SOIL - NUTRIENT RELATIONSHIPS

OF TREE SPECIES COMPOSITION AND DOMINANCE

IN THE FIELD IRRADIATION GAMMA (FIG) AREA,

WHITESHELL NUCLEAR RESEARCH ESTABLISHMENT, PINAWA, MANITOBA.

A Dissertion

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the Faculty of Graduate Studies and Research

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Master of Science

by

Calvin James Webb

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ABSTRACT

Seven nutrient parameters, hydrogen ion activity, calcium, potassium, phosphate, ammonium, nitrate,and organic matter, were measured in soil samples taken from a transect within the Field Irradiator-Gamma (FIG) area of the White-shell Nuclear Research Establishment, Pinawa, Manitoba. The relationship between these nutrients and the tree species composition and dominance of the overlying forest was interpreted using graphs and multiple linear regression equations.

Four major vegetation associations were identified along the transect: 1) larch-black spruce, 2) black spruce, 3) balsam fir-black spruce, and 4) aspen. Most of the nutrient concentrations were highest in the soils of the first two communities, and lowest in the aspen association. The low concentrations in the latter were attributed to the early successional status of the vegetation and the sandy soil. Higher levels within the evergreen communities were probably due to the high cation exchange capacity of the peat soils and to base flow of nutrients. Concentration differences between the evergreen associations were believed to result from variations in the rate of decomposition of organic matter. Tree basal area appeared to be related to a cation complex consisting of organic matter, calcium, and to a lesser extent, potassium and ammonium. The prominence of these parameters, however, was dependent on the

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successional status of the vegetation and the depth of the soil sample.

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INTRODUCTION

Canada's national wealth is very dependent upon forests and forest-based industries. In 1974 the value added—value of shipments less cost of materials and fuels—by the forest industry was 3,520,000,000 dollars (1974 Canada Year Book, 373). The rapidly increasing demand for timber products necessitates 1) increasing the land under forest management and 2) increasing forest productivity. Most harvested timber occurs on mineral soils, but necessity will probably force harvesting of trees in the marginally productive peatlands. In view of the extensive areas of peatland in Canada, 110 million hectares (Burke and O'Hare 1962, 647 as cited in Reader 1971, 2), knowledge on methods of increasing yield is important. One method which probably holds a good future for increasing yield in the forest industry is the application of chemical fertilizers. This approach can only be economical and effective after studies on the relationships between tree species composition and productivity of forests in relation to the nutrient status of the soil in unfertilized ecosystems have been conducted.

Mueller-Dombois (1964), Dammon (1971), Wali and Krajina (1973), and Page (1974) have documented forest-soil nutrient relationships in Canada, but in view of the extensive nature of the boreal forest (1972 Canada Year Book, 649) and the scarcity of relevant information, more study is necessary. This research was conducted as a pre-irradiation study of forest-nutrient relationships along the 200N cut line in the Field Irradiator-Gamma (FIG) area

of the Whiteshell Nuclear Research Establishment (WNRE)

The objectives of the research were:

1) to characterize differences in the concentrations of selected nutrients between organic and mineral soils along the transect,

2) to determine the relationship between the tree species composition along the transect and the upper 30 cm of soil, and

3) to describe and assess the relationship between the basal areas and the upper soil nutrient status along such a transect.

CHAPTER II

LITERATURE REVIEW

A. Introduction

Ecologists have always been "aware of important correlations between soils and vegetation" (Beals and Cope 1964, 777), but the study of plant-nutrient interactions is a relatively new endeavour. In most cases workers have found that other agents are relatively more important than mineral nutrition in determining the tree species composition and the growth rates of forests (Mitchell and Chandler 1939, 85). Failures to find plant-nutrient interactions in natural ecosystems (e.g. Mitchell, West, and Miller, 1966) may have resulted from the attention paid to moisture and sunlight, among others, at the expense of nutrients. This has retarded the understanding of nutrient circulation so that subsequent evaluation of nutrient levels in the plant's environment is difficult. Although methodological confusion in forest soil analysis (Gessel 1960, 224) may also account for some of the failure, the problem associated with soils analysis in the evaluation of plant-nutrient relationships is even more basic and is succintly described by Wali and Krajina (1973, 298):

> Soils analyses for all essential elements reflect only relative amounts of potentially available nutrients, often not correlated directly with plant response or species specificity. Whether these different levels of nutrients are available to plants in the final analysis is open to discussion.

The wide discrepancy between concentrations of nutrients commonly found in the soil and the lower levels at which toxicity occurs in culture solutions is evidence

that often the concentrations of nutrient extracted from
the soil are not immediately available to the plant. Until
a fraction that can be termed "plant available" is deter-
mined, progress in the study of plant-nutrient relationships
in the ecosystem will be slow.

Nevertheless, valuable insights into the interaction
between plants and nutrients have been defined and these
suggest that correlations in the field can be found. By
analyzing the nutrient concentrations within the plant
Dijkshoon (1968, 201) concluded that minerals are needed
in minimal amounts to permit plant growth and that the
requirement is species specific; exclusion of plants from
soils of relatively low nutrient concentration can, there-
fore, be expected. Mitchell (1939, 98) found that the
correlation between internal nutrient concentration and
the yield of white pine is true for other tree species also;
since there is evidence that the internal concentration of
nutrients is proportional to the nutrient-supplying capacity
of the soil (Mitchell and Chandler 1939), a relationship
between yield and extractable nutrients is likely.

Given the existence of such fundamental relation-
ships between trees and soil nutrient levels, studies of
their interaction may well bear on the generic aspects of
ecology. For instance, differences in yields between species
under varying and generally intermediate conditions of
nutrient availability could result in overlapping bell-
shaped species distribution curves as described by

Whittaker (1967). Principles of species diversity too
(Whittaker 1965, 253) might be explained by differential
growth responses under varying conditions of nutrient avail-
ability. The roughly asymptotic response of tree species
with differing nutrient demands to the fertility levels of
the soil (Mitchell and Chandler 1939, 65) suggests that
the greatest number of species would be found at interme-
diate nutrient levels. Differences in yield between species
are most pronounced at the extremes of the nutrient gradient;
on relatively infertile soils because of differences in the
extractive ability of the roots (Mitchell 1939, 105;
Childers 1959, 54) and at higher levels because of differ-
ences in the optimum concentrations for each species
(Mitchell and Chandler 1939, 65). Dominance by only a few
tree species would be the logical result of the exaggerated
differences in production under these conditions, thereby
confirming the thesis of Monk (1967) and McNaughton and
Wolf (1969) that species dominance is greatest at environ-
mental extremes.

While most of the previous discussion has centered
on interaction at the species level, relationships at the
association level can also be expected. Page (1974, 29)
observed that the availability of all nutrients (with the
exceptions of sodium and phosphorus) that he studied was
greatest under the hardwoods, and Rennie (1955, 59)
calculated that hardwoods remove four times, and other
species two times, the quantities of nitrogen, phosphorus

and potassium removed by pine. Only, however, by measuring the quantities of nutrients beneath each association and, perhaps more important, identifying the proportions of nutrients within each component of the ecosystem will ecologists be able to associate nutrient levels with vegetation associations, or vice versa.

What follows is a summary of the importance of seven soil variables on plant autecology, and a recapitulation of varied aspects of the relationship between vegetation type and the soil concentrations of each nutrient. Only seven parameters were selected for analysis because of the limited time and resources available. Moisture was not measured because the soils were saturated along most of the transect during sampling making measurement and analysis very difficult. Those selected are commonly tested in soils analysis laboratories and are quantitatively important to plant growth. Attention is centered on the more northerly forest ecosystems.

B. Soil pH

 Although pH is commonly defined as the negative
logarithm of hydrogen ion concentration, it actually
"expresses the activity rather than the concentration of
hydrogen or hydroxyl ions" (Wilde 1958, 212) and thus, is
regarded as "simply a number read on a potentiometer...."
(ibid. 213). The numerical aspect of a pH reading invites
statistical tests of the correlation between pH and various
vegetation attributes. Rarely, however, have these tests
assumed significance (e.g. Loucks 1962, 150) because,
except at the extremes of acidity or alkalinity (Wilde
1954, 89), the effects of pH on plant distribution and
production are indirect (Gordon 1964, 182); Gordon (ibid.)
found the lower limit to be the more ecologically signif-
icant extreme in natural stands of common ash, but the
general applicability of this finding is unknown.

 pH regulates plant-nutrient relationships in two
ways. First, acid conditions reduce the life functions
of bacteria and fungi which promote the decomposition of
organic matter (Moizuk and Livingstone 1966, 949), thereby
retarding the mineralization of nutrients. In contrast,
alkaline conditions may either stimulate the activity of
micro-organisms which compete with plants for available
nutrients or increase the virility of fungi which attack
tree roots, especially those of conifers (Wilde 1958, 216).
The second method relates to the form and ultimately the
quantity of nutrients available to the plant. One example

of this is that the effective hydroxyl concentration in the
soil regulates the production of ammonia gas (du Plessis and
Kroontje 1964). The greatest impact on nutrient availability,
however, generally occurs at extremes of soil acidity. Phos-
phate is fixed as slowly soluble iron and aluminum phosphate
in acid soils deficient in organic matter, and under alkaline
conditions, phosphorus as calcium phosphate is also unavail-
able to plants (Wilde 1958, 231). Nitrogen and bases are also
unavailable at low pH values (Wali and Krajina 1973, 302)
and the availability of iron, boron, zinc, and manganese
may decrease above pH 8.0 (Wilde 1958, 216). Harmful effects
on plants at pH extremes may also result from toxic accumu-
lations of elements; manganese accumulates to poisonous
levels in soils of low pH and restricted aeration (Gotoh
and Patrick 1972, 738), while compounds such as sodium,
carbonate may exist at toxic concentrations in alkaline
 soils (Wilde 1954, 89: Wilde 1958, 215).

Cases of serious harm caused by low or high pH
levels are probably rare. Most plants can grow over a range
of pH from 4 to 8 (Heinselman 1963, 329), but additional
considerations such as the length of the growing season,
the supply of total moisture available (Wilde 1954, 90;
Wilde 1958, 214) and the concentrations of nutrients in the
rooting medium (Wali and Krajina 1973, 302) ameliorate the
strictness of these boundaries.

Despite the inability to set precise limits of
pH to plant growth, soil acidity does have sociological

significance (Heinselman 1963, 342) which is best illustrated where sufficient time has elapsed for the plants to come to a relative state of equilibrium with their "total ecological requirements" (ibid 329). The soils beneath hardwoods are generally less acid than those under softwoods. This may be explained by differences in the nutrient requirements, or in the root patterns of the overlying vegetation. Challinor (1968, 288-289) accounted for higher pH values of the surface layers under red oak than those under three conifer species by the relatively high exchangeable calcium levels in the oak litter; alternatively, the shallow rooting systems of species such as spruce causes rapid recycling of calcium near the soil surface, so that the deeper soil beneath them may be slightly more acid than that from equivalent depths under other species (ibid. 289). Ovington (1953, 32) found little difference between species in the pH of fresh leaves of coniferous and hardwood species growing on alkaline soils, but on acid soils he found that the leaf pH of individual tree species varied from site to site and was closely related to the acidity of the underlying mineral soil (ibid.). Differences in pH levels between tree species of the same form also exist and may be attributed to differences in leaf acidity; Page (1974, 12), for instance, found that the pH at depths of 2.5 and 15 cm was higher under balsam fir than under black spruce.

Since correlations between pH, tree species, and vegetation types have been documented, it is logical to

expect changes coincident with ecosystem succession. Although Burgess, Johnson, and Keammerer (197, 78) found little difference in soil acidity along an age gradient, Page (1974, 24) observed such changes. For all soil and cover types the pH increased by about 0.5 units after clear cutting. The pH steadily decreased until minimum values were reached under stands 6.1 to 9.1 m high, then small increases were noticed in stands exceeding 9.1 m. The similarity in this pattern to the nutrient trends associated with succession that were described by Vitousek and Reiners (1975) suggests that the changes in pH are closely linked with the status of calcium in the soil.

To summarize the ecological correlations of pH, three trends were observed in the literature reviewed. One is that pH readings are usually higher under hardwoods than softwoods. Second, close associations between tree species and hydrogen ion activity may be found, but the strength of the association apparently depends on 1) the nature of the rooting system, 2) the calcium requirements of the species, and 3) the depth at which the pH measurement was taken. The third trend is that small changes in pH associated with the age of the forest ecosystem do occur, and may result from simultaneous changes in the status of other nutrients. Since calcium may be especially important in this respect, a general review of the ecological importance of calcium follows.

C. <u>Calcium</u>

The ecological significance of calcium is reflected by its use to characterize the cation-exchange-capacity of the soils and as an "index to general nutrient availability" (Beals and Cope 1964, 781) on the basis that calcium is the dominant macronutrient cation (Broyer and Stout 1959, 288; Buckman and Brady 1960, 74 and 347) and has a high energy of adsorption (Wilde 1958, 237). Two citations illustrate its ecological importance: 1) Wali and Krajina (1973, 307) in a study of vegetation change along a nutrient gradient found that replaceable calcium was one of five (from a total of thirty-nine variables) that was retained after step-wise elimination regression, and 2) Jeglum (1974, 122) using principal components analysis demonstrated a close relationship between calcium and the growth of black spruce.

The importance of calcium on plant distribution and production often results from the alleviation of the harmful effects of acidity by keeping the absorption and selectivity mechanisms involved in cation uptake intact (Black 1968, 327). Calcium "tends to overcome the injurious effects of excessive amounts of sodium, potassium, magnesium, aluminum, manganese and other constituents which may become toxic to the plants" (Wilde 1958, 226). Sufficient calcium must also be present to meet the heavy physiological demands of the plant community. The main function of calcium is to serve as a cementing agent (as calcium pectate for the cells of all tissues, but it also functions in the extension of

roots and root hairs, neutralizes toxic by-products formed during the growth processes (ibid.), and aids in the absorption of water and nutrients (Minotti, Williams and Jackson 1968, 692) by enhancing the permeability of the cell walls. The overall physiological importance of calcium is indicated by Mitchell's (1939, 91) finding that the differences in calcium concentration between the root and shoot of white pine seedlings were not as great as the differences for nitrogen, phosphorus, and potassium; the distribution of calcium within the plant varies with tree type (Rennie 1965, 62) and probably with the age of the tree.

Approximately thirty per cent of the cation exchange complex should be occupied by calcium if a plant's need for this element are to be met (Broyer and Stout 1959, 281). Many species have limited calcium demands and "their physiological requirements are fulfilled on most sites" (Tamm 1964, 154), while calcium toxicity is not common because most of it is absorbed by the soil (Mitchell 1939, 62). The extraction of much calcium from the soil does not mean that the physiological requirements of the overlying vegetation has been fulfilled. Low base saturation may lessen the availability of calcium (and other nutrients) to the plant (Wali and Krajina 1973, 260). Quantitative relationships between vegetation and the calcium status of the soil may, therefore, be difficult to detect.

Some general trends of the nutrient demands of tree types have been recognized. Rennie (1955, 65) calculated

that the uptake of calcium by pines is approximately one-
fifth, and by other conifers one-half that of hardwood
species; Ovington (1958b, 403) also notes the lesser
demands of pines and larch than hardwoods (ash). A clear
pattern between forest association and the calcium status
of the soil, though, has not been established. Ovington
found a lower per cent calcium in the organic layers (ibid.
393) under conifers than under hardwoods, but the difference
in the upper mineral soil was insignificant (ibid. 398).
The surface soils of treeless plots contained more
exchangeable calcium than those that were forested (ibid.).
Page (1974, 13) observed no significant differences beneath
hardwoods and softwoods growing on mineral soils. Challinor
(1968, 289) found significantly greater calcium concentra-
tions in the top inch of soil under white spruce than under
red oak and pine which was attributed to the ability of
spruce roots to concentrate this element at the soil
surface and to earthworm activity. Wali and Krajina (1973,
303) found that patterns of association varied with the
form of calcium extracted. The values of water soluble
and replaceable calcium, though, were high under aspen and
low under pine. Dammon (1971, 259) found more calcium
returned in the litter of balsam fir than in that of black
spruce, but under both species the calcium was cycled
rapidly and only five times the annual supply of calcium
was contained in the raw humus (ibid. 265).

Insufficient research and the failure to eliminate variation among soil type, age--soil calcium levels increase along an age gradient (Burgess et al., 1973, 72)-- and tree composition of the forest may explain the inefficacy in recognizing a consistent pattern between the calcium status of the soil and the overlying vegetation associations. In this respect calcium is similar to another metallic nutrient, potassium.

D. Potassium

Unlike calcium the physiological role of potassium
is mostly regulatory or catalytic rather than structural.
For instance, the carbohydrate content of the plant is
greatest when the supply of potassium is adequate because
it is thought that enzymes which break down carbohydrates
are inhibited by potassium (Broyer and Stout 1959, 294).
Potassium also functions in transformation of carbohydrates,
synthesis of proteins, and cell division (Wilde 1958, 224).
It plays a critical part in the frost hardening of plants,
is apparently responsible for reducing root rot in older
seedlings, and counteracts the harmful effects of excessive
nitrogen (ibid. 224 - 225). Potassium also stimulates the
uptake of nitrate (Minotti et al., 1968), but the magnitude
of expression of its action depends on the transport of
shoot products to the roots (ibid. 696). The potassium
requirements of the plant, however, apparently depend on
the total cation and carboxylate content of the leaves
(Dijkshoon 1969, 203), suggesting that the stimulation is
only increased demand resulting from growth. Since the
function of potassium is largely regulatory, difficulties
in assessing the quantitative relationships between
vegetation and potassium under field conditions might be
expected. The comparatively constant potasssium levels in
plants over a fairly wide range of growing conditions
(Gessel 1960, 225) suggest that even qualitative inter-
pretation is possible only at the extremes of potassium

availability. When potassium is deficient normal root growth and foliage development is hindered, while leaves that have unfolded age prematurely and die along the margins (Wilde 1958, 224 - 225).

The response by trees, however, is dynamic along a potassium gradient. The low optimal supply of potassium (Mitchell 1939, 58) and rapid recycling through plant and soil (York 1959, 155) may explain the response. Wilde (1958, 225) also noted that "the addition of potassium fertilizers increases both the growth and vigor of trees". Wikum and Wali (1974, 457) concluded that potassium was the most reliable nutrient parameter in predicting occurrence of the greatest number of species. Variations in tree size and tree species composition might, therefore, be expected along a potassium concentration gradient.

Despite the fact that atmospheric inputs are an important source of potassium and that it occurs in low concentrations in the soil (Reichle 1975, 260), patterns between plant associations and the levels of potassium in the soil are evident in the literature. The most obvious of these is that, with the exception of pines, potassium concentrations are greater in the soil under softwoods than beneath hardwoods.

Challinor (1968, 289) found more exchangeable potassium in the soil beneath white spruce than in that under red oak, white, and red pine; he hypothesized that a dense concentration of fine roots under spruce accounted for

this accumulation because "in soils relatively poor in potassium, root action tends to concentrate this element at the surface through nutrient cycling". Page (1974, 13) observed more available potassium (by weight) beneath softwoods than hardwoods and Rennie (1955, 89) concluded that the quantities of potassium taken up decrease in the order hardwoods, other conifers, and pines. Ovington (1958, 129) detected a great proportion of potassium in the litter and in the fresh leaves of hardwoods than of conifers, but he also concluded that conifers "decrease the exchangeable potassium in the soil more than hardwoods" probably as a result of the greater immobilization of nutrients within the litter of coniferous species. Biological fixation of the extremely small quantities of total and easily soluble potassium in peat and in light sandy soils (Tamm 1964, 126 and 154; Dammon 1971, 265), possibly by micro-organisms engaged in humus decomposition (Dammon 1971, 265) may explain the low concentrations found under pine by Wali and Krajina (1973, 304). The sufficiency levels for pine, however, are low (Wilde, 1958, 225; Fowells, 1959, 11).

