of 60% WHC.
Figure 17. Total available nitrogen (NH$_4^+$-N and NO$_3^-$-N) in the humus of the N$_2$PK and N$_3$PK treated plots following 0, 2, 4 and 8 weeks incubation at 20°C and a water content of 60% WHC.
Figure 18. Total available nitrogen (\(NH_4^+\)-N and \(NO_3^-\)-N) in the humus of the straw treated plots following 0, 2, 4 and 8 weeks incubation at 20°C and a water content of 60% WHC.
Under the conditions reported here, an increase in the concentration of NH$_4^+$-N is the result of mineralization of the organically bound nitrogen and is brought about by the microorganisms present in the humus. The increase in NO$_3^-$-N concentration is the result of the actions of nitrifying bacteria. Total available nitrogen rises when the sum of NH$_4^+$-N and NO$_3^-$-N increases.

Immobilization of NH$_4^+$-N by the microflora leads to a decrease in NH$_4^+$-N concentration. Nitrification can also decrease NH$_4^+$-N by oxidizing ammonium to nitrate.

Following the interactions between mineralization and immobilization, the rate at which nitrogen became available showed the following trends:

1. Additions of nitrogen significantly increased the KCl extractable NH$_4^+$-N over the controls in time zero and this trend continued over the eight week period.

2. The rate of NH$_4^+$-N production was most rapid during the first two weeks of incubation for all treatments except N$_3$. At the N$_3$ level, NH$_4^+$-N production continued fairly rapidly until the fourth week.

3. Following this two week period, NH$_4^+$-N increased only slightly during the remaining weeks for the control and N$_1$ humus. For the N$_2$, N$_3$ and N$_3$PK treated humus, NH$_4^+$-N decreased in amount.

4. In plots which received PK along with N additions, the production of NH$_4^+$-N was somewhat lower, although the differences were not always significant.
5. Generally, $NO_3^-$-N levels were low on the control, PK and $N_1$ plots, with significant nitrification not recorded until the $N_2$ treatment. On the $N_3$ humus, some nitrate-N was present before incubation began, but by the eighth week, nitrate-N production was greatly increased.

6. Humus which received nitrogen and the additional PK treatments showed some $NO_3^-$-N production at the $N_2$PK level. Nitrate-N was much higher at the beginning of the incubation period for $N_3$PK, and continued at approximately the same rate throughout the experiment.

7. On the straw plots, $NH_4^+$-N levels were significantly higher than those measured for the control. In fact, ammonium-N levels were higher than those recorded for the $N_3$PK level and almost as high as those recorded on $N_3$ humus. Nitrate-N remained low.

4.4.2 Discussion

The optimum nutrition experiment provided an excellent opportunity to study what effect increases in nitrogen supply had in changing the nitrogen cycle on a low nitrogen site. Generally, the nitrogen additions did raise the nitrogen concentrations of the humus as shown in Figure 14. In some cases however, the increases seemed much smaller than would be expected. For instance, at the $N_1$ level, 336 kg N/ha was applied over the 10 year period (Table 2), yet the nitrogen concentration was raised only slightly, from $N_0 = 1.15\%$ N to $N_1 = 1.16\%$ N. Further additions of 1,000 kg N/ha at the $N_3$
level raised the concentration only 0.09 units - down in fact from $N_2 = 1.31\% \text{ N}$ to $N_3 = 1.24\% \text{ N}$.

When total nitrogen (kg N/ha) is calculated for the treated humus (Table 6) a different picture emerges. Nitrogen content for the control was 491 kg N/ha and for $N_1$ 814 kg N/ha - an increase of 323 kg N/ha. Since 336 kg N/ha was applied, it appears that little was lost from the site.

At the $N_2$ level, total nitrogen was calculated at 749 kg N/ha or 258 kg N more than the control. Since $N_2$ received 672 kg N/ha, 414 kg N was either partly taken up by the vegetation, leached from the organic layers or volatilized into the atmosphere.

Although these processes were not actively investigated in this study, some inferences can be made. Some of the nitrogen at the $N_2$ level was probably leached out as $\text{NO}_3^-\text{N}$ due to the nature of ammonium nitrate. In contrast, very little of the $\text{NH}_4^+\text{N}$ was likely leached because it is readily held by the CEC of the humus. Nitrate-N remained the same for one month of the incubation period (Figure 15), increasing somewhat at eight weeks, so that the possibility of $\text{NO}_3^-\text{N}$ loss through nitrification does exist. Some loss of nitrogen through volatilization can not be discounted since an increase in humus pH occurred and amounts of available ammonium-N were large.

The remaining nitrogen was most likely taken up by the ground vegetation and trees. Nitrogen concentrations in the current year foliage for trees growing on the $N_2$ treated plots were actually kept at approximately 1.65% N (Weetman and Forunier, 1984). In a study of a $P. \text{banksiana}$ stand fertilized with 300 kg urea-N/ha,
Morrison and Foster (1977) were able to raise the nitrogen concentration to 1.26 % N. They calculated that 23% of the applied nitrogen was distributed within the trees after three years which was equal to 70 kg N/ha. It would be fair to assume therefore, that substantial amounts of nitrogen were taken up by the trees on the N₂ plots over the 10 year period considering the nitrogen concentration of the jack pine needles was much higher (Weetman and Fournier, 1984).

Remarkably, most of the applied nitrogen on the N₁ treated humus was immobilized within the humus layers. Low decomposition rates resulted in a large build-up of organic matter. This immobilized nitrogen represents a nutrient gain by the humus, which acts here as a large storage reservoir, releasing only small amounts of nitrogen for tree use.