Dammon's (1971) study is unique for he investigated variations in the rates of nutrient mineralization between cover types. Although the potassium concentrations in the raw humus horizons of black spruce and balsam fir cover types growing on sandy glaciofluvial deposits in Newfoundland were low, they represented twenty-one and fourteen times

the annual supply of the respective stands (<u>ibid.</u> 265).
These amounts, however, were also equivalent to eleven and
ten times the annual returns for spruce and fir respectively,
so Dammon concluded that "the rate of potassium mineralization
differs little between cover types" (<u>ibid.</u>).

The levels encountered beneath any association also
depend on the stage of development of the ecosystem.
Burgess <u>et</u> <u>al.</u> (1973, 72), for instance, found that the
levels of potassium in the soil increased with time
(although the concentrations began to decrease near the
middle of an age gradient). This may be a function of the
decrease in the potassium/calcium uptake ratio that occurs
with time (Rennie 1955, 65) which in turn is related to
1) the mineral composition of the tree--calcium is most
concentrated in the woody organs whereas potassium is
physiologically more important in the leaves-- and 2) the
decrease in the foliage/woody-organs ratio as the stand
ages. The variable time must, therefore, be accounted for
when explaining the relationship between the overlying
vegetation and the quantities of potassium (and other
nutrients) extracted from the soil beneath it.

E. <u>Phosphorus</u>

Many studies have confirmed the existence of a strong correlation between the effects of nitrogen and phosphorus. Gordon (1964, 179), for example, found that phosphorus was significantly related to height growth because it was associated with nitrogen, and Moizuk and Livingstone (1966, 949) concluded that both nitrogen and phosphorus limited the growth of red maple on sphagnum mats.

Phosphorus availability seems greatest with ammonium nitrogen. McFee and Stone (1968, 882) found that the absolute amount of phosphorus in the tops of culture grown seedlings of pitch pine and white spruce was greater when ammonium was the nitrogen source due to the greater mass of the trees, although the percentage of phosphorus in the tops was lower. A possible explanation for the increased production "is that physiologically acid ammonium salt releases enough native soil phosphorus to supply the full plant requirements compatible with the growth potential made through supplying the extra nitrogen" (Broyer and Stout 1959, 288), whereas physiologically alkaline nitrate releases considerably less phosphorus (<u>ibid.</u>).

Nitrate-phosphorus relationships, however, can be ecologically important. Beadle (1954; 1966) proposed that phosphate and nitrate are important as a unit, although phosphorus may be the more limiting of the two elements. He referenced Allard's (1942) study which concluded:
1) "that available phosphate limits the rate of secondary

succession in woodland country in Virginia" and 2) "that the building up of soil nitrogen is governed by the phosphate level, which determines the invasion rate of nitrogen-fixing legumes" (Beadle 1954, 371). These conclusions, plus the suggestion "that the anion exchange capacity be defined on the basis of the amount of phosphate bound at a certain pH level" (Wilde 1958, 240), indicate that phosphorus is a nutrient of importance in its own right.

The ecological importance of phosphorus results from its prominent physiological role. Energy released from the oxidation of carbohydrates, proteins, etc., is used to synthesize adenosine triphosphate (ATP) from adenosine disphosphate (ADP) and inorganic phosphate. The energy stored in ATP later drives synthetic reactions in the cell (Devlin 1969, 114). Phosphorus is prominent in cell division and the development of meristematic tissue. The net results are the stimulation of uptake of other nutrients, especially nitrogen (Wilde 1958, 233), and an increase in production. References to the ecological importance of phosphorus are fairly common. For example, in Sweden, Aslander (1950) found that the distribution of some conifers and deciduous trees was influenced by the soil nutrient content, especially readily soluble phosphorus (Wilde 1954, 90). In addition, Beadle (1954; 1966) concluded that soil phosphate was an important agent in determining the floristics and structures of plant communities and in the floral evolution of Australia.

Some associations between soil phosphorus and plant communities were found in the literature. Ovington (1958a, 133) found greater levels of exchangeable phosphorus under conifers than under hardwoods. Page (1974, 13) also noted that available phosphate by weight at 15 and 30 cm was greater under softwoods than under hardwoods or cutovers. The depressed quantities under cutovers may be due to leaching, but those under hardwoods are apparently due to greater uptake. Rennie (1955, 89) calculated that the quantities of phosphorus taken up decrease in the order hardwoods, other conifers, and pines. Page (1974, 13) also observed that the quantities of available phosphorus were greater under spruce than fir at 15 and 30 cm though less at 2.5 cm. In contrast, Dammon (1971) observed that despite similar amounts of phosphorus in the litter of the two species (ibid. 259) phosphorus in the raw humus decreased from fir to spruce (ibid. 261). He, therefore, (ibid. 265) concluded that the rate of mineralization was greater under fir.

In addition, some trends might be extrapolated. For instance, since the phosphorus requirements of pines and early successional deciduous species are as low as 10 to 15 ppm P_2O_5 (Wilde 1958, 223 - 224) low levels beneath these associations can probably be expected. The nature of the substrate, however, is apparently an important variable affecting phosphorus concentration. Only small supplies of total and exchangeable phosphorus are available on peatlands

(Tamm 1964, 126) and the phosphorus percentage of inorganic soils is related to soil texture, usually increasing as the texture becomes finer (Black 1968, 559). Since vegetation is often related to soil texture (Wilde 1958, 177), e.g. Wali and Krajina (1973, 269) it is possible that correlations between vegetation associations and soil phosphorus levels often exist but have been obscured by the dominant nature of soil texture or soil moisture content.

Tree growth may be correlated with the phosphorus concentration of the soil for good correlations between seedling yield and internal phosphorus concentration (Mitchell 1939, 93) and between phosphorus concentrations in the leaves of trees and the levels in the soil (Beadle 1966, 1005) have been documented. The strength of the correlation probably depends on the difference between the nature of the phosphorus extracted from the soil and that used by the plant.

The main sources are organic phosphorus and calcium-, aluminum-, and iron phosphates, but immediately available phosphorus is almost exclusively orthophosphate (Hesse 1971, 271). Some controversy exists over which forms are immediately available, but Black (1968, 586) presents good evidence supporting Hesse. The instantaneous concentration of soluble phosphate is small and must be replenished during the growth of the plant, so that the rate of replenishment may be more important than the actual concentration of phosphorus (Hesse 1971, 271).

Low sufficiency levels of phosphorus would appear to reinforce that conclusion. Kramer (1959, 86), for instance, states that only very severe deficiencies affect the photosynthetic efficiencies of plants. Swan (1960, 15 - 19) observed good tree growth in solutions with phosphorus concentrations of only 6 ppm, but levels as low as 1 ppm for pines (Fowells 1959, 11) and less than 1 ppm for many agricultural crops (Arnon as cited in Swan 1960, 35) are adequate if the phosphorus is continuously available. Under these circumstances little correlation between tree growth, tree size, and extractable phosphorus can be expected.

Others such as Wilde (1958, 224) and Mitchell (1939, 45) have proposed that much larger levels of phosphorus are necessary for even phosphorus tolerant species. Swan (1960, 15) found better tree growth in solutions of low phosphorus concentration (6.2 ppm) than in control solutions of 62 ppm phosphorus. This probably resulted from young trees being more sensitive to toxicity levels than mature trees. Two possible explanations for the inconsistency are: 1) the discrepancy amounts to the difference between minimal and more optimum phosphorus concentrations, and 2) the higher levels represent the amount of inorganic phosphorus needed to ensure that the necessary concentrations of immediately available phosphorus are produced.

A number of soil conditions, however, regulate the plant availability of orthophosphate. Soil acidity and the concentrations of aluminum, iron, and calcium are especially

important in these respects. On acid soils the fixation of
phosphorus to aluminum and iron, which is not released until
the pH exceeds 9.0 (Hesse 1971, 283 - 284), may severely
limit the availability of phosphorus to plants. Fixation is
especially critical in acid soils with little organic matter
(Wilde 1954, 89) since humates, by participation in anion
exchange, usually release adsorbed phosphorus. Phosphorus
deficiency may also be critical at higher pH values for
under these conditions it is only slightly soluble as
calcium-phosphate; Waters and Pigott (1971, 179), for
example, concluded that the failure of calcifuge plants to
flourish on calcareous soils is partly due to insufficient
phosphorus. Between the higher pH levels and 5.5--when all
phosphorus fixed to calcium is released (Hesse 1971, 283 -
284)--the solubility is directly affected by the degree of
acidity. Wali and Krajina (1973, 338), for instance,
found significant negative correlations between available
phosphorus and pH and calcium. Greatest phosphorus avail-
ability occurs in acid soils rich in organic matter (ibid.),
or to be more precise, in organic soils between pH 5.0 and
6.0 (Goodman 1968, 553); there is some doubt whether
mineralization occurs below pH 5.5 (Hesse 1971, 272).
Possibly these auxiliary conditions obscure the identification
of soil phosphorus-vegetation relationships and some of
these will certainly have to be considered when interpreting
phosphorus concentrations from the transect at Pinawa.

To summarize, it may be concluded that there is little reason to doubt the ecological importance of phosphorus. There have, however, been few illustrations of an association in natural ecosystems between tree growth and soil phosphorus levels. This may be due to: 1) the strong correlation between phosphorus and several other soil nutrients, each of which may obscure the relationship to the plants, or 2) difficulty in defining and extracting from the soil the sources of phosphorus available to the vegetation. Although answers to these hypotheses cannot be expected from this study a correlation between extractable phosphorus and the overlying vegetation may be illustrated. If so, some progress will have been made in a field of study where further documentation is necessary.

F. <u>Nitrogen</u>

Unlike some of the previously described nutrients there is considerable support for both the physiological and ecological significance of nitrogen. It is a frequently limiting plant nutrient (Vitousek and Reiners 1975, 378) which probably limits the growth of agricultural plants more often than any other nutrient (Black 1968, 405). In most forests it is at least more limiting than phosphorus (Tamm 1964, 156). An indication of this is Mitchell's (1939, 95) finding that the internal nitrogen concentration had a greater effect on the yield of seedling white pine than did phosphorus. Also, total nitrogen was one of five (from a total of thirty-nine) variables found by Wali and Krajina (1973, 307) to be useful for interpreting plant distribution.

Heavy demands for nitrogen result because of the large amounts organically fixed as proteins, especially in the foliage. The greater stimulating effect of nitrogen on the shoot growth of seedling white pine than those of phosphorus, potassium, or calcium (Mitchell 1939, 64) confirms its significance to the leafy portions of the plant. Additionally, a deficiency of nitrogen results in smaller leaves with less chlorophyll (Kramer 1959, 86).

Height and diameter growth of trees is increased by nitrogen addition (Gessel 1960, 231). The response to nitrogen additions (and the competitive ability on unfertilized sites) varies among species (Mitchell and Chandler, 1939). Mitchell and Chandler (1939) used foliar analysis

to assess the relative nitrogen supply in the soil, against
which the growth response of several tree species was
measured. The foundation for this approach was the discovery
that the nitrogen concentration in the leaves was proportional
to the nitrogen supply of the soil (ibid. 31 - 56). This
method may be valid on mineral soils only, for although
Heilman (1966, 829) found a strong correlation between the
nitrogen levels in black spruce and the nitrogen content in
the top 76 cm of mineral soil, no significant correlation on
sphagnum peats was found. Using both natural and fertilized
sites Mitchell and Chandler classified several tree species
into three groups, nitrogen-tolerant, intermediate and
nitrogen-demanding, on the basis of growth response at
different fertility levels. The correlation between the
ranking of each group and the internal nitrogen concentra-
tions of each species was only crudely defined. Therefore,
the difference in competitive ability is not necessarily
due to variability in the nutrient extractive ability of
species; basswood (a nitrogen-demanding species), for
instance, had a significantly greater internal concentration
than did trembling aspen (a nitrogen-tolerant species) on
a nitrogen deficient soil. Rather, the difference between
groups lies in the amounts of nitrogen needed to raise the
internal concentration to evoke the maximum growth response,
especially in the region of minima--"where nitrogen is
definitely a limiting factor and increments thereof result
in a growth response which exceeds a direct proportion"

(*ibid.* 68). Therefore: 1) correlations between the tree
size of each species and the concentration of nitrogen in the
soil, and 2) unique levels of nitrogen under plant associa-
tions composed of varied species but of similar nutrient
demand, might be expected in other forest ecosystems too.

Several other studies have documented an association
between variations in the vegetation and the concentrations
of nitrogen beneath them, although on mineral soils the
differences may rapidly disappear with depth (Challinor
1968, 289). Generally the soils beneath hardwood
associations contain greater concentrations of total
nitrogen than do those under softwoods (Ovington 1956, 177;
Page 1974, 13), although Challinor (1968, 289) found greater
concentrations under white spruce than under red oak result-
ing from greater amounts of organic matter beneath the
spruce. Page (1974, 13) recorded greater nitrogen percent-
ages under balsam fir than under black spruce at depths
up to 30 cm; this results from greater amounts of nitrogen
returned in the litter of fir (Dammon 1971, 259) combined
with greater rates of mineralization under the fir stands
(*ibid.* 265). The low levels of nitrogen sufficiency for
loblolly and virginia pines found by Fowells (1959, 11)
suggest that early successional and heliophytic species
are not very demanding in their requirements for nitrogen.
Although rather definite trends between vegetation and
total nitrogen content are apparent, patterns for ionic
nitrogen are probably complicated by the variability in the

forms of nitrogen used by plants.

Exchangeable ammonium and nitrate are the types
generally used, but small amounts of organic nitrogen such
as amino acids may also be utilized (Wali and Krajina 1973,
305). Most forest trees, especially tolerant conifers such
as spruce, fir, and hemlock, can utilize ammonium and perhaps
some amino acids, while exacting hardwoods such as white ash,
tulip poplar, and walnut preferably use nitrate-nitrogen
(Wilde 1958, 222). McFee and Stone (1968) and Swan (1960)
obtained results supporting the thesis that ammonium is a
superior source of nitrogen for the conifers; the latter,
for instance, found that white and black spruce, jack pine,
and western hemlock grew better in "NH_4^+ only" than in
"NO_3^- only" solution cultures even though there was less
nitrogen in the first solution (ibid. 13). This, however,
is not an inviolable rule. Using a gradient analysis
technique, Wali and Krajina (1973, 317 - 319) inferred
that lodgepole pine preferentially uses ammonium while
alpine fir utilizes both ammonium and nitrate efficiently.
In previous greenhouse experiments "douglas-fir grew well
on nitrates and poorly on ammonium compounds, Sitka spruce
while showing better growth responses with nitrates
"tolerated" ammonium compounds" (ibid. 305). No information
on the ionic preferences of hardwoods was obtained from the
literature, except that trembling aspen shows no preference
to ammonium or nitrate (ibid. 319). The general nitrogen
requirements of several eastern hardwood species, however,

are given in Mitchell and Chandler (1939).

Environmental conditions can regulate the form of nitrogen that a plant absorbs. One important variable is soil acidity. Roberge (1972, 352) found that in black spruce humus when pH was lowered soluble NH_4-N increased rapidly and exchangeable NH_4-N decreased proportionately which he attributed to either a decrease of the NH_4-N adsorbing surfaces in the humus or to mass ion displacement when the pH is lowered. Even if nitrate is available, uptake is generally depressed when the solution acidity rises above pH 6.0 - 6.5 (Minotti et al. 1968, 695), although evidence to the contrary can be found, (e.g. Wilde 1958, 222). Another mechanism for the relative increase of ammonium under acid conditions is the intolerance of nitrifying organisms to pH values below 3.8 to 4.0(Pearsall 1938b, 198). The prevalance of ammonium at low pH values is ensured because solution acidity increases when the hydrogen of the carbonic acid excreted by the root is exchanged for the bases of the exchange compound (Wilde 1958, 239).

Other modifying variables such as temperature are also important. In solution cultures high root-zone temperatures ($20^{\circ}$and 25°C) accentuated the positive response of coniferous seedlings to ammonium (McFee and Stone 1968). The presence of other nutrients also influences the proportions of ionic nitrogen that plants receive. Minotti et al. (1968, 692) found that "the time for induction of optimal nitrate uptake was dependent upon presence of ambient Ca whereas maintaining the subsequent high rate of

nitrate uptake was facilitated by K"; the effect of both elements was synergistic. Nitrate-phosphate antagonisms have also been reported (Fowells 1959, 15). Modifying variables, plus a lack of research, probably account for the absence of literature on patterns of association between plant communities and the concentrations ammonium and nitrate in the soil beneath them.

Thus far I have illustrated some associations between plant communities and soil nitrogen concentrations and concluded the strength of the relationship appears to be greater for total nitrogen than for ionic forms of this nutrient, and that this may result from environmental variables which moderate the forms of nitrogen available to plants and the uptake of these nutrients. Most of the studies that have been referenced, however, took place on inorganic substrates. Although this does not necessarily preclude some of the results from being valid on organic soils, there are some aspects of nitrogen nutrition on peat soils that are peculiar and deserve attention.

Special attention will be paid to two features that are largely responsible for the nitrogen deficiency that is common on peatlands. The first is the slow rate of microbial decomposition resulting from the strongly acid reaction of the plant remains. Since the C/N ratios of the sphagnum mat of north temperate peatlands vary from 30/1 to 70/1 (Heinselman 1963, 329) much nitrogen remains immobilized and unavailable to the vegetation for long

periods of time. The second feature concerns changes in nutrient availability that occur with peat depth.

While most of the nitrogen in mineral soils is in the upper layers, in sphagnum peat most of it is in the lower part of the profile (Heilman 1966, 830). The low concentrations of nitrogen in the upper layers of moss are explained by wide C/N ratios and low substrate densities, whereas down the profile the weight of the overlying vegetation compacts the moss and decomposition reduces the C/N ratio. Despite the reduction very little nitrogen from the lower depths is available to plants growing on the peatland. There are essentially two explanations for this (ibid. 830 - 831): 1) the decomposition rate is slow, because this is also the coldest and latest to thaw portion of the profile, and 2) very little of the nitrogen which is mineralized is absorbed because the rooting depths of trees growing on peat (especially wet peats) are very shallow. Heinselman (1963, 337), for instance, observed average rooting depths as low as 15 cm for black spruce in northwestern Minnesota.

Evidence of nitrogen deficiencies are common on trees growing on peatlands. Heilman (1966) observed chlorosis, poor growth, and reduced canopy densities resulting from low nitrogen levels, whereas black spruce growing in conjunction with alder were vigourous and had dark green foliage (ibid. 828). Size differences between good and poor sites that are probably attributable to the

effect of nitrogen are described by Heinselman (1963, 327):

> On the best sites (<u>Picea</u> <u>mariana</u>), the most abundant
> tree, attains diameters up to 15 in. and heights of
> 80 ft. But on the poorest muskegs it is reduced almost
> to a shrub, sometimes resembling the candelabra trees
> of the tundra transition.

Results as variable as these may be attributable solely to differences in available nitrogen, but an inter-relationship between nitrogen and other nutrients may also be important.

G. Organic Matter

In contrast with some of the other nutrients good correlations between organic matter (with no differentiation between litter, humus, etc.) and the overlying vegetation have been found. These probably result from its beneficial effects in mineral soils which are briefly described by Wilde (1958, 181). One is that organic matter increases the water retaining capacity of soils. Once organic matter is incorporated into the mineral soil it also has beneficial effects on soil structure, porosity, permeability and aeration. Nutrients, especially bases and ammonium-nitrogen are efficiently adsorbed to organic matter, for the cation absorption capacity of humus exceeds that of clay by several hundred per cent. Replenishment-rates also are greater within organic than inorganic soil constituents (Rennie 1955, 84). An indication of the general ecological importance of organic matter is that the per cent humus content of the soil is a variable useful in predicting tree growth in plantations (Wilde 1970, 101).

Several instances of an association between organic matter and species composition can be found in the literature. Loucks (1962, 148) observed a stronger species composition gradient associated with the A-horizon complex than with the texture-depth soil complex. Wali and Krajina (1973, 268) concluded that the organic horizons, rather than soil texture, was most responsible for the distribution of black spruce communities. Ovington's (1958) paper is especially

significant for it correlates organic matter and the consequent nutrient status to the species composition of the forest.

He noted that litter formations were related to tree species composition of the overstory, and that there were large differences between formations in the total contents of sodium, potassium, and phosphorus in the surface organic layers (Ovington 1958a, 140). The differences, however, resulted from variations in the gross amounts of organic matter rather than in chemical composition. Consequently, the total content of these nutrients was greater beneath conifers than beneath hardwoods although nitrogen levels were slightly greater under hardwood stands (Ovington 1956, 177). In addition, Ovington (1958a, 140) concluded that the amounts of exchangeable nutrients in the organic layer are small compared to those in the mineral soil.

The concentrations of organic matter and associated nutrients depend upon the maturity of the ecosystem. Ovington (1956, 177) and Page (1968, 52) observed more organic matter in the soil under forested than under tree-less plots, while Burgess et al. (1973, 72) concluded that the amount to be found depends upon the age of the forest. Vitousek and Reiners (1975, 376) emphasized the positive correlation between the organic matter content and the soil nutrient levels that occurs during ecosystem succession. No information of this nature for peatland

ecosystems was found, possibly because disturbance
(especially human alteration) is concentrated in forests
overlying mineral soils.

Nutrient availability in peatlands is generally low
because of the higher accumulation/decomposition ratios of
organic matter. Heinselman (1963, 341), for instance, noted
that the poorest sites in Minnesota peatlands had thick
accumulations of poorly decomposed sphagnum moss as the
uppermost layer, although it is not necessarily true that
deep peats are poor sites (ibid. 330). The levels of
available nutrients depend on the type of peat. Sedge
peats usually have the highest nutrient levels, and
sphagnum the lowest, while those in feather moss and woody
peats are intermediate (Wilde 1958, 172; Loucks 1962, 150).
Nikinov and Minkina (1961, 67) observed that woody peats
are usually more strongly decomposed than those of moss, and
that woody plants deposit peats of a higher ash content
than do mosses under similar conditions. McVean (1963,
661) concluded that Eriophorum-Sphagnum peat had adequate
supplies of potassium, calcium, magnesium and phosphorus
for the nutrition of pine seedlings, but the rate of
nitrogen mineralization was insufficient to satisfy the
growth requirement. Dried colloidal peat released sufficient
nitrogen, but phosphorus then became the limiting nutrient.
Nutrient availability in peatlands is governed by the
oxygen content and redox potential of the water (Nikinov
and Minkina 1961, 67) which regulates the rate of decomposi-

tion of organic matter. Unfortunately there is little information on the relationship between peat type and the species composition of the overstory. Reader (1971, 187 – 188) found the rates of litter decomposition increased with peatland succession, but no generalizations concerning decomposition rates, nutrient availability, and tree species occurrence in peatlands can be made.

In summary, the role of organic matter in mineral soils is largely as an exchange complex, while in peat soils it serves mostly as a nutrient reserve. Dissimilarities in tree species composition and growth rates have been associated with differences in the humus content of mineral soils and it is reasonable to assume that consequent differences in available nutrients explain some of the variation in vegetation cover. Similar effects on peat soils have apparently not been documented, but in view of the variance in nutrient availability between peat types, they can be expected there too.

CHAPTER III

GENERAL DESCRIPTION OF THE STUDY AREA

A. Location

      The FIG area of WNRE near Pinawa, Manitoba is
located approximately 120 km northeast of Winnipeg (Figure
1a) mostly within the northeast quarter of section 22, town-
ship 14, range 11E (Figure 1b). FIG is a circularly enclosed
area (100 m in diameter) of mixed forest which has been set
aside "to study the effects of chronic irradiation on the
biota" (Dugle and Thibault 1972, 1). Within FIG there is
a grid network of north-south and east-west cut lines at
100 m intervals. All positions are located with reference
to the centre (ONS OEW) where the irradiator is located
(Figure 1c).

B. Geology

      The bedrock geology of WNRE consists of Precambrian
rocks (MacPherson 1971, 15) composed of granites and granite
gneisses of the Superior Porvince in the Canadian Shield
(ibid. 17). Glaciolacustrine deposits 9 to 24 m deep
overly the bedrock (Ackerman 1973, 2).

      Lacustrine clay is present throughout FIG, but is
covered by sand or organic matter. The sand is from 0 to
2.7 m thick and at 250W progressing from east to west
changes from well-graded, fine to medium aoelian sand to
poorly graded, gravelly lacustrine sand (ibid. 10). The
aoelian sand is more than ninety-nine per cent quartz
(ibid. 11).

Figure 1. Location of study area

      a. Location of WNRE at Pinawa, Manitoba

      b. Location of Field Irradiator Gamma (FIG)

         area – Dugle and Thibault (1972, 2)

      c. Location of study transect within FIG

WHITESHELL NUCLEAR
RESEARCH ESTABLISHMENT

Pinawa

Winnipeg River

Red River

44

11

59

15

WINNIPEG

1

0   10   20   30 km

25 | 31 | 32 | 33 | 34 | 35 | 36

24 | 30 | 29 | 28 | 27 | 26 | 25

HWY 11

WINNIPEG RIVER

15 | 19 | 20 | 21 | 22 FIG | 23 | 24

12 | 18 WNRE | 17 | 16 | 15 | 14 | 13

1 | 7 | 8 | 9 | 10 | 11 | 12

N

POWER LINE •—•—•

WNRE BOUNDARY —··—··—

ROADS:
  PAVED
  GRAVEL

0   MILES   1

0   km   1

6 | 4 | 3 | 2 | 1

HWY 211

study transect

46
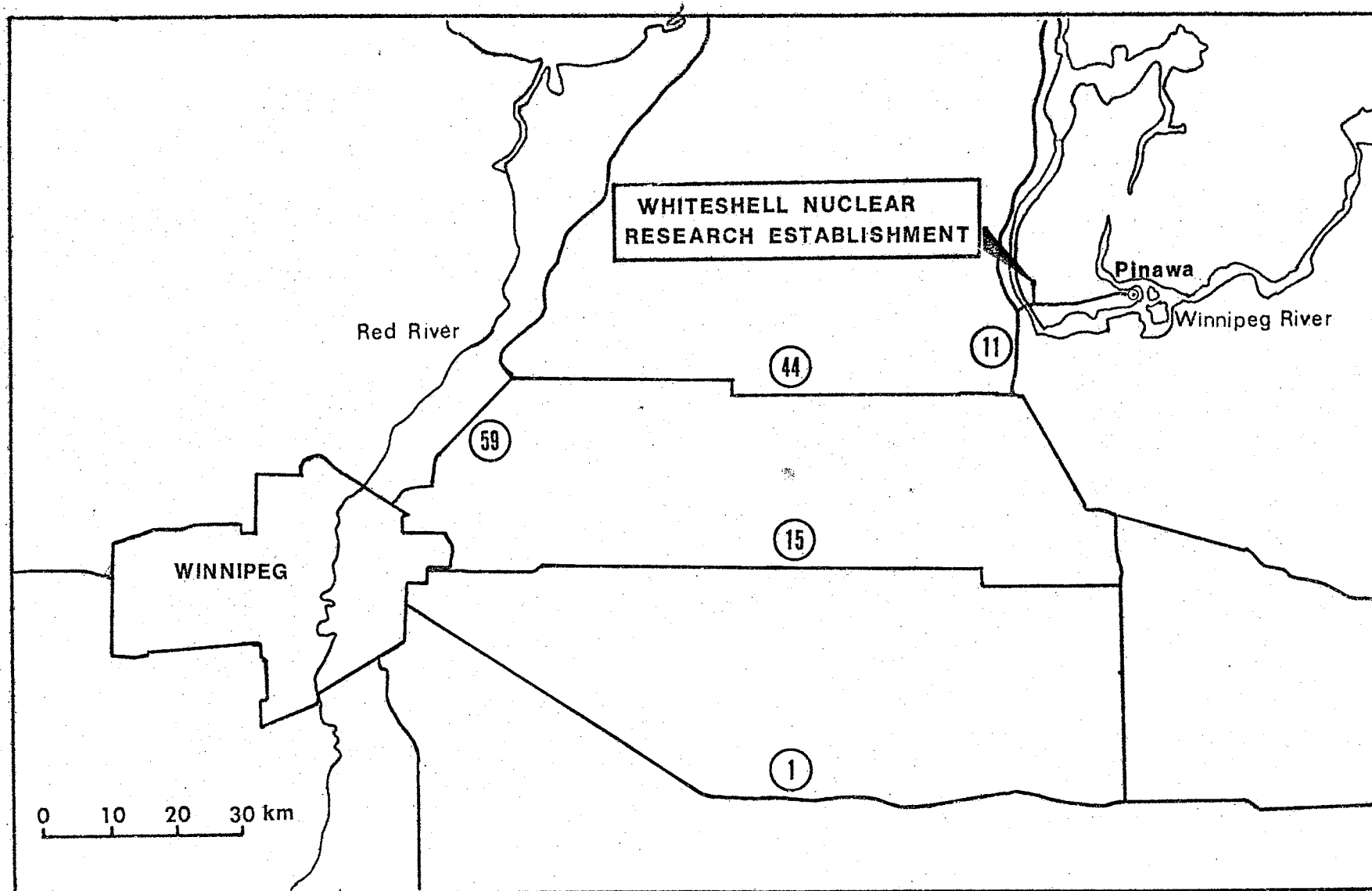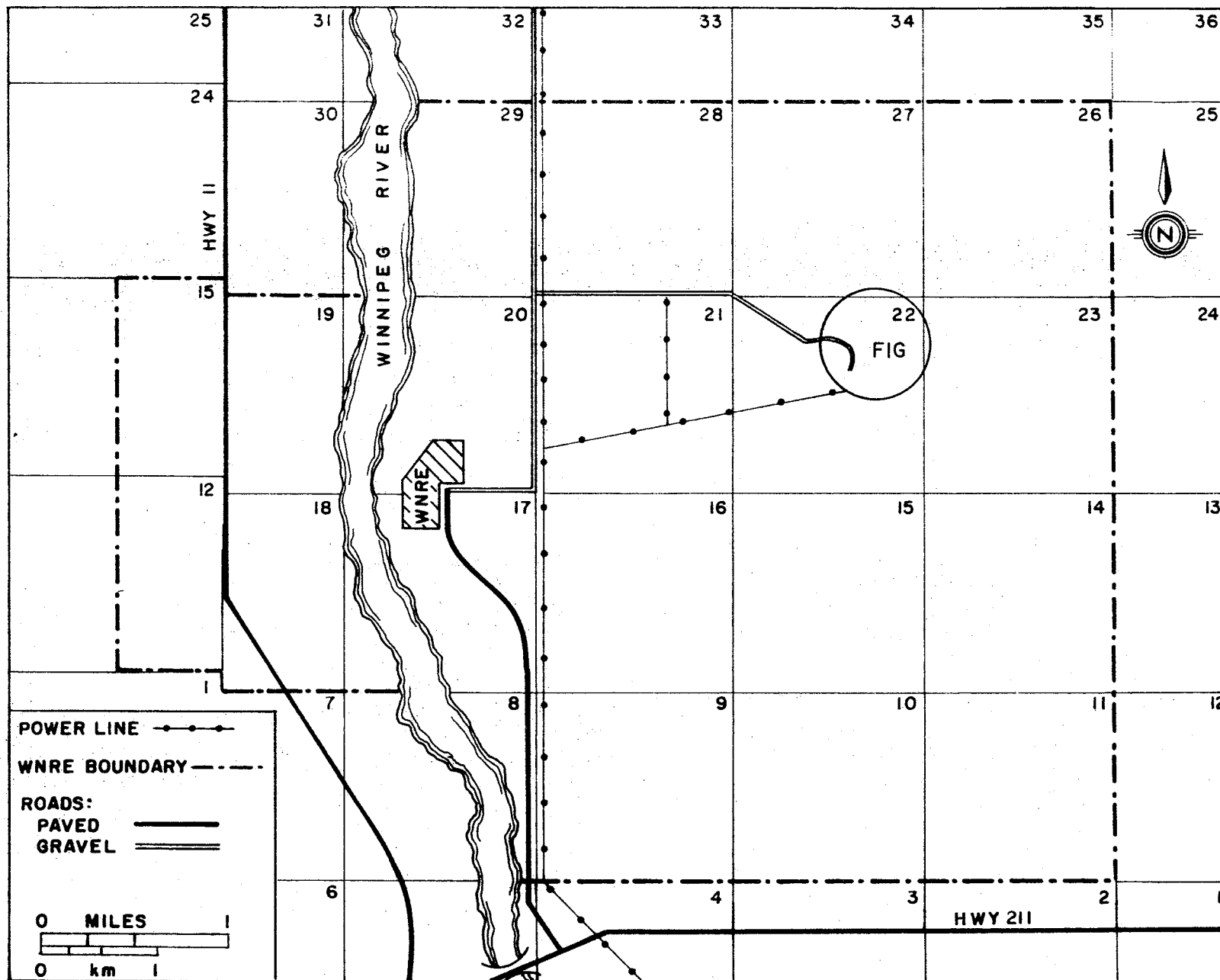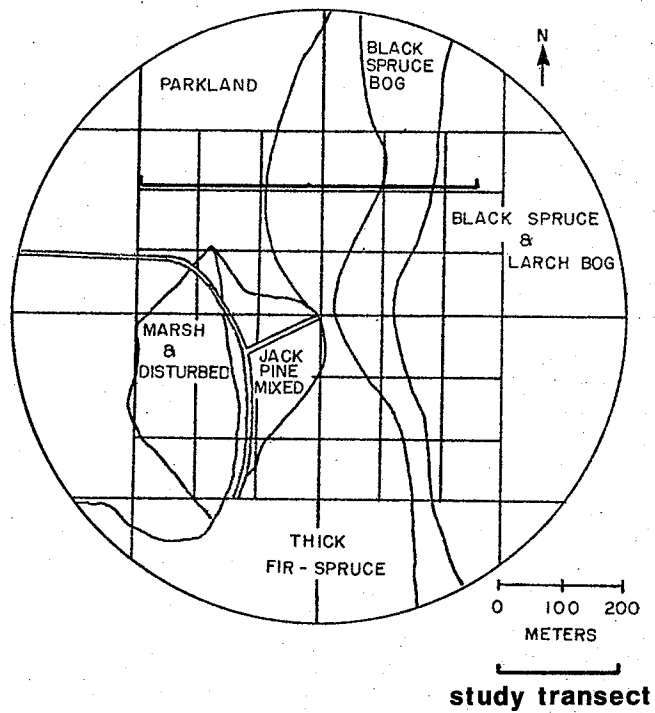
C. Topography

The topography of FIG slopes eastward from the sand towards the bog. The change in elevation from 300W to OEW is approximately 4.2 m (ibid. 56).

D. Climate

Pinawa is located in the north central portion of the North American continent and has a typical continental climate characterized by "rainfall with an early summer maximum, and wide ranges of annual, monthly, day to day, and diurnal temperatures" (Bell 1974, 28). Pinawa is near the middle portion of the belt of prevailing westerlies (ibid.). Three main fronts, the Polar, the Maritime Arctic, and the Continental Arctic fronts, determine the climate although only the first two are distinguished in the summer since no source for Continental Arctic air exists then (ibid.).

Since the climatological station at the WNRE has only recently been established there are still insufficient data with which to summarize the climate of the area. The following data were, therefore, taken from Climatic Normals for Seven Sisters Falls which is located approximately 6 km south-east of the research site and is surrounded by vegetation types similar to those at Pinawa.

TABLE I

CLIMATE OF SEVEN SISTERS FALLS (1931 - 1966)

MEAN	YEARLY	JULY	JANUARY	MAXIMUM(mo)	MINIMUM(mo)
TEMPERATURE(^{o}C)	7.8	31.0	-12.3	31.0(July)	-12.3(January)
RAINFALL(cm)	36.9	6.73	trace	7.49(June)	0.00(January)
SNOWFALL(cm)	94.7	0.00	17.8	19.6(March)	-----
TOTAL PRECIPITATION(cm)	46.43	6.73	1.78	7.52(June)	1.45(February)

E. Soils

Four major soil series are found within FIG, the
Woodridge Series, the Shallow and Deep Peat complex, and the
Lee River Series. The main features of the descriptions given
by Smith and Ehrlich (1967) are presented.

1. Woodridge Series

These sandy soils have developed on sand and gravel
beach and outwash deposits "which may be underlain by a
strongly calcareous, stony glacial till within 30 inches
of the surface" (ibid. 92). Dry soil conditions, resulting
from moderate surface runoff and rapid internal drainage, is
a consequence of the coarse parent material and mantle.
Grey wooded soils "characterized by a thin, organic surface
layer; a deep, leached, light greyish brown A horizon and a
brown, textural B horizon" (ibid.) are typical of the
Woodridge Series. Ackerman (1973, 11), however, describes
the soil on the aoelian sands as a degraded dystrical brunisol.

Dry soil conditions, rather than nutrient deficiencies,
are the major obstacle to the agricultural use of these soils.

2. Lee River Series

Only a small part of FIG is occupied by this clay soil which occurs in areas of poor drainage, particularly along the margins of shallow organic soils. Internal drainage, is slow because of the fine texture of the parent material and a high water table. While the surface layer consists of fibrous peat that varies from 15 to 46 cm deep, the parent material is an alkaline, slightly to moderately calcareous lacustrine clay; the soil is classified as peaty orthic humic gleysol.

3. Shallow Peat Complex

Shallow peat, 30 to 94 cm deep, occurs in poor to very poorly drained areas at the margins of extensive areas of deep peat and lies over moderately fine to fine textured calcareous lacustrine sediments (ibid. 82) that are neutral to moderately alkaline in reaction. The layer of peat is described by Smith and Ehrlich:

> the organic soil complex consists of several soil types differentiated on the type and degree of decomposition of the vegetation from which the peat was formed. The dominant soil type is fibrous shallow peat developed on medium to strongly acid peat. The upper portion of the organic layer is a mixture of fibrous feather mosses and sphagnum, while the lower portion consists of one or more compact layers of moderately or well developed peat derived from sedge or a mixture of wood and sedge. (ibid.)

Nutrients that limit the growth of agricultural crops (and probably trees) on these soils are phosphorus, manganese, boron, copper, molybdenum and zinc.

4. <u>Deep Peat Complex</u>

This peat ranges from 0.9 to 3.7 m underlain by
moderately to strongly calcareous lacustrine clay. Smith
and Ehrlich (1972) have differentiated three organic soil
types based on regimen or water movement pattern.