As nitrogen additions are increased, transformation processes are greatly altered. Total nitrogen content, although higher than the control, decreases compared to the N₁ level. Available nitrogen increases substantially, especially on the N₂ and N₃ treated plots. Nitrification, first beginning at the N₂ level, becomes a major factor with the N₃ treatment. The increased potential for leaching loss of NO₃⁻-N probably accounts for the majority of nitrogen lost from the forest floor. After 10 years, only 628 kg N/ha remained of the 1,344 kg N/ha which had been applied, indicating that over 714 kg N/ha was lost or taken up by the vegetation.

With increased nitrite and nitrate production in spite of the low pH, the potential for chemodenitrification exists. Nitrite is readily transformed to nitrous acid which can be further oxidized to
nitric oxide and nitrogen dioxide. Most of the NO$_2$ so produced will react further with H$_2$O to form nitric acid and nitrous acid, but some of the NO and NO$_2$ is likely to escape. The significance of this reaction in soil has been in dispute for some time, but Nelson (1982) considers the chemical decomposition of nitrous acid an important avenue of nitrogen loss in acidic soils. Conditions favouring biological denitrification are likely to occur only infrequently, and should not result in major losses of nitrogen.

Ammonia volatilization probably does not account for large nitrogen losses either. However, volatilization can occur even at low pH ($N_3 = pH 4.9$) when organic matter of high nitrogen content decomposes (Freney et al., 1981).

Application of PK alone affected the nitrogen transformations as seen in Figures 14 and 17 and Tables 6 and 7. Decreased nitrogen concentrations as well as a reduction in the decomposition rate, very likely led to the build up of organic matter (Figure 9). However, the total nitrogen content of the humus as well as the supply of available nitrogen increased somewhat when compared to the controls. Additions of phosphorus have been shown to improve the ability of plants to recover mineral nitrogen from soils by approximately 20% (Black, 1968). Increased nitrogen uptake from the mineral soil may have contributed to increased nitrogen in the litter returning to the forest floors. When nitrogen was added with the PK, the opposite results were achieved; nitrogen concentration and decomposition rates increased but available nitrogen decreased. Furthermore, nitrification was somewhat reduced during the incubation experiment when
compared to humus treated with nitrogen alone. Viro (1963) reported similar results when phosphorus was added to incubating humus samples.

This interplay of nitrogen and phosphorus illustrates the interconnection between these two elements. Unfortunately, the linkage between nitrogen and phosphorus is not sufficiently understood. For example, Walker et al. (1959) reported that nitrogen fertility can be improved by application of phosphorus, and in this investigation available nitrogen did increase on the PK treated plots. Additions of nitrogen and PK decreased nitrogen availability however, exemplifying that the important effects of phosphorus on the mineralization processes probably involve the relative requirements of these elements by the decomposer organisms (Cole and Heil, 1981).

Nitrogen relations in the straw treated humus were very interesting and contrary to expectations. Concentrations of total nitrogen was very high (1.38% N) and the release of NH$_4^+$-N during the incubation period was likewise high. This translated into total and available nitrogen contents equal to or greater than those found on plots receiving 672 - 1,344 kg N/ha!

Weetman and Algar (1974) have speculated on the absence of nitrogen immobilization on a substrate with such a high C/N (>100) ratio. They attributed this to all or part of the following: reduced competition from the ericaceous vegetation for the limited nitrogen supply, increased nitrogen availability due to the decomposing ground vegetation or possible nitrogen-fixation on the straw layer.

Agricultural research has shown that application of substrates with high C/N ratios need not reduce decomposition of organic residues.
Studying the dynamics of carbon and nitrogen in a simulation model, McGill et al. (1981), noted that high C/N ratio of 100 had no effect on plant processes although it stimulated microbial growth. In this investigation, decomposition rates were found to be high on the straw treated humus. Ferguson (1967) reported that application of straw had not depressed cereal yield, but had in fact, increased production. Similarly, tree volume production was substantially increased on the straw plots (Weetman and Fournier, 1984).

Part of the answer may possibly lie in the addition of more easily decomposable carbohydrates as an energy source for microorganisms. Coupled with the reduction in nitrogen demand plus the nitrogen released by the decomposing ground vegetation, increased nitrogen was available for tree growth. Litter quality was possibly better, with enough nitrogen returning to the forest floor to enable a thriving microbial population to exist on the straw layer. Additionally, the higher pH of the straw as well as its better moisture holding capacity, possibly contributed to the creation of more desirable environmental conditions for microbial growth.

Although mycorrhizae were not investigated in this study, an increase in the organic matter (straw) may have led to an increase in mycorrhizal development. Mikola (1969) noted that soil moisture was very important for mycorrhizal formation because moist soils prevent mycelia from drying; hence survival is greater. Moist soils also offer better substrates for sporophore production and spore germination and a corresponding increase in mycorrhizal formation on tree roots. The straw-treated humus may have retained moisture longer than
the thin humus layer of the control plots and so promoted mycorrhizal
growth and increased nutrient procurement for the trees.

4.5  **Carbon and Decomposition**

4.5.1  **Results**

The results for the carbon (% C) and the C/N ratio are given in Table 8. With reference to this data, the conclusions are:

1. % C increases with low nitrogen additions at the N₁ level.
   Larger applications have no further effect.
2. The C/N ratio increases at the N₁ level and decreases again to control levels at the N₂, N₃ treatment levels.
3. Additions of PK alone increases the % C, and C/N ratio to their highest levels. Additions of nitrogen reduce the % C somewhat and decrease C/N ratio to control levels.
4. % C for the straw treatment reflect those values found at the control level. The C/N ratio however, is the lowest at C/N = 32.