An acid fibrous moss (mostly sphagnum) peat that is
usually from 1.8 to 3.7 m deep is the most extensive soil
type. The upper 0.9 to 1.8 m consists of coarse to medium
fibred sphagnum while the layers below are formed from
either sedges and mosses or sedges and wood. A very acid
surface layer is characteristic of this soil type.

A layered fibrous moss peat soil, usually 0.9 to
2.1 m deep, often occurs between treeless sedge peats or
on the upper margins of bogs near mineral soil margins.
Fibrous layers of sphagnum and feather mosses occur in the
upper 15 to 61 cm while the rest of the profile is composed
of moderately well decomposed woody and sedge or sedge and
moss peat. "The significant difference between this soil
and the previously described soil is that it is more
compacted, contains considerably less sphagnum moss, receives
water from mineral soils and the surface peat layers are
less acid" (<u>ibid.</u> 42 - 43).

The third peat type, sedge peat, is unlikely to
occur in the FIG area.

Little is known about vegetation-nutrient relation-
ships in the deep peats because of their low agricultural
value. In fen peats, however, phosphorus, potassium and

copper appear to limit production (<u>ibid</u>. 44); probably
these also limit growth in the other deep peat types.

F. <u>Vegetation</u>

The vegetation of the Whiteshell Nuclear Research
Establishment lies within the Lower English River section of
the boreal forest (Rowe 1972). Much of the vegetation is
successional. Dugle (1972, 47) predicts that "most of the
WNRE areas would have a white spruce-fir, black spruce, or
river-deciduous forest climax."

Two main forest types are represented in FIG. Slightly
over one half of FIG consists of a black spruce-labrador tea -
sphagnum community, while a mixed broad-leaved and needle-
leaved forest dominates the remainder of the area (Dugle 1969,
3). FIG has been disturbed by logging, gravel-pit operations,
tree removal, and burns (1929, 1938, and 1961) (<u>ibid</u>. 1).
The mixed forest shows more disturbance than the evergreen
associations (<u>ibid</u>. 29).

Each soil type has a characteristic vegetation cover.
Open stands of jack pine (<u>Pinus</u> <u>banksiana</u> Lamb. = <u>P</u>. <u>divaricata</u>
(Aiton) Dumont) is the native (Smith and Ehrlich 1967, 92),
although not true climax vegetation, on the Woodridge soil.
<u>Populus</u> <u>tremuloides</u> Michx. (aspen) is also common on it. In
FIG, however, the stand of jack pine is very small (Dugle,
1969a, 33) and the forest consists of many species whose dom-
inance varies with location. The other main species include
<u>Abies</u> <u>balsamea</u> (L.) Mill. (balsam fir) <u>Betula</u> <u>papyrifera</u>
Marsh. (paper birch) <u>Fraxinus</u> <u>nigra</u> Marsh. (black ash)

Larix _laricina_ (Du Roi) K. Koch (larch) _Picea_ _glauca_

(Moench) Voss (white spruce) _Picea_ _mariana_ (Mill.) BSP.

(black spruce) _Populus_ _balsamifera_ L. (balsam poplar), and

Populus _tremuloides_. Dugle (1969a; 1972) may be consulted

for a more complete description of the mixed forest. For

author citations and nomenclature see Dugle (1969b) and

Dugle and E. Lakany (1971).

Vegetation on the shallow peat consists mostly of

black spruce or black spruce and larch with under vegetation

consisting of sphagnum and feather mosses, some alder and

bog birch (Smith and Ehrlich 1972, 82). Cedar is also listed

on the map accompanying the soils report, but Dugle (1969b;

1971) reported none in the FIG area. Balsam fir, which was

not mentioned by Smith and Ehrlich (1972), is common on the

shallow peat within FIG.

Black spruce and larch are the two main tree species

found on deep peat, but there are great differences in the

degree of forest cover between the two soil types. On the

acid, fibrous moss peat the trees are stunted and occur in

semi-open stands, but on the mineral-influenced type the stands

are "well-stocked and merchantable." (Smith and Ehrlich 1967,

42).

On Lee River clay soils balsam poplar, black spruce, and

larch with shrubby understories of willow and alder are

common. Approximations to all but the last forest type are

outlined in Figure 1c.

CHAPTER IV

METHODS

A. The Field Sample

1. Location

This study was conducted along a transect from 250E to 300W, 200 m north of the irradiation tower. Sampling along a transect rather than random sampling within FIG was chosen because 1) working along a transect involved fewer logistic problems and 2) the data was to be assessed with respect to the topographic gradient. A transect 550 m long was chosen because it adequately traversed the major vegetation associations within the area. The transect was judged to be distant enough from the irradiation tower so that ecological disturbance due to previous irradiation (at 19 h/da since March 2, 1973) was minimal. Subsequent data obtained by Dugle(pers. comm.) tend to confirm the validity of this assumption. Dose rates during 1973 - 1974 for six sites along the transect are as follows: OEW (closest to the tower) - 33.65 mrad/h, 100W - 26.72 mrad/h, 150W - 16.92 mrad/h, 200W - 9.67 mrad/h, 250W - 10.72 mrad/h, 300W - 3.59 mrad/h.

2. Sampling the Vegetation

a) Shape and Size of Quadrats

Although rectangular plots are more efficient for sampling vegetation than are square plots (Oosting 1956, 42), the latter were used for logistic reasons. Firstly, in heavily forested areas the long sides of rectangles are difficult to lay in a straight line. Secondly, rectangular quadrats placed perpendicularly to the ecological gradient

would result in more plots to sample; the increase in efficiency would not have compensated for the extra work needed to sample, and to analyze the data from, more quadrats. Ten by ten metre quadrats were used since these dimensions are generally satisfactory for sampling the overstory of a forest in northerly forests (ibid. 48; Cain and de Oliveira 1959, 146).

b) Mensuration

A preliminary investigation into forest composition was conducted to gather information used in proposing a sampling scheme. From the mid-point of each ten metre quadrat along the cut line the relative dominance of the four most common species near that point was visually assessed; the results were nearly identical to those of others working under the direction of Dugle (pers. comm.). The vegetation, by quadrats, was grouped into associations of similar composition. The proportion of the length of the transect that each association occupied was the principal criterion used to decide the representation of each association in the sample of a stratified random sampling scheme. The proportions were slightly weighted towards the deciduous forest because it was believed that as the influence of water becomes less pronounced, the nutrient medium is more heterogeneous and requires more intensive sampling.

The associations that were recognized, the length of the transect they occupied, and the number of quadrats sampled from each are as follows:

1. Larch-black spruce association, 250E to 190E - 3 quadrats

2. Black spruce association, 180E to 70E - 4 quadrats

3. Balsam fir - black spruce association, 60E to 10E - 3 quadrats

4. Balsam fir association, OEW to 70W - 4 quadrats

5. mixed deciduous - evergreen association, 80W to 250W - 12 quadrats

6. Trembling aspen association, 260W to 300W - 4 quadrats

Within each quadrat the circumference of all tree trunks greater than 5 cm in circumference at breast height was recorded. The circumference of each trunk of aspen in clones, or paper birch having grouped trunks, was measured rather than summing the totals to calculate the circumference of each tree. Dugle and Bols (1971) and Dugle (pers. comm.) were consulted in the identification of the species of spruce within the FIG area. Except for those trees felled along the cut line, only the circumference of live trees was measured. For felled trees the circumference of the trunk below the cut was used to calculate the basal area which may be, therefore, slightly overestimated. These measurements were included in the sample on the rationale that the trees would have been alive had they not been removed for the survey lines. Since tree growth extends to September at the latest (Fraser 1960, 203) the circum-

ference of the trees were measured in August and September
of 1973 in an attempt to minimize variation that would
result from sampling during active growth.

3. Sampling the Soil

a) Depth

Samples were taken at depths of 0 - 15 and 15 - 30 cm
below the soil surface. In view of the shallow rooting
systems of some of the species found along the transect,
e.g. aspen (Maini, 1968, 55) and black spruce (Heinselman
1963, 337; Rowe 1956, 64), it was thought that sampling
at these depths would correspond to the zones of greatest
uptake by the trees. In the case of black spruce, which is
known to have rooting depths as shallow as 15 cm (Heinselman
1963, 337), samples from 0 - 15 and 15 - 30 cm may corre-
spond to zones of active and negligible uptake respectively.

b) Method

The soil samples used for laboratory analysis were
each composite samples of eight soil cores (Wilde 1958,
181) taken in a roughly zig-zag fashion (Jackson 1958, 24)
across the quadrat. The eight cores for each of the 0 - 15
and 15 - 30 cm depths were placed in a plastic bucket and
mixed until 'homogeneous'; in the wetter peats where the
soil corer would not extract a sample, sampling was done
by hand. A sample of this mixture was then placed in a
polyethylene bag. Before sealing the bag two droppers-
full of toluene were added to retard microbial activity
during transport to the laboratory (Black 1965, 1188).

The samples were stored at below freezing temperatures until they were ready for analysis (ibid. 1181).

(c) Time

Ecological and practical considerations were used in the decision to sample the soil in the autumn. The annual fall accumulation of nutrients represents the maximum amount which is available to the vegetation in the springtime (Weetman 1961, 15) and which would best differentiate plant-nutrient interactions along the transect. Foster and Gessel (1972, 451) found a significant increase in soil calcium added by litterfall and that the "forest floor received increased amounts of K and Ca from stemflow in the autumn". In addition, Pearsall (1938b, 195) recommended avoiding periods of active utilization of nutrients by plants because some easily soluble nutrients would not be detectable then, and sampling at a time of year when the activity of different associations is as close as possible. Because deciduous and evergreen trees occur along the transect, fulfilling both these criteria would mean sampling in mid-winter when snow and temperature conditions make sampling impractical. Autumn rather than spring was chosen because of the dryer conditions that prevail.

All but eleven quadrats were sampled late in October, 1973. The remaining samples of peat were taken in the third week of May, 1974. These samples were left until spring because the frozen peat surface made accessibility easier, and where possible, removing cores of ice and peat with the sampler gave somewhat more quantitative samples.

B. Laboratory Treatment of the Soil Sample

1. Drying the Soil Sample

(a) Disadvantages

Drying the soil is considered standard procedure when immediate analysis of the sample is not possible. Drying, however, alters the physical and chemical properties of the soil sample. Physical changes may result from "irreversible dehydration causing cementation of clay particles which are then not dispersed" (Hesse 1971, 14). Increasing the temperature and the drying time generally causes the greatest alteration in the chemical status (ibid. 12).

Except for soils containing sulphur compounds (ibid. 19) the hydrogen ion activity is only slightly altered by drying the sample and some change results from alteration of the carbon dioxide content of the soil (Jackson 1958, 42). The difference in pH between fresh samples and those dried at temperatures up to $105^{\circ}C$ has been found to be small and "almost within the limits tolerated in the chemical method" (Riehm 1956, 104).

The change in the inorganic phosphorus content of the sample depends on the soil pH. Mineralization induced by drying increases as the pH approaches neutrality (Hesse 1971, 271). In acid soils the increase is very temperature dependent; air drying acid soils may increase the acid extractable phosphorus by ten to thirty per cent (Jackson, 1958, 155), but by drying at high temperatures the water

or dilute acid extractable phosphorus may be increased in excess of one hundred per cent (ibid. 155; Hesse 1971, 13). Less phosphorus is extracted from dried alkaline soils than from fresh samples and it has been demonstrated that a decrease in the pH of alkali soils increases phosphorus mineralization upon drying (Hesse 1971, 271). In addition, changes in aluminum and iron induced by drying are thought to disturb the phosphorus fixation capacity of some soils (ibid. 13). Mineralization may not be great when the peat soils are dried. Hesse (1971, 470) states that air drying flooded soils may not affect the amounts of extractable phosphorus.

Large increases in exchangeable potassium have been noted as the drying temperature is raised (ibid. 128; Jackson 1958, 130), but Riehm (1956, 104) observed a small decrease in exchangeable potassium after fresh soil was dried at $105^{\circ}C$. One possible explanation for the difference is that exchangeable potassium is increased after drying if it is present in concentrations less than a milliequivalent (meq) per 100 g of soil, but decreases at concentrations in excess of that (Hesse 1972, 18).

Although calcium is the most common exchangeable cation in the soil (Buckman and Brady 1969, 74 and 347) no changes in the status of exchangeable calcium after drying the soil have been reported.

Drying has little effect on the total nitrogen content of a soil sample (Hesse 1971, 12), but modification of

the inorganic fraction is pronounced. The change is largely temperature dependent.

> Air-drying a soil seems to have little effect upon the nitrifying organisms, and consequently on re-wetting the increased mineral nitrogen fraction will appear as nitrate, whereas if the soil had been dried at higher temperatures the nitrifiers would have been killed and on re-wetting there would be an accumulation of ammonium nitrate (ibid. 13).

Oven drying at higher temperatures may explain Bremner's conclustion that "changes which have been observed in the ammonium content of soils as a result of drying have been more pronounced than the changes in nitrate content." (Bremner 1965, 1182). Although a consistent pattern of change resulting from drying is difficult to ascertain (ibid. 1183), there is little doubt that the alteration can be large.

(b) Justification

Despite the chemical changes, it is advantageous to dry the sample before storage and analysis. Samples stored in the moist state for even short periods of time undergo microbial change with concomitant alteration in the status of organic matter and the ions in the soil. Another advantage is that weighing, sieving, and sub-sampling of soils (especially waterlogged ones) is easier if the sample has been dried (Hesse 1971, 496; Jackson 1958, 32).

There is also some support of a more theoretical nature for drying the soil. "There is reason to believe that certain chemical reactions are hastened by the drying

process and that dried samples are, therefore, more nearly at equilibrium." (Jackson 1958, 42). Ions such as nitrate can change within such short periods of time due to natural causes that "in order to compare soils it is essential to standardize by air drying even though the results may be different from those which one would obtain in the field" (Hesse 1971, 12).

Because of the convenience, standardization, and reproducibility attainable by soil drying, and because no special emphasis is being placed on knowing the exact concentration of nutrients in the soil beneath the vegetation, the soils were dried in this study.

(c) Discussion

To facilitate rapid drying, the soil is spread onto flat trays and placed in a cabinet with circulating warm air. Hesse (1971, 12) recommended that the temperature should not exceed 35°C with the relative humidity between 30 and 70 per cent while Jackson (1958, 31) suggested at least partial air-drying at temperatures between 25° and 35°C and relative humidities of 20 to 60 per cent. In some laboratories up to 70°C or higher were used (Williams and Riehm 1956, 31).

(d) Procedure (Appendix A)

2. Sieving and Storing

(a) Sieving

A soil fraction of less than 2 mm in size contains virtually all soil nutrients and facilitates mixing. With

sandy soils humus particles must be ground and restored to the sample (ibid.; Black 1968, 222 - 226). No attempt, however, was made to grind the peat samples.

(b) Storage

Since immediate nutrient analysis of the soil samples was not possible, convenient and effective methods of storing the samples were considered. Hesse (1971, 16) suggested screw capped glass jars which prevent contact of the soil with ammonia and other laboratory fumes which not only alter the pH of the soil (Jackson 1958, 44), but its ionic properties as well. Because of the greater ease of transport and storage, relative freedom from breakage, and low cost, the soil samples were stored in plastic bags. Although Hesse (1971, 16) asserted that storage in plastic containers can result in changes in the clay minerals (and, therefore, the cation exchange capacity) of the soil, there appears to be little support for this hypothesis.

Reagents such as toluene or chloroform can be added to the soil in small quantities to retard microbial action, but some researchers have found them to be ineffective and that their use can disrupt subsequent chemical analysis (Bremner 1965, 1181). Deep freeze storage is also used to retard microbial alteration. Gasser (as cited in Bremner ibid.) found no change in inorganic nitrogen when soil samples were stored at $-10^{\circ}C$ for 32 days, but Allen and Grimshaw (as cited in Bremner ibid.) did find changes in samples stored at $-15^{\circ}C$.

Bremner (<u>ibid</u>. 1182) concluded that storage at cold temperatures is not a satisfactory method for preserving the status of inorganic nitrogen in the soil.

Cold storage of the samples was used for two reasons:

1. since the degree of microbiological activity is a function of temperature, cold storage at least retards disruption of the mineral status and

2. storage in a freezer effectively eliminates exposure of the sample to the atmosphere of the laboratory.

(c) <u>Procedure</u> (Appendix A)

3. <u>Analysis of the Soil Sample</u>

(a) <u>Hydrogen-Ion Activity</u>

(1) <u>Methods of Analysis</u>

The acidity of the soil is not properly reflected by pH measurements. They express hydrogen ion activity, but not the activity of other ions such as iron, magnesium, and aluminum which also influence soil acidity (Hesse 1971, 35). Nevertheless, the measurement of soil pH tells much about associated soil properties, especially mineral status and nutrient availability (<u>ibid</u>. 19), and characterizes the soil as a medium for plant growth (Jackson 1958, 38).

The pH of soil solutions is commonly measured colorimetrically. Although colorimetry is accurate to within 0.2 of a pH unit (Hesse 1971, 28) and is convenient to use in the field (<u>ibid</u>. 26) there are many disadvantages

associated with it (Jackson 1958, 51; Peech 1965, 915 - 916; Kolthoff and Laitinen 1941, 52; Hesse 1971, 28).

The pH of the samples were measured electrometrically because of the many sources of error inherent in colorimetric pH measurement and the tedious length of the proper colorimetric procedure as outlined by Kolthoff and Laitinen (1941, 47). Although there are inaccuracies in this method, they are not as severe as those previously described.

Liquid junction potential is "the most important source of error when using the glass electrode-calomel system" (Hesse 1971, 24). The error is minimized by using a saturated KCl (or NH_4NO_3 when K would interfere) solution in the glass electrode (Jackson 1958, 41). An asymmetric potential across the glass membrane occurs "even when solutions of the same H^+ ion activity are on the two sides" (ibid.), but frequent calibration of the glass electrode in a solution of known pH corrects this. Kolthoff and Laitinen (1941, 100) note that in strong acid solutions there are positive deviations from the pH and that negative deviations occur in strong basic solutions; while the range of variation depends on the composition of the glass, soil solutions are not likely to make this problem a severe one. As in colorimetry, the electrometric method is subject to salt error, but this is minimal (Jackson 1958, 41) and can be standardized "by taking measurements in potassium chloride solution rather than in water" (Hesse 1971, 24).

There are many advantages to measuring pH electro-
metrically. Accuracy is one of these; measurements to
0.2 of a pH unit or better can be made (_ibid._). It is
rapid, convenient, and inexpensive. The method does not
expel dissolved gases such as carbon dioxide--this would
alter the pH--from the system under measurement (Jackson
1958, 41) and "the observed e.m.f. electromotive force
is unaffected by the presence of oxidizing or reducing
agents or of capillary-active substances such as proteins"
(Kolthoff and Laitinen 1941, 102). The glass electrodes
can be used in coloured, turbid and colloidal solutions
(_ibid._) and in thick fluids, pastes, and gels (Jackson 1958,
41). Because the current passing through the cell is
small, correct results are obtained even in unbuffered
solutions (Kolthoff and Laitinen 1941, 102).

(2) _Ratio of Solution to Soil_

Hesse (1971, 21) and Jackson (1958, 44) recommend
that electrometric pH measurements be taken from a
saturated soil paste since this brings all soils to an
equipotential moisture status. Dilution of the soil with
a solution is the more common practice because it is more
convenient and less complicated than bringing the soils to
the same moisture status, and no specially shaped electrodes
(_e.g._ spear shaped) are necessary.

The accuracy that is sacrificed by using a soil
dilution varies with the ratio of soil to solution.
Higher pH readings are obtained, "regardless of the initial

pH of the soil..." (Peech 1965, 917), as the proportion of water to soil is increased. The rise in pH from sticky point to a water/soil ratio of 10/1 is usually 0.2 to 0.5 pH unit, but in some neutral and alkaline soils the rise may be one or more units (Jackson 1958, 42).

(3) Time for Equilibration

Hesse (ibid. 30) recommends that soil suspensions be allowed to stand for an hour before measurement to allow equilibration of the soil with the solution. This also allows equilibration of the soils to the carbon dioxide pressure of the atmosphere (Peech 1965, 920), but for most practical soil testing, the pH may be read immediately (Jackson 1958, 46).

(4) Dilution Solvent

Normally the soil is diluted with water, but there are several advantages to using salt solutions as the solvent. Normal KCl is often used because the pH values are affected less by biological and meteorological phenomena than they are in water and, therefore, better reflect the intrinsic character of the soil (Peech 1965, 918). Alternatively, the soil may be diluted with 0.01M $CaCl_2$. Peech (1965, 919) remarks that pH readings in 0.01M $CaCl_2$ using a 2/1 solution/soil ratio are approximately 0.5 units lower than a similar measurement in water. Wali and Krajina (1973, 335) found a difference of 0.7 to 1.1 units difference in measurements made in water and in $CaCl_2$ using a 2.5/1 ratio of solvent to organic matter; the

correlation coefficient between the two series of measure-ments was 0.895.

The decision to measure hydrogen ion activity in a $CaCl_2$ suspension was based on the advantages of the method outlined by Peech (1965, 918 - 919):

1. soil pH measured in 0.01M $CaCl_2$ is independent of dilution over a wide range of soil/solution ratios.

2. the soluble electrolytes contributed by non-saline soils in a 2/1 0.01M $CaCl_2$/soil suspension are insignificant so that the observed pH is nearly independent of the initial amount of salts in the soil.

3. a 0.01M $CaCl_2$ solution approximates the total electrolyte concentration of the soil solution at optimum field water content; a 2/1 $CaCl_2$/soil suspension, therefore, more nearly reflects the soil pH under field conditions than does an equivalent soil-water suspension.

4. "Because soil suspensions are flocculated in 0.01M $CaCl_2$, the errors due to liquid junction potential can be minimized by placing the calomel in the clear supernatant liquid" (ibid. 919).

(5) Procedure (Appendix B)

(b) Calcium and Potassium

(1) Calcium: Methods of Analysis

Calcium can be measured in many ways. Classically, calcium is determined complexometrically using EDTA, but problems associated with this method include 1) inter-ference from many ions (elimination of which complicates

the procedure), 2) choice of a suitable indicator solution,
and 3) inaccuracies in end-point determinations (Hesse 1971,
109 - 110). With care, 3 per cent precision is possible
(ibid. 121). A gravimetric technique by which calcium is
determined as the oxalate by titration with cerate or
permanganate was described by Jackson (1958, 89 - 96).
For routine determinations interferences are almost
negligible (ibid. 90), but the method is "far too tedious
to be commonly employed" (Hesse 1971, 90).

An emission spectrophotometric method was chosen
for the analysis of calcium because 1) it is simple, 2) it
is well suited to the analysis of alkali metals, 3) many
samples can be analyzed quickly, and 4) the necessary
equipment was readily available. Although Rich (1965,
864) described the method as less precise than good chemical
methods, Herrman (1963, 330) assessed it more favourably.
Analysis by flame, however, is not without problems.

Interference from aluminum, iron, phosphorus, and
sulphur occurs in spectrophotometric analysis of calcium.
Although Shaw and Veal (1956, 333) concluded that direct
aspiration of the extract is for practical purposes as
satisfactory as more elaborate procedures of removing the
interference (e.g. Rich 1965), for the sake of precision an
attempt was made to minimize it. Of the two methods
available to accomplish this--extraction of the interfering
ions or the addition of 'releasing' elements-- the latter
was chosen because of its simplicity, efficiency, and

"freedom from loss or contamination" (David 1960b, 789).
Errors may arise from self-absorption, but dilution is only
necessary if calcium concentrations are high. Further
details on sources of error and appropriate corrections,
and definitions of technical terms peculiar to flame
emission and atomic absorption spectrophotometry can be
found in Rich (1965) or David (1960b).

(2) Potassium: Methods of Analysis

There are several ways to measure potassium once it
is in solution. Volumetric, gravimetric, and colorimetric
procedures are described by Jackson (1958, 111 - 130).
These methods are simple and inexpensive (ibid. 112), but
the many steps (each being a potential source of error)
involved in each procedure precludes their use, except in
cases where the equipment necessary for the other methods
is unavailable (Hesse 1971, 137 - 138). Turbidometric
and glass electrode methods are more simple and less time
consuming. The variability in the number of precipitation
nuclei for the cobalt/nitrite precipitate minimizes the
accuracy of the former method (Jackson 1958, 121).
Measurements using the glass electrode are accurate and
reproducible if appropriate corrections for sodium inter-
ference are made (Hesse 1971, 138), but the equipment was
unavailable for this study. In view of the availability
of equipment and of the benefits previously mentioned
potassium was analyzed by flame. Difficulties in analysis
by this method are outlined later in the text.

(3) Choice of an Extraction Solution

Several solutions are available for the extraction of calcium and potassium. In analysis by flame two solutions, neutral 1N ammonium acetate (NH_4OAc) and .2N ammonium chloride (NH_4Cl) are commonly used. Although the emission intensities of neutral 1N NH_4OAc and .2N NH_4Cl are the same (Shaw and Veal 1956, 328), there are several advantages and disadvantages associated with each extractant.

The optional procedure of Shaw and Veal (ibid. 331) in which an NH_4OAc extract is directly aspirated is fast and simple and may be of sufficient accuracy. Only the NH_4OAc extracts of soils low in calcium and magnesium should be directly aspirated because magnesium depresses calcium emission (ibid. 331). There is no depression in ammonium chloride solutions (ibid.), but if the standard procedure of Shaw and Veal (1956, 331) is adopted much preparation is necessary before they can be aspirated.

Both NH_4OAc and NH_4Cl extract interfering ions from the soil. Those in the NH_4OAc solutions are low (ibid. 330; Rich 1965, 862) and are of little effect whereas David (1960a, 496) found that "ammonium chloride afforded considerable protection against interference with calcium absorption by silicate, but had little effect on inter-ference by phosphate and aluminium." All ammonium salts tend to overestimate exchangeable calcium in soils because of some dissolution of free carbonates and attempts to correct for this are usually unsatisfactory (Heald 1965,

1000). This was, however, of little concern; in a pre-
liminary analysis the Soil Testing Department at the
University of Manitoba described the calcium carbonate
($CaCO_3$) content of soil samples from sites 60 - 70E, 20 -
30W and 190 - 200W as "very low".

Of the two extractants, neutral 1N NH_4OAc was used
because only it offered the combination of extraction of
low levels of interfering ions and rapidity of analysis
made possible by direct aspiration.

(4) Ratio of Solution to Soil

For inorganic soils a 25/1 ratio of extraction
solution volume to soil weight is commonly used (e.g.
Shaw and Veal 1956, David 1960a, Evans and Grimshaw 1968),
but instead we used a 10/1 ratio suggested by Pratt (1965,
1027). Possible disadvantages of using a low ratio are
inadequate cation replacement, large percentage analytical
error with soils of very low cation content, and inter-
ference with Ca and Mg flame emissions by aluminum and
phosphate (Shaw and Veal 1956, 331). The decision to
overlook these hazards was based on practical considerations.
The Soil Testing Service of the University of Manitoba found
75 ppm potassium in a sample taken from the site 190 - 200W.
By extension to the rest of the inorganic soils, it was
assumed that a 10/1 ratio would provide potassium con-
centrations in the extracts that were within the optimum
concentration range of the spectrophotometer, i.e.,
concentrations covering 20 - 80 per cent of the trans-

mission scale of the spectrophotometer (Cooke, 1969, 11).
The soil extract could, therefore, be directly analyzed
for potassium. Similarly it was estimated that a 100/1
ratio would be appropriate for the organic soils; the
potassium concentrations of two organic soils from sites
20 - 30W and 60 - 70E were 585 and 600 ppm respectively.

Although greater concentrations of calcium than
potassium were expected it was felt that because of the
expanse of the standard curve most samples could be
accomodated within the optimum concentration range and
that the soil extracts could be directly analyzed.

(5) Method of Extraction

Shaw and Veal (1956, 331 - 333) present a standard
and an optional procedure for the extraction of calcium
from soil. The latter was chosen for reasons previouvly
explained. It, however, was abbreviated by not centrifuging
the filtered extract. That step was considered expendable
because it largely duplicates filtration in the removal of
suspended particles in the extraction solution. I used
extracts filtered on Whatman no. 40 paper and experienced
no problem with nebulizer blockage, but to reduce the
chance of shredding the use of Whatman no. 540 paper is
recommended when it is available.

(6) Interference and its Correction

Phosphate, aluminum, silicate, iron and sulphate
interfere in the determination of calcium concentrations

by forming compounds stable at the temperature of the flame (David 1960a, 501). While Evans and Grimshaw (1968, 413) concluded that suppression by aluminum and iron was most critical in ammonium acetate extracts, Evans and Veal (1956, 330) found the depression by phosphate to be more serious than that of aluminum. Strontium or lanthanum are commonly used to eliminate the interference.

Strontium is a more efficient releasing agent than lanthanum (David 1960a, 499; Dinnin 1960, 1478). Although Dinnin found that high strontium emission at 422.7 mu made it "almost completely unusable" (ibid. 1478), David (1960a) reported no such effects in analysis by atomic absorption spectrophotometry with strontium concentrations of 1500 ppm. Lanthanum gives a much lower background emission at full release than does strontium (Dinnin 1960, 1478). The disadvantages of using lanthanum prohibited its use in this study. It can only be used at 422 mu (Dinnin 1960, 1478) and the limits of tolerance given by Evans and Grimshaw (1968, 414) are lower than those of strontium that David (1960a, 499) reported. Lanthanum salts are also considerably more expensive than those of strontium and are often so heavily contaminated with calcium that even with corrections made for the contamination, the accuracy is much reduced (Cooke 1969, 20).

Interference is less of a problem in potassium than in calcium analysis; David (1960a, 498) found no depression of potassium absorption when he varied the

concentrations of phosphate, aluminum, and sulphate from
0 to 160 ppm and silicate from 0 - 64 ppm. Calcium enhances
potassium absorption, but this can be nullified by adding
a suppressant (Atomic Absorption Methods Sheets, K5).
David's precedent (ibid. 500)was followed and potassium
was measured in solution with 1500 ppm strontium.

Although failure of the hollow cathode lamp
necessitated the measurement of potassium by emission
rather than by absorption the above conclusions are valid
because the interferences previously discussed are chemical
reactions occurring in the flame. Radiative interference and
ionization are more critical sources of error in analysis
by emission.

Radiative interference was probably minimized
because a spectrophotometer equipped with a monochromator
and variable slit width was used to detect the resonance
line (Rich 1965, 855). Ionization is a problem in hot
flames and is most evident when only "one alkali metal is
present and when the concentration of this element is low
(< 10 ppm)" (ibid. 852). The low temperature air-propane
flame was not used because of its instability. No other
measures to reduce ionization were taken, but because of
the 'perfect' nature of the standard curve for potassium
its effect was probably negligible.

(7) Standard Curves

A range for the potassium standard curve was
chosen that would theoretically allow good sensitivity,

but which would obviate dilution of most of the soil extracts. Previous data obtained for potassium (cf. ante p. 71 - 72) was used to estimate its concentration in the extract; the mid-summer values were extended considerably to allow for fall accumulation of nutrients and for strong positive deviations. Calcium standards were prepared in approximately the same concentrations as potassium because their levels in the soil extract were not expected to greatly differ.

Exact reproducibility of standard curves is not possible by simply resetting the controls of the spectro-photometer to their previous values, but they can be duplicated by spraying some of the standard solutions and adjusting the instrument to its previous readings (Cooke 1969, 11); in this way the curve was regularly checked throughout the sample as a precaution against short-term instrument instability.

(8) Procedure (Appendix C)

C. Phosphorus

(1) Extraction Solution

Interest was focused on immediately available phosphorus (Hesse 1971, 271) which is largely inorganic orthophosphate. Orthophosphate complexes mostly with calcium, iron, and aluminum and its availability from them depends on the soil conditions under which they are found. Since the solubility of inorganic phosphorus is largely pH dependent numerous extraction solutions covering a broad pH range have been used to extract it from the soil.

Dilute mixed acid solutions are used to dissolve greater amounts of iron phosphate (Olsen and Dean 1965, 1042). A good mixed extraction solution is one of dilute acid fluoride. The fluoride ion complexes the Al^{+3} and Fe^{+3} ions with consequent release of phosphorus; the acid dissolves the calcium phosphates and prevents precipitation (as calcium phosphate) of phosphorus released by the aluminum and iron (Jackson 1958, 159). Correlations of plant uptake or plant yield with phosphorus extracted by solutions of dilute acid fluoride have been good (cf. Hesse 1971, 274 - 275).

For calcareous, alkaline, and to a lesser degree neutral soils, alkaline extraction solutions are best (ibid. 273). In such soils most of the phosphorus is bound to calcium. A 0.5M $NaHCO_3$ solution at pH 8.5 precipitates the calcium as calcium carbonate with subsequent release of phosphorus. This solution also extracts greater quantities of phosphorus from aluminum and iron than other extractants when used on acid soils (Olsen and Dean 1965, 1045). Secondary precipitations using this extractant are minimal because the concentrations of aluminum, calcium, and iron remain low (ibid.). High correlations between $NaHCO_3$ extractable phosphorus and uptake of phosphorus by plants have been found (ibid. 1046).

The choice of extraction solutions was narrowed to sodium bicarbonate and dilute acid fluoride because these gave the best correlations with plant response over

the greatest variety of soils. Although both solutions remove the same forms of phosphorus from the soil the latter was chosen for two reasons. The first is that the forms of phosphorus which are important to plant nutrition are extracted with greater success with it than with sodium bicarbonate (Hesse 1971, 275). Second, although dilute acid fluoride can be used on a variety of soils (Jackson 1958, 155), it is most successful on acid ones (Olsen and Dean 1965, 1040). Therefore, this solution appeared most suited to extracting phosphorus from the mostly acid and heterogeneous soils along the transect.

(2) Method of Analysis - Colorimetry

Colorimetric methods are almost exclusively used in phosphorus analysis because they are the simplest and quickest of the methods available and are capable of a high degree of accuracy (Hesse 1971, 289). Two methods, one combining phosphorus with molybdate and the other with vanadomolybdate, are commonly used. A molybdenum blue method was chosen because it is the more sensitive of the two.

By using $0.03N$ NH_4F in $0.025N$ HCl to extract phosphorus it was necessary to use chlorostannous acid to reduce to molybdophosphoric acid. This reducing system combines good sensitivity (Jackson 1958, 138) with relative freedom from interfering ions (ibid. 145). Normally interference is from ferric iron; in low concentrations interference is depressed by adding an excess of

tin chloride to the test solution (Hesse 1971, 271), and
by using the procedure of Olsen and Dean (1965) the limit
of tolerance to iron was extended to 75 ppm (ibid. 1040).

(3) Procedure

The procedure of Olsen and Dean (1965, 1035 - 1049)
was used in the measurement of dilute acid-fluoride
extractable phosphorus. The phosphate standards were
extended to 2 ppm.

(d) Nitrogen

(1) Introduction

Inorganic nitrogen, mostly ammonium and nitrate,
occurs in small amounts in the soil. For instance, ammonium
constitutes no more than five per cent of the total soil
nitrogen in surface soils, but in excess of thirty per cent
can be present in certain subsoils (Bremner 1965, 1180).
When rates of mineralization are not considered, the deter-
mination of nitrate and ammonia is of limited use for
estimating available nitrogen (Hesse 1971, 183). Rate
measurements were not taken because the standardization of
environmental conditions is difficult, they are time con-
suming, and do not bear directly upon the objectives of
this thesis.

(2) Ammonium

Methods of Analysis

Colorimetry by Nessler's reaction is commonly used
to analyze for ammonium because it is more sensitive than
many other methods (Taras 1958, 97). Chemical interference

is a major disadvantage when using this method. Magnesium, manganese, iron and sulphide cause turbid conditions because of insolubility in alkaline solutions, or production of precipitates with iodine and mercury. Some of the soil samples from the transect were tested using Jackson's (1958, 195 - 196) procedure, but severe chemical interference led to the rejection of this method.

Distillation methods are commonly used when testing for ammonium because 1) they can be used on coloured extracts (Bremner 1965, 1184), 2) separate extractions for the determination of ammonium and nitrate are unnecessary (ibid.), 3) once the extract is filtered from the soil it needs no further preparatory treatment (Hesse 1971, 180), and 4) the results are precise and accurate (Taras 1958, 75). Although most distillation methods are tedious, time-consuming, and subject to interference by organic nitrogen compounds, Bremner (1965, 1185) corrected this by using a short distillation period and by using magnesium oxide to eliminate interference by alkali-labile organic nitrogen compounds. The procedure given by Bremner (ibid. 1195 - 1198) was used in the analysis for ammonium.

Although analysis by micro-diffusion offers all the advantages of distillation the unavailability of suitable diffusion cells (Bremner 1965, 1207 - 1208) at the time of analysis prevented the adoption of this method.

Procedure

The soil samples were shaken for 10 min (ibid.

1190) with 1N KCl using an equilibrium extraction procedure (<u>ibid.</u>). Soil dilution ratios of 10/1 for inorganic soils and ranges from 100/1 to 20/1 for peat soils, depending upon the degree of decomposition, were used to extract the ionic nitrogen. Ammonium was determined using the steam distillation procedure with magnesium oxide (Bremner 1965, 1195 - 1198).

(3) <u>Nitrate</u>

<u>Methods of Analysis</u>

"Nitrate in soil extracts can be determined either by reduction to ammonia which is then liberated by alkaline steam distillation and titrated, or colorimetrically, either directly or after reduction to nitrate or ammonia" (Hesse 1971, 180). The nitro-phenoldisulphonic method is the most important of the colorimetric procedures for direct analysis of nitrate (Jackson 1958, 197). The accuracy of this method using a spectrophotometer is about five per cent (Hesse 1971, 182) and the sensitivity is about 0.01 ppm (Taras 1958, 145). Serious interference caused by ions and coloured extracts occurs when using the nitro-phenoldisulphonic method. This method was rejected because it is tedious and time consuming, and others were considered.

One of these, the brucine method, is sensitive to approximately 0.1 ppm of nitrate; best results, however, are obtained from 1 to 4 ppm (Taras 1958, 141). The method has two serious shortcomings: 1) "failure to conform

to Beer's law in the wave length region of greatest absorption" (ibid.), and 2) variability in colour development.

The hydrazine reduction method using a Technicon Auto Analyzer Unit appeared to be the most ideal method for nitrate analysis. Its primary advantage is speed of analysis, 40 samples per hour. The precision of this technique compares favourably with those previously mentioned; for example, Kamphake, Hannah, and Cohen (1967, 213) found standard deviations of 0.024 and 0.073 ppm for concentrations of 1.0 and 10.0 ppm of nitrate after 25 randomly distributed analyses of each concentration. The sensitivity of this method is easily increased to 0.01 ppm (ibid. 215). In addition, there is minimal chemical interference.