4.5.2  **Discussion**

In general, there is a correlation between the C/N ratio of organic matter and nitrogen mineralization during decomposition, with low ratios favouring nitrogen release. However, available carbon may also limit microorganism activity, so that the C/N ratio is not as sensitive to the nitrogen mineralization rate as could be expected. Evaluating the results for the optimum nutrition and straw experiment, the ratio was generally found inadequate in explaining transformation processes.
TABLE 8. Percent carbon, and the C/N ratio of the treated humus.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>% C</th>
<th>C/N</th>
</tr>
</thead>
<tbody>
<tr>
<td>N₀</td>
<td>43.9</td>
<td>38</td>
</tr>
<tr>
<td>N₁</td>
<td>47.2</td>
<td>41</td>
</tr>
<tr>
<td>N₂</td>
<td>47.7</td>
<td>36</td>
</tr>
<tr>
<td>N₃</td>
<td>47.4</td>
<td>38</td>
</tr>
<tr>
<td>N₀PK</td>
<td>53.1</td>
<td>48</td>
</tr>
<tr>
<td>N₁PK</td>
<td>51.1</td>
<td>43</td>
</tr>
<tr>
<td>N₂PK</td>
<td>49.4</td>
<td>38</td>
</tr>
<tr>
<td>N₃PK</td>
<td>49.2</td>
<td>36</td>
</tr>
<tr>
<td>Straw</td>
<td>44.6</td>
<td>32</td>
</tr>
</tbody>
</table>
Compared to the controls, the C/N ratio of the N\textsubscript{1} treated humus was higher. This value corresponds well to the lower decomposition rate factor (k = 0.0155) calculated for N\textsubscript{1} when compared to the control (k = 0.0237). Indeed, most of the nitrogen added was found immobilized within the organic layers as the high carbon to nitrogen ratio would indicate. However, heavier nitrogen applications did not decrease the C/N ratio significantly below the control, although decomposition factors and especially available nitrogen increased greatly.

Addition of PK alone increased the C/N ratio considerably. With increased nitrogen applications however, C/N ratios reflect those recorded from the humus receiving nitrogen alone. Similar increases due to phosphorus and potassium were reported by Viro (1963).

The straw treated humus had the lowest C/N ratio of all treatments. Earlier discussions have already indicated the high mineralization rates this humus exhibited. The high C/N ratios traditionally associated with straw had decreased to \(C/N = 32\) indicating that much of the carbohydrates in the straw had rapidly decomposed over the 10 year period.

Other researchers have speculated on the differing quantities of nitrogen mineralized from organic matter with similar C/N ratios. In his incubation experiments, Benoit (1974) reported a net immobilization of \(\text{NH}_4^+\) in black spruce humus, but with jack pine humus, constant rates of nitrogen mineralization was recorded. According to Zöttl (1960), no valid conclusions can be made about the nitrogen
supply from the C/N ratio, when material dissimilar in decomposability is compared.

From the literature, it appears that the organic chemical composition of litter plays an important role in nitrogen release. For example, lignin may be more of a determinant in decomposition rates than the C/N ratio (Swift et al., 1979). Percentages of lignin have been shown to increase with increased nitrogen fertilizer applications (Berg and Straaf, 1980). Nilsson (1973) investigated the suppressing effect of lignin on cellulose decomposition and his observations support the concept that the lignin acts as a barrier enclosing the carbohydrates. This barrier must first be degraded before the cellulose and the hemicellulose components can be decomposed.

However, lignin content will affect the decomposition rate only if it is a dominant chemical fraction towards the later stages of decomposition. Berg and Straaf (1980) present some suggestions regarding the interaction of carbon and nutrients (nitrogen):

1. At least three groups of carbon compounds affect the rate of decomposition - the soluble compounds with a rapid turnover rate, the somewhat slower cellulosics and hemicellulosics and the slowest turnover compounds containing lignin or lignified carbohydrates.

2. Elements such as nitrogen and phosphorus influence decomposition rates of needle litter when soluble compounds and parts of the un lignified carbohydrates were already degraded.
3. As the concentration of lignin increased, the influence of plant nutrients decreased.

4. A high lignin level initially can negate the stimulating effect of plant nutrients on decomposition rates.

4.6 Cation Exchange Capacity (CEC) and the Cations $K^+$, $Ca^{++}$ and $Mg^{++}$

The CEC of the humus determined at field pH with the sodium chloride method is given in Table 9. Since the CEC here is a measure of the reversibly adsorbed cations retained by the organic matter, this value will be relatively high due to the active organic fractions. Increases in CEC can also be expected when the pH rises (Thompson and Troeh, 1978). Table 9 shows that the CEC for the control is 42 meq/100 g, with a slight increase to 48.3 meq/100 g at the N$_3$ level as more nitrogen is added. This increase is probably directly attributed to a rise in the pH following the saturation of the exchange sites with $NH_4^+$ ions. Camire (1981) also noted a higher CEC in jack pine humus following increases in the pH after higher rates of urea fertilization.

Addition of PK significantly raises the CEC. Again, the higher pH recorded on these plots probably accounts for most of the increase (Figure 13).

The addition of straw increased the CEC of the humus. Increased decomposing organic matter may have led to higher oxygen-containing functional groups with a larger adsorption capacity.