Nitrate has been successfully determined in 2N KCl extracts using the hydrazine reduction method in the Soil Testing Laboratory at the University of Manitoba (C. M. Cho, pers. comm.). Another distinct advantage of this method then is that nitrate can be measured in the same soil extract as ammonium.

One disadvantage, however, of the hydrazine reduction technique is that a separate analysis for nitrite is necessary; since copper and hydrazine solutions reduce nitrate to nitrite, the true nitrate concentration can only be determined after subtracting the concentration of NO_2-N originally present. On the assumptions that 1) nitrite is present in only low concentrations in the soil

and that 2) it is rapidly converted to nitrate, no effort was made to investigate the concentration of nitrite in the soil extract.

Procedure

The same extracts used in the determination of ammonium were used for nitrate analysis. These determinations were conducted by the Soil Testing Department of the University of Manitoba using the hydrazine reduction method.

(e) Organic Matter

(1) Methods of Analysis

Carbon exists in basically four forms in the soil (Jackson 1958, 205): 1) carbonate mineral forms such as $CaCO_3$, $MgCO_3$, $CaCO_3$, CO_2 and the HCO_3^{--} and CO_3^{--} ions of more soluble salts, 2) condensed organic carbon such as charcoal, graphite, and coal, 3) altered and resistant organic residues of plants, animals, and microorganisms which may be termed humus, and 4) little altered organic material which is subject to rapid decomposition. The indirect methods (Broadbent 1965, 1397) of analysis for organic matter estimate only organic carbon by measuring either the carbon dioxide evolved during wet or dry combustion of organic carbon, or the extent of reduction of a strong oxidizing agent, usually chromic acid. Lack of suitable equipment prohibited the adoption of the first method, and to a lesser extent, the second.

Jackson (1958, 206) describes the latter technique as "rapid and popular", and it has the advantage that only the

most active forms of carbon--oxidizable organic matter--
are measured. There are several disadvantages that lead
to the rejection of this method. One of these is that
several agents such as chloride, nitrate, iron (II) and
higher oxides of manganese (Hesse 1971, 212), interfere
with the analysis. Difficulties in colorimetric end-point
determinations can result in rather large errors by the
inexperienced analyst although the difficulty depends on
the indicator used. Another problem which is especially
applicable to the inexperienced analyst is finding the
right proportions of oxidizing reagent to the weight of
soil (Hesse 1971, 214), particularly for soils of higher
organic matter content. This difficulty would be important
in soil samples taken from the eastern end of the transect
at Pinawa. The last, and rather irritating, disadvantage
is in the expression of results. Oxidizable matter can be
reported as per 100 gm of soil (Jackson 1958, 206 - 207), but
in order to make comparisons between soils "conversion factors
from oxidizable matter to carbon and organic matter are often
employed" (ibid. 207). The conversion value varies with the
specific method of analysis and the type of soil (Hesse 1971,
215: Allison 1965, 1373), and with the depth of the soil
sample (Broadbent 1965, 1397; Jackson 1958, 206); conversion
values for each different group of soils must be obtained
(Allison 1965, 1373) by using a combustion procedure.

In view of the unsatisfactory aspects of the indirect

methods, direct analysis—in which the organic matter is destroyed and the loss in weight of the soil is used as a measure of the organic content (Broadbent 1965, 1398)—was considered. Destruction of the organic matter is accomplished by either oxidation of the organic matter with hydrogen peroxide or ignition at high temperature. The former is comparable to the chromic acid methods for estimating oxidizable carbon (Hesse 1971, 211). The advantage of this method over ignition is that the "low temperature permits the retention of the hydroxyl and strongly sorbed water in the mineral colloids" (Jackson 1958, 222), but it has two "serious limitations in that the oxidation of organic matter by this reagent is incomplete, and the extent of oxidation varies from one soil to another" (Broadbent 1965, 1398). The problem of a conversion figure to organic matter is a major limitation to the use of this method. Ignition at high temperatures quantitatively oxidizes organic matter, but the loss in weight often exceeds that of organic matter because of decomposition of minerals in the soil (ibid.).

Therefore, in view of the equipment and time available a simple loss on ignition test was judged to be most appropriate for the measurement of organic matter, especially since the errors of ignition at high temperatures may have been overestimated (Hesse 1971, 210). Even so, since most of the water loss from the mineral constituents occurs from 450 - 600°C (ibid.) keeping the temperature

below 450°C is preferable. Although ignition at low

temperatures fails to completely discriminate between

organic and mineral matter, especially in soils containing

amorphous materials (Jackson 1958, 225), the gravity of

this error is reduced in our case because many of the

samples from the study transect are organic. The

advantages of the method include quantitative oxidation

of organic matter (Broadbent 1965, 1398), simplicity, and

probably reproducibility since it is largely the organic

carbon that is ignited (cf. Jackson 1958, 205).

(2) Procedure (Appendix D)

CHAPTER V

RESULTS AND DISCUSSION

A. Introduction

A single linkage cluster analysis computer program described in Davies (1971, 420 - 423) was used to classify the forest. Simple similarity coefficients were calculated on the presence or absence of tree species in each quadrat. The input data is presented in Table II, and the clustering by quadrats is illustrated in Figure 2.

This diagram illustrates the division of quadrats according to dominance by evergreen (240E to 40W) and by deciduous species (70W to 290W). Furthermore, it indicates that the trees along the transect are essentially divided into four communities. First, the larch-black spruce association is characterized by the presence of these two species and one hundred per cent similarity in species composition of the quadrats. Second, the black spruce community is distinguished by the dominance of black spruce and one hundred per cent similarity between quadrats. Third, the balsam fir-black spruce community is characterized by the presence of fir and black spruce encompassing the rest of the evergreen-dominated portion of the transect. Fourth, the aspen community is characterized by the dominance of aspen poplar and by relatively high tree species composition. Most quadrats cluster at the ninety per cent level of similarity while those clustering at the one hundred per cent and eighty-one per cent levels are not described separately because they encompass only small and scattered portions of the transect.

TABLE II
INPUT DATA FOR SINGLE LINKAGE CLUSTER ANALYSIS COMPUTER PROGRAM

Quadrat	Larix laricina	Picea mariana	Picea glauca	Picea sp[a]	Abies balsamea	Pinus banksiana	Betula papyrifera	Populus tremuloides	Populus balsamifera	Ulmus americana	Fraxinus nigra
230 – 240E	2	2	1	1	1	1	1	1	1	1	1
220 – 230E	2	2	1	1	1	1	1	1	1	1	1
210 – 220E	2	2	1	1	1	1	1	1	1	1	1
160 – 170E	1	2	1	1	1	1	1	1	1	1	1
100 – 110E	1	2	1	1	1	1	1	1	1	1	1
90 – 100E	1	2	1	1	1	1	1	1	1	1	1
70 – 80E	1	2	1	1	1	1	1	1	1	1	1
60 – 70E	1	2	1	1	1	1	1	1	1	1	1
30 – 40E	1	2	1	2	2	1	1	1	1	1	1
20 – 30E	1	2	1	2	2	1	1	1	1	1	1
0 – 10W	1	1	1	1	2	1	1	1	1	1	1
10 – 20W	1	2	1	1	2	1	1	1	1	1	1
20 – 30W	1	2	1	1	2	1	1	1	1	1	1
30 – 40W	1	2	1	1	2	1	1	1	1	1	1
70 – 80W	1	2	1	1	2	1	2	1	2	1	2

a. Spruce which could not be identified as either white or black (Dugle and Bols 1972).

TABLE II (continued)

Quadrat	Larix laricina	Picea mariana	Picea glauca	Picea sp.[a]	Abies balsamea	Pinus banksiana	Betula papyrifera	Populus tremuloides	Populus balsamifera	Ulmus americana	Fraxinus nigra
90 – 100W	1	2	1	1	2	1	2	2	1	1	1
100 – 110W	1	2	1	1	2	1	2	2	2	1	1
110 – 120W	1	2	2	1	2	1	2	2	2	2	1
120 – 130W	1	1	1	1	2	2	2	2	2	1	1
130 – 140W	1	1	1	1	2	1	2	2	1	1	1
140 – 150W	1	1	2	2	2	1	2	2	1	1	1
170 – 180W	1	2	1	2	2	2	2	2	1	1	1
180 – 190W	1	2	2	1	2	2	1	2	1	1	1
200 – 210W	1	2	1	1	2	2	2	2	1	1	1
210 – 220W	1	1	1	1	2	1	2	2	2	1	1
220 – 230W	1	2	1	1	2	1	2	2	2	1	1
240 – 250W	1	1	1	1	1	1	1	2	1	1	1
260 – 270W	1	1	1	1	1	1	2	2	2	1	1
270 – 280W	1	1	1	1	1	1	2	2	1	1	1
280 – 290W	1	1	1	1	1	1	2	2	1	1	1

FIGURE 2. Clustering by quadrats

LEVEL OF SIMILARITY

```
75      80      85      90      95      100
```

- 230 – 240 E
- 220 – 230 E   **Larch – black spruce**
- 210 – 220 E
- 160 – 170 E
- 100 – 110 E
- 90 – 100 E   **Black spruce**
- 70 – 80 E
- 60 – 70 E
- 30 – 40 E
- 20 – 30 E
- 0 – 10 W   **Balsam fir –**
- 10 – 20 W   **black spruce**
- 20 – 30 W
- 30 – 40 W
- 100 – 110 W
- 220 – 230 W
- 90 – 100 W
- 120 – 130 W
- 130 – 140 W
- 170 – 180 W
- 200 – 210 W
- 210 – 220 W   **Aspen**
- 240 – 250 W
- 260 – 270 W
- 270 – 280 W
- 280 – 290 W
- 70 – 80 W
- 110 – 120 W
- 140 – 150 W
- 180 – 190 W

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75      80      85      90      95      100
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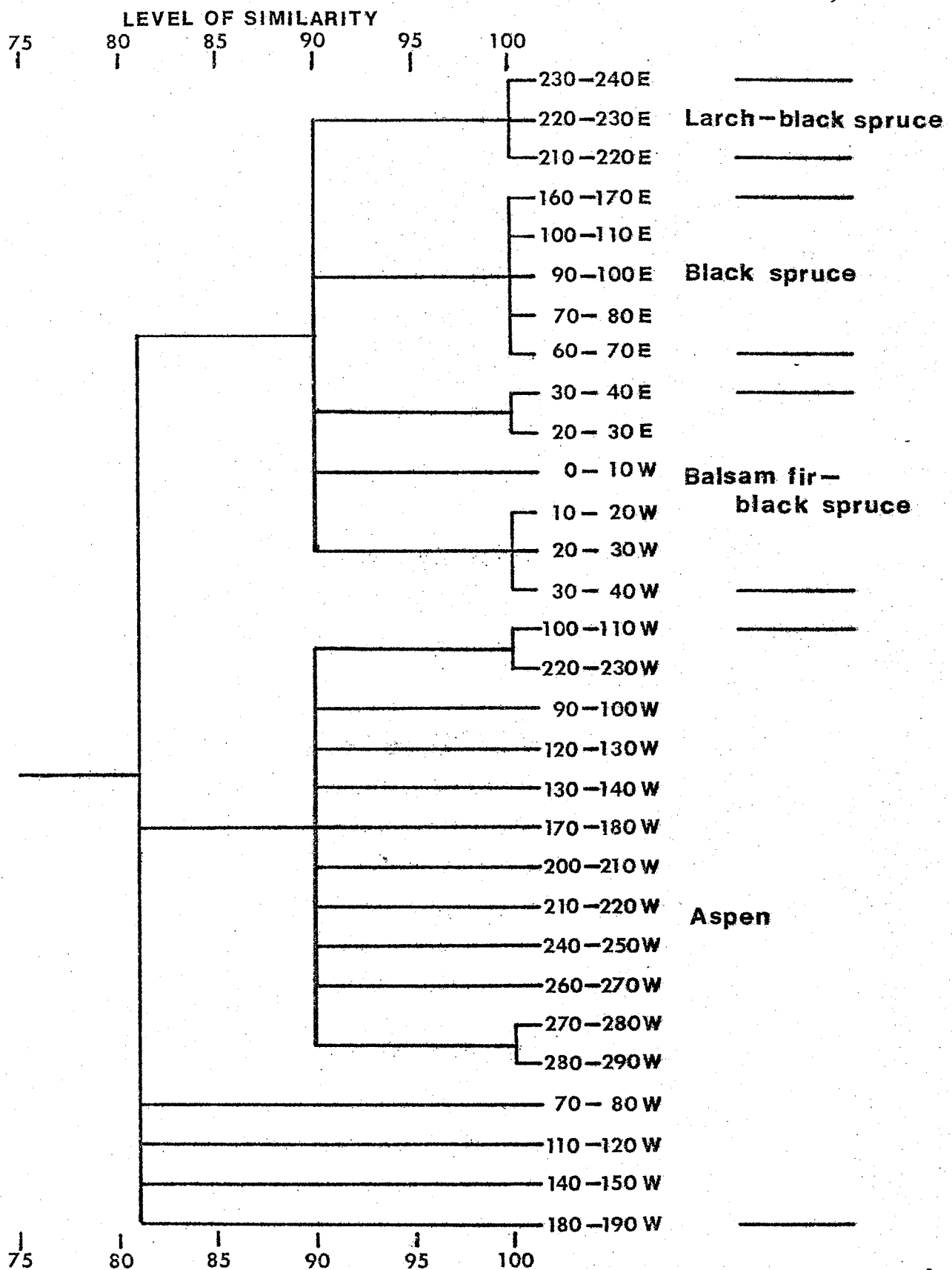
It was concluded that most of the description and analysis of nutrient data within this chapter would be organized in relation to four tree associations.

B. Description and Interpretation of Laboratory Results in Relation to Tree Cover along the Transect

1. Hydrogen-Ion Activity

The pH readings increased from the larch association and peaked within the balsam fir - black spruce community (Figure 3). Thereafter the pH levels declined but in an undulating fashion. Although there was some correspondence between zones of similar pH and associations of vegetation, the boundaries may overlap. Most of the pH readings differed between sample depths, but no relationship of the forest to the magnitude of the difference or to the pattern of difference (i.e. whether the pH of the upper sample exceeded that of the 15 - 30 cm sample, or vice versa) could be detected.

Six zones having similar pH were subjectively recognized. The first consisted of high soil acidity levels and included samples from 240E to 210E. Like the rest of the zones too few samples were measured to indicate whether there was a statistical difference in pH between the 0 - 15 cm and 15 - 30 cm depths. From samples 170E to 20E another zone with maximum pH values ranging from 6.1 to 6.6 was distinguished. The lower soil samples seemed to have a greater pH than did those from the 0 - 15 cm depth and the differences appeared greatest at the western extreme of this area. This may indicate an ecologically important change in the rooting environment for it is at this western extreme that balsam fir first appeared along the transect. The third zone consisted of samples exceeding pH 6.5 with the pH of the 15 - 30 cm samples usually exceeding those from 0 - 15 cm.
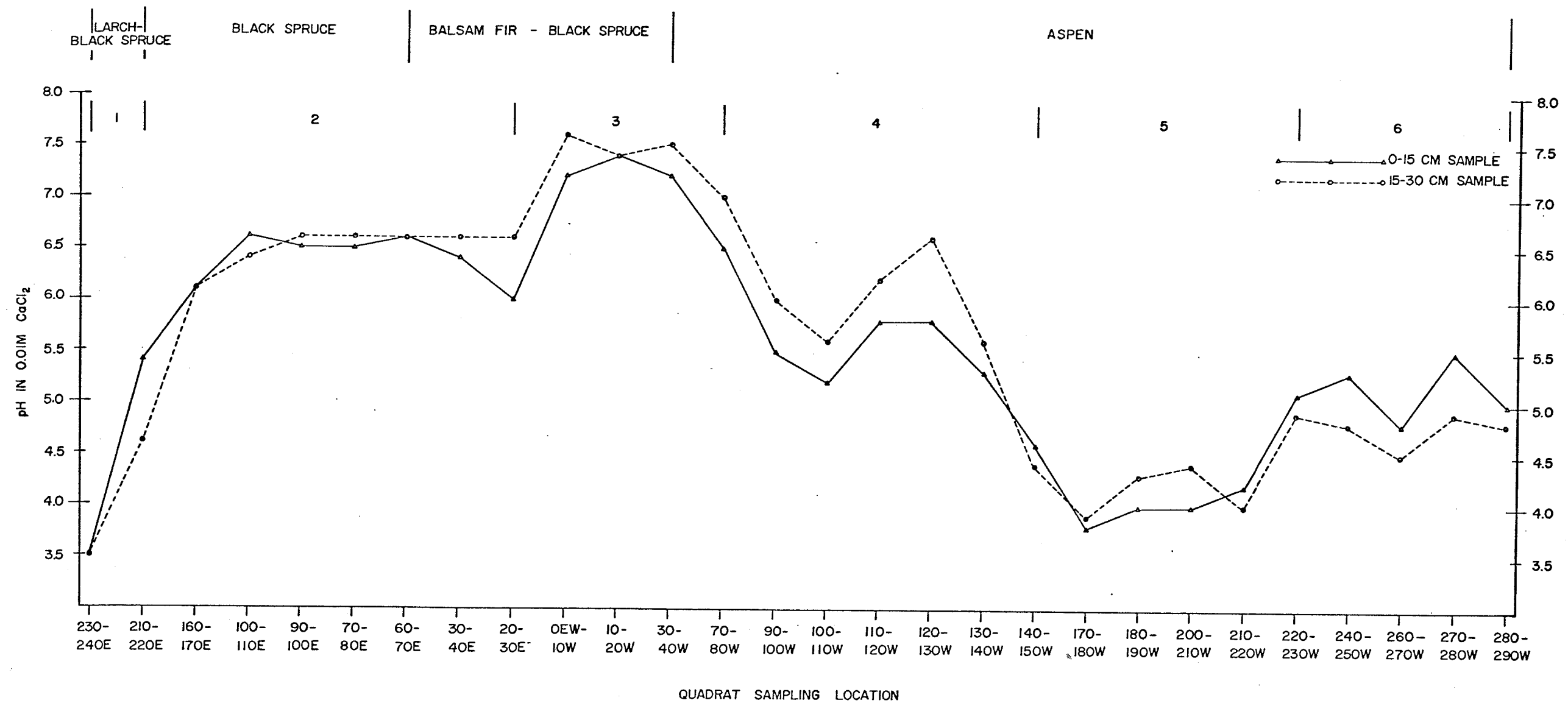
FIGURE 3

pH (in 0.01M CaCl$_2$) ALONG THE TRANSECT

OEW is the most eastern sample of this zone. The relatively greater dominance of balsam fir at this point suggested that the rise in pH is ecologically important. Although the western extreme of the third zone was recognized as 8OW, on the basis of data for other soil parameters, quadrat 70 to 8OW may be more appropriately included in the fourth zone in which the soil acidity fluctuated considerably from site to site, and the pH of the 15 - 30 cm samples apparently exceeded that of the upper depth. The fifth zone included samples from 14OW to 22OW. With the exception of zone 1, the soil was most acid in this section with pH ranging from 3.8 to 4.6. The pH of the 15 - 30 cm sample seemed greater than that from O - 15 cm in three of the five quadrats within this zone, and a similarity in pH from 18OW to 22OW was apparent. The remaining portion of the transect (zone 6) was characterized by a moderate rise in pH with readings ranging from 4.5 to 5.5, and by pH levels that appeared higher in the O - 15 cm samples.