The impact of fertilization on the exchangeable cations $K^+$, $Ca^{++}$ and $Mg^{++}$ is given in Table 9. Concentrations of these cations
TABLE 9. Exchangeable bases $K^+$, $Ca^{++}$, $Mg^{++}$ (me/100 g), CEC (me/100 g) and Base Saturation (%) of the treated humus.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>$K^+$ (me/100 g humus)</th>
<th>$Ca^{++}$ (me/100 g humus)</th>
<th>$Mg^{++}$ (me/100 g humus)</th>
<th>CEC</th>
<th>BS %</th>
</tr>
</thead>
<tbody>
<tr>
<td>N0</td>
<td>3.09</td>
<td>5.09</td>
<td>0.76</td>
<td>42.95</td>
<td>21</td>
</tr>
<tr>
<td>N1</td>
<td>1.60</td>
<td>5.61</td>
<td>0.65</td>
<td>43.21</td>
<td>18</td>
</tr>
<tr>
<td>N2</td>
<td>1.49</td>
<td>6.70</td>
<td>0.67</td>
<td>46.35</td>
<td>12</td>
</tr>
<tr>
<td>N3</td>
<td>1.41</td>
<td>6.66</td>
<td>0.67</td>
<td>48.70</td>
<td>18</td>
</tr>
<tr>
<td>N0PK</td>
<td>2.86</td>
<td>12.68</td>
<td>0.68</td>
<td>45.80</td>
<td>35</td>
</tr>
<tr>
<td>N1PK</td>
<td>2.90</td>
<td>13.15</td>
<td>0.65</td>
<td>45.50</td>
<td>37</td>
</tr>
<tr>
<td>N2PK</td>
<td>2.01</td>
<td>15.54</td>
<td>0.66</td>
<td>52.45</td>
<td>35</td>
</tr>
<tr>
<td>N3PK</td>
<td>3.02</td>
<td>11.90</td>
<td>0.69</td>
<td>51.95</td>
<td>30</td>
</tr>
<tr>
<td>Straw</td>
<td>2.90</td>
<td>6.97</td>
<td>1.42</td>
<td>48.12</td>
<td>24</td>
</tr>
</tbody>
</table>
in the humus is given in Table 10. Results of these two tables can be summarized as follows:

1. The control plots had the highest exchangeable $K^+$ values.
2. Additions of PK increased the exchangeable $K^+$ and $Ca^{++}$ but had no effect on $Mg^{++}$.
3. Increasing nitrogen additions reduced $K^+$ significantly and increased $Ca^{++}$ somewhat on plots not receiving PK additions.
4. Potassium concentration decreased significantly with increased nitrogen additions but application of PK kept concentrations at around 0.08% K.
5. Concentrations of calcium also increased significantly with PK additions but nitrogen additions had no effect.
6. Magnesium remains constant at 0.03% Mg regardless of treatment.

Following increased application of ammonium nitrate, large amounts of $NH_4^+$–N are introduced into the organic layers. Under moist conditions, the $NH_4^+$ ions can easily displace $K^+$ ions from the exchange complex because these two ions have the same valency and similar size. With more $K^+$ ions in solution, the potential for increased leaching exists, especially considering the mobile nature of $NO_3^-$–N added in the form of ammonium nitrate and as a result of nitrification. Indeed, exchangeable $K^+$ ions decreased with increased nitrogen additions as did the concentration of K in the humus.

Whereas other researchers have also noted decreases in Ca and Mg concentrations following nitrogen fertilization (Beaton et al., 1969; Otchere-Boateng and Ballard, 1978), there was no decrease in these
TABLE 10. Average concentrations (%) of phosphorus, potassium, magnesium and calcium in the treated humus*.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td>N0</td>
<td>0.12a</td>
<td>0.09e</td>
<td>0.03a</td>
<td>0.22a</td>
</tr>
<tr>
<td>N1</td>
<td>0.11a</td>
<td>0.06b</td>
<td>0.03a</td>
<td>0.23a</td>
</tr>
<tr>
<td>N2</td>
<td>0.11a</td>
<td>0.05b</td>
<td>0.03a</td>
<td>0.30a</td>
</tr>
<tr>
<td>N3</td>
<td>0.11a</td>
<td>0.04a</td>
<td>0.03a</td>
<td>0.24a</td>
</tr>
<tr>
<td>N0PK</td>
<td>0.15b</td>
<td>0.08d</td>
<td>0.03a</td>
<td>0.45b</td>
</tr>
<tr>
<td>N1PK</td>
<td>0.16bc</td>
<td>0.08d</td>
<td>0.03a</td>
<td>0.65b</td>
</tr>
<tr>
<td>N2PK</td>
<td>0.19cd</td>
<td>0.07c</td>
<td>0.03a</td>
<td>0.51b</td>
</tr>
<tr>
<td>N3PK</td>
<td>0.17d</td>
<td>0.08d</td>
<td>0.03a</td>
<td>0.44b</td>
</tr>
</tbody>
</table>

*Values in the same vertical column followed by the same letter are not significantly different (P <0.05).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td>N0</td>
<td>0.12a</td>
<td>0.09a</td>
<td>0.03a</td>
<td>0.22a</td>
</tr>
<tr>
<td>Straw</td>
<td>0.14b</td>
<td>0.09a</td>
<td>0.06b</td>
<td>0.30b</td>
</tr>
</tbody>
</table>

*Values in the same vertical column followed by the same letter are not significantly different (P <0.05).
cations noted here. Possibly, the increased CEC following increases in pH associated with the larger nitrogen additions, enabled more of these divalent cations to be adsorbed onto the exchange sites. This reduced the presence of Ca\(^{++}\) and Mg\(^{++}\) ions in solution and prevented their loss through leaching.

Humus which had received the PK treatment showed higher potassium and calcium and concentrations. The increase in calcium was due to the 12-16% Ca content of the superphosphate fertilizer. Potassium concentrations did decrease somewhat with larger nitrogen doses but results were not significant. There was no change recorded for the Mg\(^{++}\) ion and concentrations remained at 0.03%.

4.7 Phosphorus

The addition of PK significantly raised phosphorus levels in the treated humus as shown in Table 11. However, considering that these plots received 336 kg P/ha over 10 years, very little phosphorus remained in the organic layers. Since increased levels of phosphorus in the jack pine foliage, which occurred on PK treated plots (Weetman, unpublished data), cannot account for the bulk of this loss, leaching is assumed to have been large.

Generally, organically bound phosphorus is considered very immobile and the immobility of phosphorus in soils has been reported by many researchers. Studying the loss of phosphorus from fertilized peat in containers under field conditions, Malcolm et al. (1977) found that up to 60% of the added phosphorus was leached from the system. They suggest two characteristics which largely determine the rate of
TABLE 11. Average total phosphorus (kg/ha) in the treated humus.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>P (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N₀</td>
<td>51.3</td>
</tr>
<tr>
<td>N₁</td>
<td>77.9</td>
</tr>
<tr>
<td>N₂</td>
<td>62.9</td>
</tr>
<tr>
<td>N₃</td>
<td>55.8</td>
</tr>
<tr>
<td>N₀PK</td>
<td>81.7</td>
</tr>
<tr>
<td>N₁PK</td>
<td>102.9</td>
</tr>
<tr>
<td>N₂PK</td>
<td>98.6</td>
</tr>
<tr>
<td>N₃PK</td>
<td>93.7</td>
</tr>
<tr>
<td>Straw</td>
<td>81.2</td>
</tr>
</tbody>
</table>
phosphorus leaching: the solubility of the phosphate fertilizer and
the phosphorus adsorption capacity of the organic matter. Superphos-
phate is fairly soluble at the lower pH range and low phosphorus
adsorption capacity of the humus must also be suspected. Fox and
Kamprath (1971) demonstrated that in acid (pH < 4.6) soils containing
no inorganic colloids, phosphorus adsorption was low, resulting in
high phosphorus mobility.

4(b) SEEDLING GROWTH AND NUTRITION

In order to determine whether the changes in the humus brought
about by repeated fertilization and the straw application would affect
seedling growth and nutrition, a bioassay experiment was performed.
The results of the dry matter production and nutrient uptake of jack
pine seedlings grown on the treated humus are discussed.

4.8 Seedling Growth

4.8.1 Results

After growing in the greenhouse for six months, seedling dry
matter production for each treatment was determined. Total seedling
weights and the component shoot and root weights are presented in
Figure 19. In Table 12, the root/shoot ratios for each treatment are
listed. The results for all variables are summarized below:

1. The addition of nitrogen did not significantly affect seedling
   shoot weights. However, shoot biomass did increase at N1
Figure 19. Average dry matter production (grams) of seedlings grown on treated jack pine humus for six months.
Table 12. Root/shoot ratios of seedlings grown on treated jack pine humus*.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>R/S (± S.D.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N0</td>
<td>0.56 ± 0.13a</td>
</tr>
<tr>
<td>N1</td>
<td>0.65 ± 0.07bcd</td>
</tr>
<tr>
<td>N2</td>
<td>0.69 ± 0.11cd</td>
</tr>
<tr>
<td>N3</td>
<td>0.69 ± 0.08d</td>
</tr>
<tr>
<td>N0PK</td>
<td>0.60 ± 0.09abc</td>
</tr>
<tr>
<td>N1PK</td>
<td>0.58 ± 0.06ab</td>
</tr>
<tr>
<td>N2PK</td>
<td>0.66 ± 0.11cd</td>
</tr>
<tr>
<td>N3PK</td>
<td>0.78 ± 0.07d</td>
</tr>
</tbody>
</table>

*Values in the same vertical column followed by the same letter are not significantly different (P <0.05).

<table>
<thead>
<tr>
<th></th>
<th>R/S (± S.D.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N0</td>
<td>0.56 ± 0.13b</td>
</tr>
<tr>
<td>Straw</td>
<td>0.36 ± 0.07a</td>
</tr>
</tbody>
</table>

*Values in the same vertical column followed by the same letter are not significantly different (P <0.05).
level, only to decline as more nitrogen was added, falling below the control at N3.

2. Root biomass responded significantly to nitrogen additions with greatest root growth again at the N1 level, but declining at higher nitrogen levels. Root weights were still marginally higher at N3 compared to the controls.

3. The addition of PK increased root and shoot biomass for all but the N3 PK level, however, the differences were generally not significant.

4. For the straw treatment, root and shoot weights were significantly different compared to controls.

5. There were no significant differences in the root/shoot ratios for treatments receiving nitrogen additions and PK applications, although ratios were generally greater at higher nitrogen levels. In contrast, the root/shoot ratios for the straw experiment were significantly lower than the controls.

4.8.2 Discussion

Using dry matter production as a measure of growth, the results show that for the optimum nutrition experiment, seedlings grown on humus treated with low levels of nitrogen additions attained the highest biomass production. With the addition of phosphorus and potassium, dry matter production was increased a further 11% over the group which did not receive these nutrients. Additional large nitrogen additions decreased seedling oven dry weights on both -PK and +PK plots to below control values (N3-PK = 0.473 g; N3+PK = 0.470 g).
Both agricultural and forest research has found a decrease in the root/shoot ratio with increasing amounts of nitrogen and phosphorus application (Rohrig, 1958; Paavilainen and Norlamo, 1975). This is attributed to the stimulating influence these nutrients, especially nitrogen, have in increasing shoot growth. Thus, although the root biomass also increased, the ratio of roots to shoots decreases.

Results recorded in this study did not agree with these findings. In fact, the rate of growth was greater for the roots than the shoots resulting in an increase in the root/shoot ratio.

The depression in yield which occurred on humus treated with high levels of nitrogen may have been caused by physiological disorders within the seedlings. When levels of nitrogen nutrition are increased, the levels of amino acid concentration also increases since they are not being used because of a shortage of other plant nutrients (Mengel et al., 1979). With very high levels of available $\text{NH}_4^+$, amino acid synthesis cannot keep pace and $\text{NH}_4^+$ is stored within the plant cell. Research with agricultural plants has shown that $\text{NH}_4^+$ can be toxic to plants and reduce yields (Jungk, 1967; Maynard and Barker, 1969).