The correspondence between pH zones and vegetation associations becomes less distinct progressing from east to west along the transect. The first zone corresponded with the larch - black spruce association and although the most eastern border of zone 2 corresponded with the begining of the black spruce association, the western extreme overlapped the balsam fir - black spruce community. The western border of the third zone overlapped slightly with the aspen forest. No correspondence of pH zones and

sub-associates of trees in the aspen forest was found.

Only a generalization between the type of vegetation cover and the pH levels along the transect was possible. With the exception of the larch - black spruce association, the pH within the evergreen associations was greater and less fluctuating than that within the aspen forest. There was no apparent relationship between pH and the amount of vegetation cover. This suggested that differences in pH does not result from differential uptake of cations and anions by the vegetation along the transect.

Although the differences in pH between the two sample depths was least in the black spruce association, no relationship of tree cover to the magnitude of the difference could be detected elsewhere along the transect. Neither the associations of trees, basal area, nor differences in cover type (evergreen vs. deciduous) were apparently related to whether the pH levels of the 0 - 15 cm sample exceed those at 15 - 30 cm or vice versa.

More fundamental explanations for some of the pH levels may exist. Higher pH values at the 15 - 30 cm depth within the evergreen associations might be expected because of its relative proximity to the calcareous clay zones beneath the peat. One possible explanation for the exceptions is that these were pockets of deeper peat where root extraction of cations had lowered the pH. The changes in pH with depth described by Smith and Ehrlich (1967, 82) were not well defined in the peats along the transect.

From the description of Woodridge fine sand given
by Smith and Ehrlich (ibid. 93) a slight increase in pH was
expected from the 0 - 15 cm to the 15 - 30 cm depth. This
trend was not always observed along the transect. Except
for one site (140 - 150W) soil acidity was greatest in the
0 - 15 cm sample up to 210W; the amount by which the pH of
the lower sample exceeded that from 0 - 15 cm may be a
function of 1) proximity of the 15 - 30 cm sample to the B
horizon or 2) the fraction of the illuvial layer that was
sampled. From 210 - 290W pH of 0 - 15 cm sample seemed
greater.

This pattern in upland sites may be related to
differences in internal drainage. The reverse trend at the
western extreme of the transect might be explained by
relatively impeded soil drainage resulting from a locally
heavier soil texture and/or a more level microtopography.
Less drainage resulting from greater interception of rain-
fall by the vegetation cannot be used to account for the
reversal, for the vegetation cover at this extreme of the
transect was no less variable and was often less than on
sites east of 210W. Hypothetically, from 80 to 210W
percolation of water through the soil displaced the cations
and deposited them lower in the soil profile, thus increasing
the pH at depths of 15 - 30 cm; deposition down the slope
gradient (Ackerman 1973, 39) may explain the higher pH
levels of the 15 - 30 cm samples within the peat soils
where there was no internal drainage.

2. <u>Calcium</u>

(a) <u>Preliminary Remarks</u>

Duplicating the results of the first sample run
proved to be a problem; the final results of the second
analysis were higher than those of the first by an average
of 1189.4 ppm ($P < 0.01$). This probably resulted from a
difference in instrument adjustment between replications.
The disparity was relatively small (10.8 ppm) and insignifi-
cant ($0.20 > P > 0.10$) before multiplication by dilution
ratios. Because the difference only assumed significance after
multiplication by the dilution ratios the data were accepted
for use in this thesis.

(b) <u>Discussion of Results</u>

Higher concentrations of calcium in the peat soils
than in the inorganic soils and the large quantities of
calcium extracted from the peat are two features of Figure 4.
The higher concentrations in the peat soils were attributed
to their greater total cation exchange capacity and to an
influx of nutrients (Ackerman 1973, 39). The discovery of
snail shells from the 15 - 30 cm samples of some peat sites
suggested that some of the calcium may be derived from the
shells.

The concentrations from 230 - 240E were comparable to
some sites with much lower organic matter contents (<u>e.g.</u> the
upper samples of 110 - 120W and 120 - 130W). The organic
matter may differ in two ways causing the cation exchange
capacity to be lower than at the other peat sites.
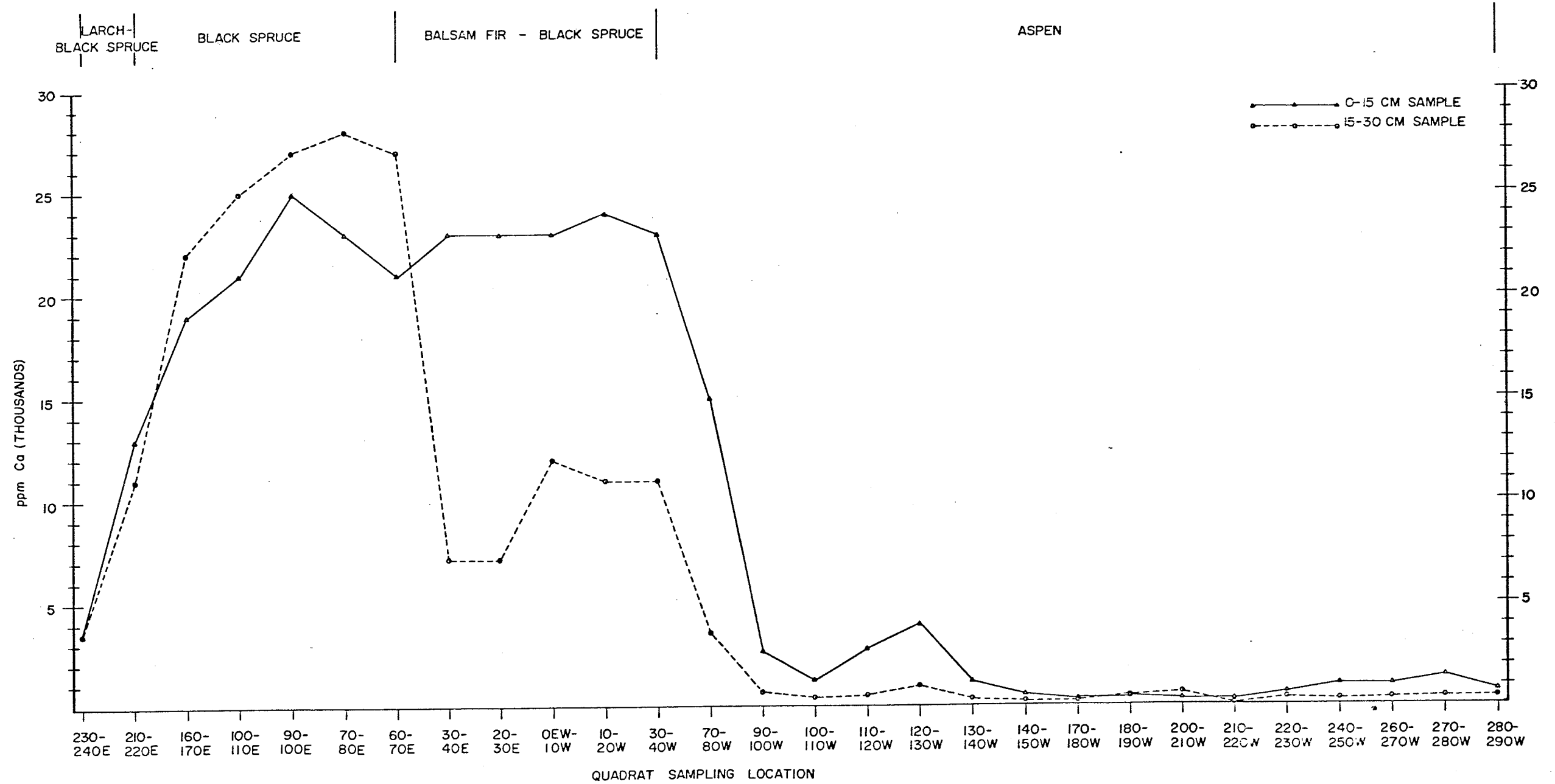
FIGURE 4

CALCIUM CONCENTRATIONS ALONG THE TRANSECT

1) There may be differences in the specific composition of the moss cover. For instance, the ratio of <u>Sphagnum</u> sp. to <u>Hypnum</u> sp. or other brown mosses may be greater than at the other sites. Forest production is better on the latter type of moss Wilde 1958, 169 - 170).

2) The low pH at site 230 - 240E suggested that decomposition may be retarded and the capacity of the organic matter to adsorb cations would be reduced.

Calcium concentrations in the 0 - 15 cm samples were generally higher than those from 15 - 30 cm. Exceptions to the trend were those five sites in the black spruce association which may be due to better decomposition of matter in the lower sample. This may also be a reflection of a "burying effect" (Heilman 1966, 830) common in peatlands. The greatest difference in calcium levels between the two depths occurred from 40E to 80W. What makes this interesting is that balsam fir appears in the peatland sample at 40E and except at 70 - 80W, fir is prominent along that portion of the transect. This does not, however, reflect utilization by this species, but rather a lower organic matter content in the 15 - 30 cm sample.

The calcium concentrations over all the sites were highly correlated with the per cent organic matter; the correlation coefficient at the 0 - 15 cm depth was 0.90 ($P < 0.01$) while that for the 15 - 30 cm depth was 0.86 ($P < 0.01$) Calcium concentrations in the 0 - 15 cm samples under the

black spruce and balsam fir - black spruce associations were similar.

Since calciphilous trees need no more than 1000 ppm of calcium (Wilde 1958, 226) the concentrations in the peat soils were sufficient to permit maximum tree growth. In the aspen forest, good tree growth in conjunction with low calcium concentrations suggested that the species are not calcium demanding. This was deducted from the fact that early successional species generally have low nutrient demands. Also, the very strong relationship between organic matter and extracted calcium ($r = 0.99$, $P < 0.01$ for the 0 - 15 cm sample from 70 - 290W; $r = 0.096$ $P < 0.01$ for the 15 - 30 cm sample) suggested that only moderate concentrations of calcium were available to the vegetation. The hypothesis cannot be adequately tested without growth and radiotracer experiments.

The depressed concentrations of calcium may also be related to the acid conditions that prevailed in the upland association. The significant correlation between pH and calcium lent creditility to the hypothesis. The correlation coefficient for the 0 - 15 cm sample from 90 - 290W was 0.81 ($P < 0.01$). Site 70 - 80W was excluded from the test because the upper layer of soil was similar to those of the lowland sites. When it was included the correlation co-efficient dropped to 0.70 ($P < 0.01$). The coefficient for the 15 - 30 cm sample from 80 - 290W was 0.67 ($P < 0.01$).

3. Potassium

(a) Preliminary Remarks

The final results of the first replicate were higher than those of the second by an average of 64.8 ppm (P<0.01) An explanation for this is operator error and instrument instability. In order to obtain similar instrument response to the standard solutions the controls of the spectrophotometer were set differently between replications; a drop in oxidant flow (5 1/min to 4.2 1/min) that occurred when cylinder air was replaced by line air may have necessitated this modification. Differences between the standard curves and analytical sensitivities of each replication would be a logical result of the variation.

The difference in the intercepts of the standard curves (which may also be due to imprecise preparation of the standard solutions) explains much of the average difference of 1.85 ppm (P<0.01) between duplications before multiplication by dilution factors. The intercept for the first curve was slightly negative (-0.007) while that for the second was positive (0.01); this means that if all else were equal, (by using the formula $x = \frac{y - a}{b}$) the concentrations in the first replicate of samples would be higher than those of the second. The difference when multiplied by the extract/soil ratio, explains the large difference reported previously.

Results based on the average of two readings were regarded as useful because I was interested mainly in the

relative concentrations at the sites.

(b) <u>Discussion of Results</u>

Two features of Figure 5 are particularly distinctive. First, potassium concentrations were highest in the peatland sites; the high cation exchange capacity of organic matter and base flow of nutrients probably explain this. Second, the potassium concentrations were lower (using a paired difference test $\bar{D} = 157.15$ ppm, $P < 0.01$) from the 15 - 30 cm sample than the 0 - 15 cm sample. The explanations for this are: 1) root uptake was greatest from the 15 - 30 cm depth, and 2) the percentages of organic matter were reduced at the lower depth.

The difference in potassium concentration between layers was the lowest in the aspen association. Two possible explanations are that the root system is concentrated below the 30 cm depth so that little difference due to nutrient uptake is found, and the porosity of the sandy soil allows enough leaching of potassium to ameliorate the disparity between layers. The first explanation is doubtful because roots often impeded sampling of the soil with the auger and because species such as aspen are known to have shallow rooting systems (Maini 1968, 51 and 55). If the second were true, explaining the high levels of phosphate would be difficult. Most likely the small difference was a product of sampling technique. The shallow organic horizons were mixed with much inorganic soil to constitute the sample from the 0 - 15 cm depth and the small difference in potassium concentrations was a consequence of the
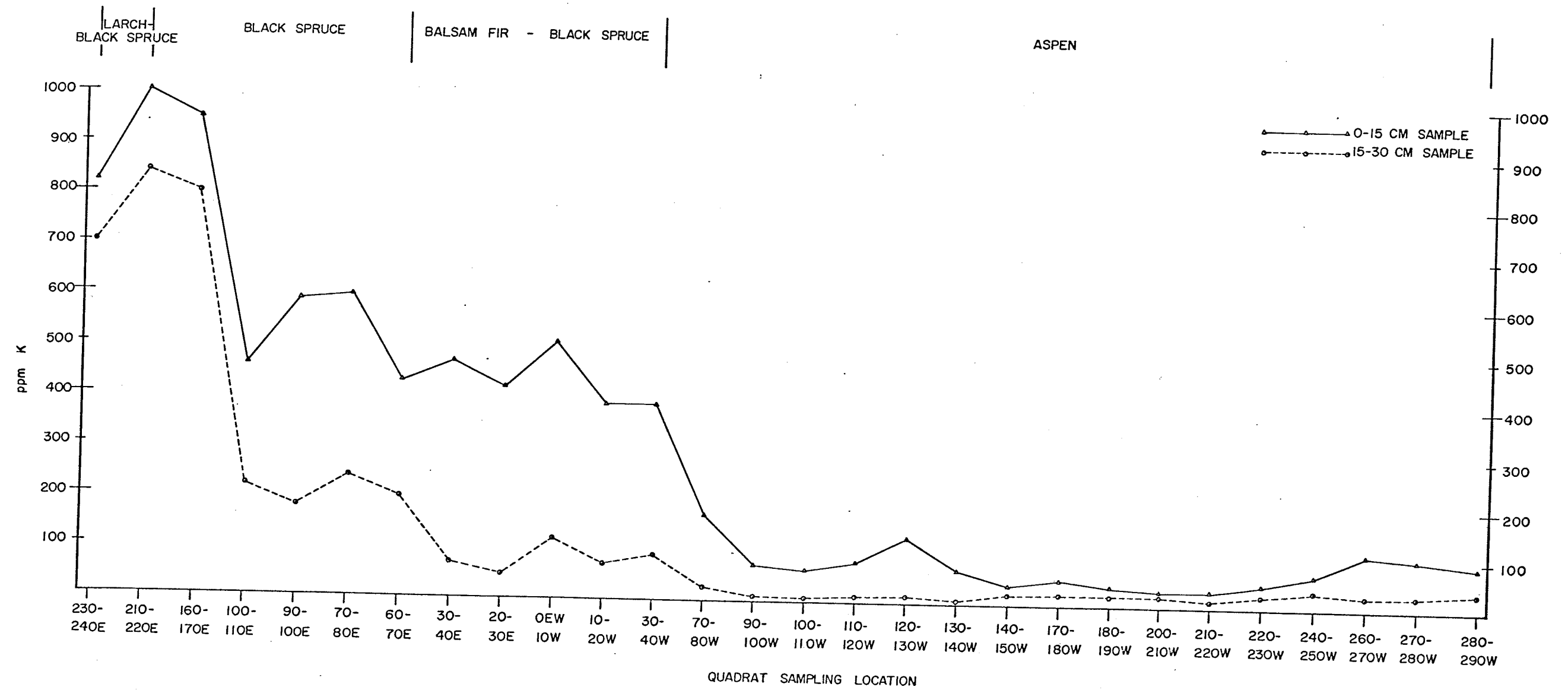
FIGURE 5

POTASSIUM CONCENTRATIONS ALONG THE TRANSECT

similarity in physical composition of the samples from the two depths. The significant linear relationships between organic matter percentage and potassium levels support this hypothesis. For the 0 - 15 cm sample r = 0.88 (P < 0.01) while that for the lower depth was weaker with r = 0.77 P < 0.01). Differences in resource utilization by the associations may account for the weaker relationship in the latter equation.

Concentration differences were greatest in the soils of the evergreen associations. From 110E to 40W the differences in potassium concentrations between depths were more pronounced than those within depths. The lower concentrations in the 15 - 30 cm samples were due to a substantial reduction in organic matter content, suggested by the significant correlation between potassium concentration and organic matter (r = 0.95 P < 0.01). The higher levels of potassium in the 0 - 15 cm samples which were not significantly correlated with organic matter (r = 0.45, P > 0.05) suggested that potassium may be in excess of that adsorbed by organic matter and that biological interpretations for potassium levels may be appropriate. The similarity of potassium concentrations at the 0 - 15 cm depth appears to support Dammon's (1971, 265) conclusions that the potassium regimes and rates of potassium mineralization in black spruce and fir associations were the same. The slight difference between associations may reflect greater uptake of potassium by fir than by spruce.

The potassium concentrations were highest from 240E to 110E, but the disparity between the two depths was less than in the rest of the evergreen community. The difference was not due to lower levels of organic matter at the 15 - 30 cm depth (no statistical test was conducted because of the small number of samples) and appeared to reflect the influence of uptake. The high potassium concentrations were associated with a reduction in density, growth rate (Dugle et. al. 1974, 30), and size of trees. If potassium were limiting, the condition primarily responsible for the reduction in uptake is unknown. At the most eastern sites the highly acid conditions probably restricted uptake, but the shift of pH from 160E to 110E was so small ($\bar{x}$ = 6.1 to 6.5) that the restricting effect of acid conditions was doubtful. Two reasons to doubt that the shift adversely affected nutrient uptake are: 1) pH is still at a medial level and 2) trees are very adaptable with respect to acidity (Wilde 1958, 212 - 218). Alternatively, the plants may be absorbing sufficient quantities of potassium. The high potassium concentrations may only represent accumulations by the organic matter from the minerotrophic waters that move slowly through the bog. No satisfactory answer to the question is possible with the present data.

With the possible exceptions of 240E to 210E, there is some question whether potassium is limiting anywhere along the transect. Examination of nutrient poor uplands revealed that in some of the samples from the 15 - 30 cm

depth the potassium concentrations are close to 150 ppm, a level satisfactory for exacting species (Wilde 1958, 225). Although the concentrations were often lower, it is possible that the potassium available to trees was underestimated since normal ammonium acetate rather than boiling normal nitric acid was used as the extracting solution. If the concentrations are not underestimated the presence of undemanding species such as jack pine suggests that most of the species were adapted to low nutrient levels and do not suffer from potassium deficiency. If evergreens such as balsam fir and black spruce can grow where potassium concentrations are lowest then potassium would seem available where the levels of this nutrient are much higher.

4. Phosphorus

(a) Preliminary Remarks

Jackson (1958, 161) described phosphate concentrations from 3 to 7 ppm as low, from 7 to 20 ppm as medium, and greater than 20 ppm as high. Most of the values along the transect greatly exceed 20 ppm. Inflated levels of orthophosphate from several sites were expected because preliminary tests conducted by the Soil Testing Service of the University of Manitoba revealed high concentrations of phosphate. The values reported for the 0 - 15 cm sample of sites 60 - 70E, 20 - 30W, and 190 - 200W were 57.6, 41.6 and 24.6 ppm respectively, still much lower than those illustrated in Figure 7.