The most interesting aspect of the bioassay experiment is that the growth results generally show the same trends as those found for the mature jack pine stand. Figure 20 graphically presents a comparison of the total periodic volume growth response of the stand (Weetman and Fournier, 1984) and seedling dry matter production, both expressed as a percent of the control set at 100%. Greatest stand volume
Figure 20. Periodic total volume increment (1970-1979) in m³/ha of the jack pine stand and total seedling dry weight (6 months) in grams expressed as percent of the control N₀.
increment and seedling biomass was attained with low levels of nitrogen plus the addition of PK. At the N$_3$ and N$_3$PK levels, negative growth (compared to control = 100%) or extremely low growth response is also recorded for both seedling and stand response.

However, some anomalies did occur. Whereas the addition of PK alone increased seedling weight, this treatment reduced stand response considerably. At the N$_2$ and N$_2$PK levels of nutrient additions, seedling response was generally low, whereas stand response was still high.

The straw treatment again provided an interesting comparison to the optimum nutrition experiment. Seedling biomass production was highest on the straw treated humus with gains of 77% over the control. Stand response was 46% greater than the control and equal to the response recorded at the N$_1$-PK (44%) and N$_2$+PK (45%) levels.

Taking into account the limitations inherent in bioassay experiments, plus the fact that seedlings were grown on the top organic layers and not the whole soil profile, the bioassay was sensitive enough to reflect general the trends observed at the stand level.

4.9 Seedling Nutrition

4.9.1 Results

In order to evaluate the nutritional status of the seedlings grown on the treated humus, analysis of foliar macronutrient concentrations were conducted. The results are presented in Figure 21, Table 13 and summarized below:
Figure 21. Average foliar nitrogen concentrations (± standard deviation) of the seedlings grown for six months on the treated humus.
TABLE 13. Average foliar concentrations of nitrogen, phosphorus, potassium, magnesium and calcium of jack pine seedlings grown on treated humus*.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td>N&lt;sub&gt;0&lt;/sub&gt;</td>
<td>1.47a</td>
<td>0.17a</td>
<td>0.36bc</td>
<td>0.11a</td>
<td>0.38a</td>
</tr>
<tr>
<td>N&lt;sub&gt;1&lt;/sub&gt;</td>
<td>1.39a</td>
<td>0.18a</td>
<td>0.31ab</td>
<td>0.13c</td>
<td>0.45b</td>
</tr>
<tr>
<td>N&lt;sub&gt;2&lt;/sub&gt;</td>
<td>1.75bc</td>
<td>0.21b</td>
<td>0.31a</td>
<td>0.14d</td>
<td>0.51c</td>
</tr>
<tr>
<td>N&lt;sub&gt;3&lt;/sub&gt;</td>
<td>1.78c</td>
<td>0.21b</td>
<td>0.30a</td>
<td>0.14d</td>
<td>0.51c</td>
</tr>
<tr>
<td>N&lt;sub&gt;0&lt;/sub&gt;PK</td>
<td>1.45a</td>
<td>0.21b</td>
<td>0.45d</td>
<td>0.12b</td>
<td>0.41ab</td>
</tr>
<tr>
<td>N&lt;sub&gt;1&lt;/sub&gt;PK</td>
<td>1.51ab</td>
<td>0.20b</td>
<td>0.38c</td>
<td>0.12b</td>
<td>0.44b</td>
</tr>
<tr>
<td>N&lt;sub&gt;2&lt;/sub&gt;PK</td>
<td>1.38a</td>
<td>0.24c</td>
<td>0.32ab</td>
<td>0.12b</td>
<td>0.52c</td>
</tr>
<tr>
<td>N&lt;sub&gt;3&lt;/sub&gt;PK</td>
<td>1.52ab</td>
<td>0.25c</td>
<td>0.30a</td>
<td>0.14d</td>
<td>0.61d</td>
</tr>
</tbody>
</table>

*Values in the same vertical column followed by the same letter are not significantly different (P <0.05).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td>N&lt;sub&gt;0&lt;/sub&gt;</td>
<td>1.47a</td>
<td>0.17a</td>
<td>0.36a</td>
<td>0.11a</td>
<td>0.38a</td>
</tr>
<tr>
<td>Straw</td>
<td>2.16b</td>
<td>0.16a</td>
<td>0.41b</td>
<td>0.11a</td>
<td>0.32a</td>
</tr>
</tbody>
</table>

*Values in the same vertical column followed by the same letter are not significantly different (P <0.05).
Nitrogen

1. Significant differences were observed in the nitrogen concentrations were observed only in those seedlings growing on the N$_2$ and N$_3$ treated humus.

2. Nitrogen concentrations were highest however, on seedlings grown on the N$_2$ and N$_3$ treated humus with nitrogen levels at 1.75% N and 1.78% N respectively. Control levels were recorded at 1.46% N.

3. Lowest nitrogen levels occurred in seedlings growing on the N$_1$, and N$_2$PK treated humus at 1.39% N and 1.38% N respectively.

4. Additions of PK reduced foliar nitrogen concentrations by about 7%. Likewise, as Figure 21 shows, nitrogen concentration variability between the nitrogen levels was reduced on PK treated humus.

5. Straw treated humus produced the highest nitrogen levels in seedlings (2.16%N) and results were significantly different from the control (1.46% N).

Phosphorus

1. Addition of nitrogen significantly increased phosphorus concentrations.

2. Additions of PK further increased phosphorus levels in seedlings by more than 20% over those growing in humus which did not receive a PK treatment.

3. Phosphorus concentration was significantly lower in seedlings growing on the straw treated humus.
**Potassium**

1. In contrast to phosphorus, additions of nitrogen decreased foliar potassium levels significantly.

2. Additions of PK could not offset this decline although potassium levels were significantly higher in seedlings grown on PK treated humus than in those which grew on humus not receiving this treatment.

3. The potassium concentration of straw treated seedlings were significantly higher than the control.

**Magnesium and Calcium**

1. Additions of nitrogen significantly increased foliar magnesium and calcium levels.

2. Additions of PK had no effect on Mg or Ca levels in seedling foliage.

3. Straw treated humus also had no effect on foliar Mg and Ca levels.

4.9.2 Discussion

The critical level of foliar nutrient concentration is generally defined at that point where yield attains 90% of the possible maximum (Ulrich, 1952; Richards and Bevege, 1972). According to Swan (1970), foliar nutrient concentrations for jack pine are in the critical to adequate range at N = 1.3%; P = 0.16%; K = 0.33%; Ca = 0.10% and Mg = 0.07%. Results for the bioassay experiment showed that seedling nitrogen, phosphorus and magnesium nutrition were sufficient for most treatment levels. Potassium levels were generally within the critical
limits and could be considered adequate in only a few cases. Calcium concentrations however, were very high and more than adequate for all treatment levels. Magnesium levels are also considered adequate for all treatments.

Generally, conditions in the greenhouse were such that, irrespective of treatments, the humus seemed capable of releasing sufficient nitrogen for adequate seedling nutrition. Humus which had received little or no nitrogen additions and whose nitrogen concentration was low (Section 4.4.1, Figure 14), did not necessarily induce low nitrogen levels in seedling foliage. For example, at the $N_0PK$ level, humus concentration was 1.11% N, yet seedlings growing on this treatment level had higher nitrogen concentrations than seedlings growing on humus which had received the equivalent of 672 kg N/ha.

Data on seedling dry matter production and stand basal area increment (Figure 20) indicated a substantial response to moderate applications of nitrogen. Seedling response was highest on the $N_1PK$ treated humus. Sustained high growth response of the jack pine stand was also achieved with repeated light doses of nitrogen with additions of PK as supplied with the $N_1PK$ treatment regime. Seedling nitrogen concentrations generally fluctuated between $+1.4 - +1.5\%$ N over the treatment levels $N_0$, $N_1$ and humus receiving PK additions (Figure 21). Optimum foliage % N for the stand was 1.4% N (Weetman and Fournier, 1984).

Nitrogen fertilization can affect the concentrations of other nutrients in the foliage. Some researchers have found decreased foliar P, K, Mg and Ca levels following nitrogen additions (Krauss,
1969; Timmer, 1979) which have been attributed to either antagonistic or dilution effects. In this study, nitrogen additions raised P, Mg and especially Ca levels significantly.

Nitrogen application promotes plant uptake of phosphorus in several agricultural crops (Grunes, 1959). However, it has also been reported that nitrogen depresses phosphorus uptake by pine seedlings (Fowells and Krauss, 1959). This may be partly explained by the effect nitrogen fertilization has in retarding mycorrhizal development and hence, in decreasing phosphorus uptake. However, Taber and McFee (1972) found that nitrogen can also increase phosphorus absorption. Increases in the nitrogen concentrations caused an increase in respiration rates with a corresponding increase in ATP demand. Thus, nitrogen addition may have increased metabolic activity and created a demand for increased phosphorus. Increased mineralization rates which occurred in the humus following heavier nitrogen application, may also have released immobilized phosphorus in the organic matter. With more phosphorus available for plant uptake, concentrations of this nutrient increased in the seedling foliage.

Potassium levels were within the lower end of the critical range for all treatments which received high nitrogen additions. The average potassium concentration of nitrogen treated humus (Table 10) was also low and, as discussed earlier, is probably due to the mobile nature of $K^+$—especially following fertilization. Seedling potassium levels were higher on PK treated humus but a similar decline in foliar potassium occurred as increased amounts of nitrogen were applied.
The low growth response of the seedlings and the jack pine stand on plots receiving high N additions, may be due to a deficiency in boron and other micronutrient levels. According to Ballard (1983), soils which have high concentrations of available N may aggravate or induce deficiency in boron. These conditions were certainly met on high N plots. Unfortunately, no boron analysis was conducted on the seedling foliage.

Since plant growth is a factor not only of nutrient intensity but also balance (Shear et al. 1948), the ratios of one nutrient to another is important when striving for maximum yield. Ingestad (1966) expressed as a ratio several macronutrients to nitrogen (N = 100). Values for Pinus sylvestris, an ecologically similar tree species, are thought to be in the following range (Ingestad, 1979):

\[
\begin{array}{cccccc}
N & P & K & Ca & Mg \\
100 & 14 & 43 & 6 & 6 \\
\end{array}
\]

Only the relative phosphorus to nitrogen ratio for the PK treated seedlings approached or exceeded the above stated value for P. sylvestris. All values for potassium were below the recommended values, while those for calcium and magnesium were higher.

Simple ratios of the major nutrients N, P, K, Ca and Mg are also used to express nutrient balances for a number of tree species. Interpretations of these element concentration ratios have recently been published by Ballard (1983). Looking first at the N/P ratios, the values for the optimum nutrition experiment were between 5.5 and 8.5. These ratios would indicate no P deficiency in seedling foliage. The N/P ratios for the straw experiment were higher at 13.5 and a possible P deficiency may be indicated.
The K/Ca ratio may also be useful in identifying possible potassium calcium imbalances since these two nutrients are known to be antagonistic (Mengel, 1972). Bjorkman (1953) noted nutritional imbalances in Norway spruce when K/Ca was 0.3, but a much healthier green colour when K/Ca was 0.9. Seedlings growing on the various treated humus had lower K/Ca values with increasing nitrogen additions, from $N_1 = 0.95$ to $N_3 = 0.59$ and for PK treatments $N_1PK = 0.86$ to $N_3PK = 0.49$. The straw treatment had a K/Ca ratio of 1.28 which possibly illustrates that optimum K/Ca ratios may well lie higher than 0.5 for jack pine.

Depression in yields which occurred at certain nutrient levels, in spite of adequate nitrogen nutrition, may well have been caused by certain imbalances in macro- and micro-nutrient levels. It appears, that diagnosis of nutrient deficiency is fairly straightforward, but determining optimum foliar nutrient concentrations is not. Much more research is required in this area of tree nutrition in order to set up reliable nutrient balances for our major tree species.
5.0 SUMMARY

The optimum nutrition experiment and the straw treatment provided an excellent opportunity to study the effect of sustained nitrogen additions and a large carbohydrate application to the forest floor of a jack pine stand and on certain aspects of the nitrogen cycle. The results showed that some nitrogen transformation processes were greatly affected within the organic layers of the forest floor. And yet, the buffering capacity of the humus and its resistance to change was remarkable, considering the magnitude of some of the treatments. In evaluating the observed treatment impacts, the following conclusions are drawn:

1. The addition of nitrogen drastically changed the ground vegetation. Mosses, lichens and ericaceous shrubs were greatly reduced at higher nitrogen applications, to be replaced by exotic species such as Sambucus, Aster and Viola.

   The straw treatment effectively smothered the ground vegetation. Only after 10 years did the original ground cover begin to regain control over the area.

2. Repeated low additions of nitrogen effectively increased humus weight by 65% and depth by 2 cm. Heavier nitrogen applications reduced both weight and depth. Humus which had received the additional PK treatments, exhibited similar trends; however, the changes in weight and depth were smaller.

   Weight of the straw treated plots was 35% higher but there was little effect on depth.
3. The lowest decomposition rates observed were for humus receiving low nitrogen additions, indicating slow nutrient turnover and nitrogen immobilization. Addition of PK alone also resulted in low rates and this was attributed to phosphorus decreasing the decomposer populations. Increased nitrogen raised decomposition rates markedly, indicating higher nutrient release.

Decomposition was also high on the straw treatment, approaching values found on high nitrogen addition plots. In spite of high C/N ratios associated with straw, this treatment seemed to be supporting an active microbial population.

4. The decrease in pH commonly associated with ammonium nitrate fertilizer was observed at low nitrogen levels. As nitrogen additions increased, pH values rose, possibly due to saturation of exchange sites with $\text{NH}_4^+$ which in turn acts as a base in accepting $\text{OH}^-$ groups remaining after water reacts with ammonium nitrate. Humus receiving the additional PK treatments had consistently higher pH values due to the calcium content of the superphosphate fertilizer.

The pH of the straw treated plots was also higher than the control. Quite possibly, the original pH of the straw was higher.

5. Nitrogen concentration of the humus was raised significantly only when 672 kg N/ha was applied and decreased with the higher nitrogen application, probably due to increased leaching losses. Addition of PK alone depressed nitrogen concentrations, but when applied in addition with nitrogen, concentrations of nitrogen were increased.
Straw plots had one of the highest humus nitrogen concentrations at 1.38% N.

6. All treated plots recorded higher total nitrogen (kg/ha) than controls, with humus receiving the low level of nitrogen additions containing the largest amount of nitrogen. High nitrogen plots apparently lost much of the applied nitrogen. Indications point to a very tight nutrient cycling at low levels of nitrogen input.

7. Results of the aerobic mineralization study confirm that nitrification was proceeding, in spite of pH < 4, on high nitrogen plots. As expected, available nitrogen increased as more nitrogen was applied, but additions of PK generally depressed available nitrogen on plots receiving nitrogen.

Straw plots showed high amounts of available nitrogen but no nitrification was observed.

8. Large additions of nitrogen had no effect on the C/N ratio, but PK applications increased C/N, especially when none or little nitrogen was applied.

The straw treatment had the lowest C/N ratio of all treatments.

9. The CEC rose steadily as more nitrogen was applied which is attributed to the increase in humus pH. Base saturation declined with increased nitrogen levels - most likely due to increased leaching loss of NO$_3^-$ . Potassium seemed to have caused most of the decline as magnesium and calcium levels remained fairly constant. Additions of PK significantly increased CEC as well as exchangeable bases.
10. Although PK applications did increase phosphorus levels in the humus, much of the applied phosphorus was leached from the organic horizons.

11. Humus derived from sustained low additions of nitrogen plus application of PK resulted in the highest seedling biomass and this correlated with stand response. Seedlings grown on the straw treated humus exhibited the greatest response of all treatments.

12. Seedling nitrogen concentrations were adequate for all treatments and reflected the ability of the humus, under greenhouse conditions, to release sufficient nitrogen. Additions of nitrogen increased foliar phosphorus, calcium and magnesium levels but decreased potassium concentrations. Treatments with PK depressed nitrogen concentration but increased foliar phosphorus and calcium levels but had no effect on potassium.

   Seedlings growing on straw treated humus had the highest nitrogen concentration of all treatments but the lowest levels of phosphorus.

13. Foliar nitrogen concentrations could not be correlated with seedling biomass production. Possible other factors which influenced growth are low foliar potassium levels and very low K/Ca values.

   Seedlings grown on the straw treated humus had more balanced nutrient relationships.
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Janna W. Kumi

List of Publications and Symposia