There are several possible explanations for the high values obtained in this experiment. One is that the Soil Testing Laboratory used a pH 8.5 sodium bicarbonate extraction solution, whereas a dilute acid-fluoride solution was used in this study. Acid-fluoride extracts more calcium and aluminum phosphate than does sodium bicarbonate (ibid. 159). It is possible that silica extracted by the fluoride ions may have positively interfered with the analyses of extracts from the sandy soils. Soil samples used in this experiment were taken in late October - early November of 1973 and May 1974, while those analyzed at the University of Manitoba were gathered in late July, 1973. Lower concentrations could be expected in the latter samples because they were taken at a time of high photosynthetic activity and,

therefore, of high nutrient uptake. Drying the soils above room temperature for a relatively long period of time may have raised the phosphate concentrations. Hinman (1970, 181) found an increase in sodium bicarbonate extractable phosphorus after storage at low temperatures.

Contamination is not responsible for the high concentrations. All water used during the analysis and in the preparation of reagents and standards was double distilled. The blank sample always exceeded 98 per cent transmission when first inserted into the colorimeter.

There was some concern that adjusting the volume of extraction solution/weight of soil ratios to bring the concentration of phosphorus in the soil extract to within the range of the calibration curve, rather than varying the aliquot size of the extract as recommended by Hesse (1971, 291) might have accounted for the very high phosphorus results. This hypothesis was rejected because Bel'skiy, Kulakovskaya, and Rozina (1961, 1246) recommended that a solvent/soil ratio of 50/1 be used for determining available phosphorous in peat-bog soils. Similarly high ratios of 80 and 40/1 were used in the analysis of peat soils in this study. Also, the averages of two replicates, using both methods of adjustment, for fifteen randomly selected samples were compared using a paired t-test; the average difference in concentration (6.2 ppm) was not significant (t = 0.71, P > 0.05).

Therefore, since no known source of error accounted for the high nutrient concentrations, and since several plausible explanations for the levels existed, the phosphate values were accepted as valid for interpretation in this study.

(b) Discussion of Results

Besides the high levels of phosphorus at the sites along the transect, the outstanding feature of Figure 6 is the abrupt reversal in concentration with respect to sample depth at site 140 - 150W. East of this site the phosphorus levels in the 0 - 15 cm samples exceeded those from 15 - 30 cm, but to the west a reversal was apparent. Lower concentrations at 15 - 30 cm were expected at all sites because that depth corresponds to the zone of maximum root density for black spruce, balsam fir (Heinselman 1963, 337; Dammon 1971, 261) and perhaps for poplar species (Maini 1968, 51 and 55). East of 140W the differences between depths was greatest in the evergreen associations, possibly because the trees were still actively photosynthesizing when the soil samples were removed. The reversal west of 140W is, however, inexplicable. One possibility is that phosphate was chemically bound to an unmeasured variable that existed at high levels in the 15 - 30 cm sample. Calcium (binding phosphate as $CaHPO_4$) was not this variable, for as Figure 5 shows, the calcium levels were generally lower at the 15 - 30 cm depths from 140W to 290W.

The concentrations of phosphate in the larch - black spruce association were high; nearly 600 ppm were found at site 230 - 240E, although the levels at 210 to 220E were considerably lower. The concentration difference between sample depths is great. Since the basal areas of the trees were low, the difference is apparently not due only to nutrient uptake from the lower depth, but possibly due also
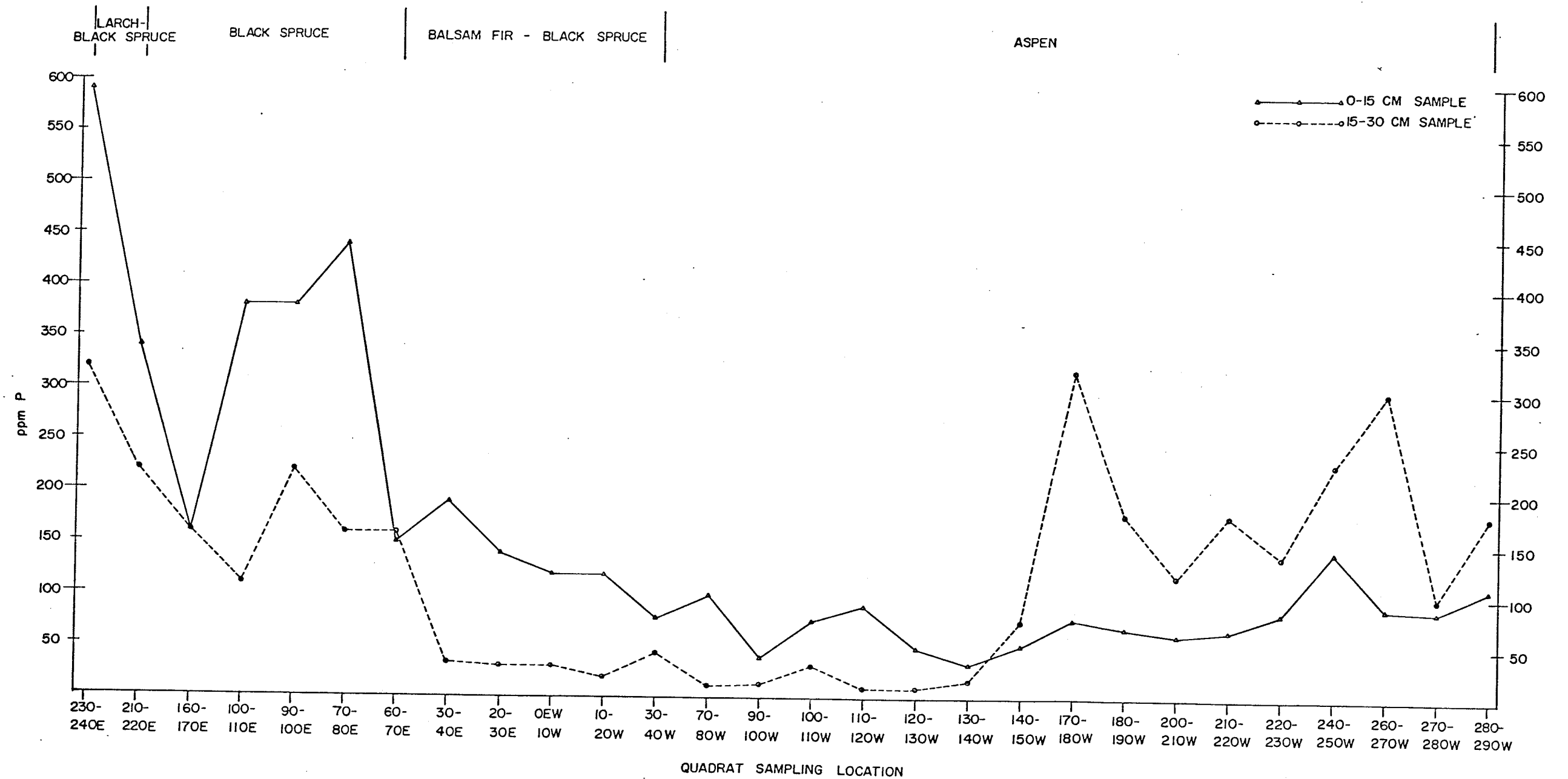
FIGURE 6

PHOSPHORUS CONCENTRATIONS ALONG THE TRANSECT

to differences in decomposition of organic matter. With the
general exception of sites 140 - 290W, the phosphorus con-
centrations from 15 - 30 cm were the highest along the transect.
High levels of this nutrient, in conjunction with low basal
area of the trees suggested that phosphorus was largely
unavailable to the vegetation. The highly acid conditions
could prevent the uptake of phosphorus by causing physiological
harm to the vegetation, by retarding decomposition of organic
matter, and causing phosphorus to be bound in forms unavail-
able to plants. Anaerobic conditions may also explain the
slight uptake.

Phosphate levels in the black spruce association
were also high, although the averages appear slightly lower
than those in the larch - black spruce community. There was
a large and uneven rise in phosphorus concentrations from
160E to 70E; thereafter, the decline was rapid and the
levels at site 60 to 70E approximate those at 160 - 170E.
Phosphate was slightly less concentrated in the 15 - 30 cm
samples than in the larch - black spruce association, and
approximate 160 ppm. There was a large difference in
phosphorus concentration between depths in three of the five
sites, but no difference existed in quadrats 160 - 170E and
60 - 70E. Low phosphate levels in the black spruce community
were expected because of the favourable pH conditions and the
large quantities of timber which were found on these sites.
Explanations for the high concentrations are hypothetical.
They are apparently not due to high calcium concentrations

because calcium levels at the 0 - 15 cm depth of the balsam fir - black spruce association generally exceed those of this vegetation zone, but the concentrations of phosphate are considerably reduced, and calcium in the black spruce association was highest in the 15 - 30 cm samples, although more phosphorus was found in the 0 - 15 cm samples. Another possibility is that the extraction solution hydrolyzed some protein to give unrealistically high available phosphorus values. This explanation is doubtful because high concentrations were also found in the sandy soils where there was little organic matter. The most plausible explanation is that phosphorus was relatively unavailable to the vegetation. The largest basal area per tree in the black spruce community was found at site 60 - 70E with lower phosphate concentrations than the other samples. An environmental variable other than pH may have retarded the decomposition of organic matter and uptake of mineralized phosphorus. The unknown condition may be aeration because redox can control both decomposition and plant uptake, and decomposition was more rapid in the balsam fir - black spruce association where the peat is less thick and where better aeration would be likely.

Phosphorus levels in the 0 - 15 cm samples at the eastern extreme of the balsam fir - black spruce community were approximately the same as those of the 15 - 30 cm samples of the black spruce asociation. The concentrations decreased

toward the western extreme of the community. Because of the
good mineralization of organic matter and the general rise in
basal area towards the west of this association, the lower
levels were apparently due to increased nutrient uptake.
Concentrations of plant-available phosphorus at the 15 - 30 cm
depth were low and relatively stable. Explanations are:
1) this is the zone of maximum root density, and 2) organic
matter from which phosphate can be mineralized was reduced.
The latter explanation may be more important because at
site 60 to 70E the phosphate and organic matter levels were
both high, while at site 30 to 40E phosphorus concentrations
were associated with reduced percentages of organic matter.

The aspen community was characterized by low con-
centrations of phosphorus in the 15 - 30 cm sample east of
sample 140 - 150W and high levels to the west. The low
levels probably resulted from small initial concentrations
of phosphate (the area is not very successionally advanced)
and high nutrient uptake. The high concentrations to the
west of this site are essentially without ecological
explanation. In addition to those possibilities mentioned
on page 112, another is that the forest along this portion
of the transect is more successionally advanced and the high
concentrations at 15 - 30 cm result from leaching. The
slight rise in concentrations in the upper sample towards
the west supports this explanation. Although areas within
FIG were burned as late as 1961 (Dugle 1969, 1) it is doubt-
ful that the resulting increases in available phosphorus

(Scotter as cited in Rowe and Scotter 1973, 455) would
remain until now. Phosphate levels in the 0 – 15 cm samples
at the western portion of the transect were similar to those
at the same extreme of the balsam fir – black spruce community
despite large differences in the percentages of organic matter.
The comparatively high concentrations in the aspen community
indicate that mineralization of phosphorus was rapid.

5. <u>Ammonium</u>

The highest concentrations of ammonium were found in the peat soils and concentrations from the 0 - 15 cm depth generally exceeded those from 15 - 30 cm (Figure 7).

Ammonium levels in the larch - black spruce association were high. This probably reflects slow rates of mineralization (especially conversion to nitrate) and/or little uptake by the vegetation. Although ammonium is most concentrated in the quadrat with the largest basal area, there are too few samples to reliably claim that there is any relationship between this nutrient and basal area. There were large differences in ammonium concentration between the 0 - 15 cm and 15 - 30 cm samples. Apparently nitrogen circulates mostly within the upper few centimeters of peat. This may be due to the shallow rooting nature of the trees concentrating the nutrients in the upper layer (Challinor, 1968). Because of the low tree density the understory probably exerts a more dominant influence on nutrient circulation than the arboreal elements. The acid conditions negate the responsibility of uptake for the lower levels at 15 - 30 cm. The concentrations of ammonium in the 15 - 30 cm sample modelled those of the upper sample. There are two possible explanations for this trend. One is that as the concentration in the upper layer increases, more nutrient is available to escape uptake and to be moved down the profile. Alternatively, this may indicate that, given equal decomposition, the concentrations present in the 15 - 30 cm sample are proportionate to those
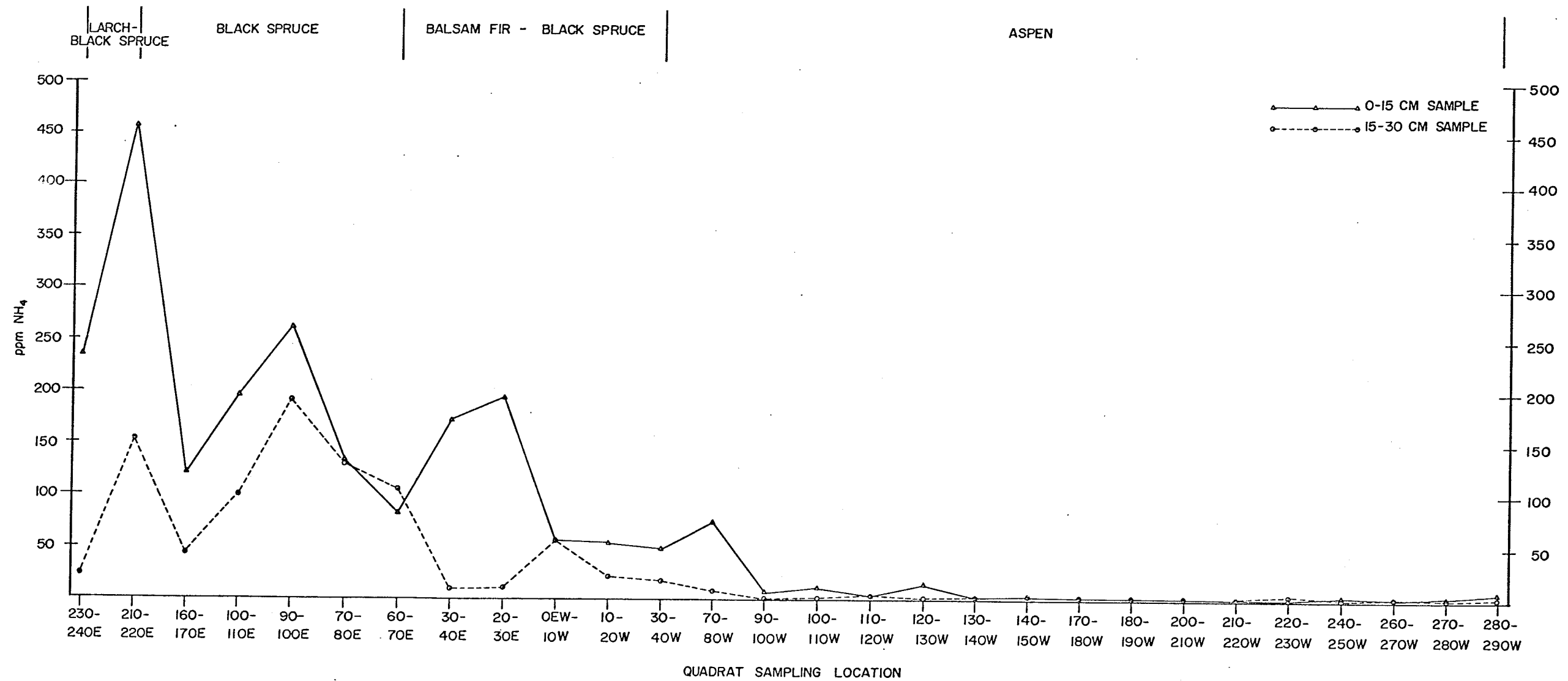
FIGURE 7

AMMONIUM CONCENTRATIONS ALONG THE TRANSECT

in the 0 - 15 cm layer.

As in the larch - black spruce association, ammonium-nitrogen was high along the black spruce segment of the transect. Slow rates of decomposition of organic matter (Challinor 1968, 280; Dammon 1971, 266) and nitrogen mineralization under spruce probably accounted for this. Except for site 60 - 70E there was less ammonium in the 15 - 30 cm than in the 0 - 15 cm sample. The most plausible explanation is that the organic matter at the lower depth was better decomposed than that above it. More nitrogen mineralization in conjunction with uptake by the trees could account for the lower nutrient levels at the 15 - 30 cm depth. That the roots of black spruce are commonly found at 15 cm below the soil surface (Heinselman 1963, 337; Dammon 1971, 261) lends credibility to the hypothesis. A more shallow rooting system might impede the circulation beyond the upper horizon (Challinor, 1968) thus keeping the concentration in the 15 - 30 cm layer relatively low. No supporting evidence for either hypothesis is available. At site 70 - 80E there was little difference in ammonium concentration between sample depths, while at 60 - 70E the concentration from the 15 - 30 cm sample was higher than that of the 0 - 15 cm sample. No explanation other than sample heterogeneity is offered. Of some interest is the rise in nitrogen from 170E - 90E, followed by a decline to 60E. This is not significantly related to basal area (15 - 30 cm depth: $r = 0.77$, $P > 0.05$) and no explanation for the trend is available.

The top 15 cm of balsam fir – black spruce association showed high ammonium levels from 40 – 20E, but a sizeable reduction occurred from OEW to 40W. The variation in nutrient concentration is apparently a function of tree species dominance. From 40 – 20E black spruce was dominant whereas balsam fir dominated the western portion of the association. Lower concentrations of ammonium from OEW to 40 W probably represent losses by nitrification, uptake, and leaching. The lower organic matter contents in the 15 – 30 cm samples probably account for the reduced amounts of ammonium found there. Despite the low number of samples, the correlation coefficient of 0.90 was significant at the five per cent level. At this depth there was more ammonium and organic matter in those quadrats dominated by balsam fir than under black spruce. Since nitrogen is mineralized more slowly under the latter (Dammon 1971, 266), and organic matter decomposes more rapidly under balsam fir than under black spruce (ibid. 265), the reversal in the expected trend must eigher result from the proximity of the clay parent material to the surface or from sampling error.

Site 70 – 80W is transitional to the aspen forest of the uplands. The 0 – 15 cm sample was largely organic while the lower stratum, like the soil to the west of this site, was largely sandy. There was more ammonium in the 0 – 15 cm sample than in those quadrats dominated by balsam fir to the east. A few trees of small circumference and high

diversity suggested that the vegetation in this quadrat
is early successional. The high ammonium levels were
probably due to release after disturbance (Page 1974, 25).
The ammonium concentration at the 15 - 30 cm depth was high,
relative to the sand samples to the west of this quadrat.
The relatively high organic matter percentage supplemented
by accumulation due to leaching is a likely explanation.

Along the rest of the transect low levels of ammonium,
showing little or irregular differences in concentration with
respect to depth, make the detection of a nutrient pattern
in relation to vegetation cover difficult. Ammonium concentra-
tions were significantly related to the percentage of organic
matter at the 0 - 15 cm depth ($r = 0.79$, $P < 0.01$). No
significant relationships of ammonium concentrations to basal
area existed in the aspen forest. Hypotheses of a technical
nature may explain the apparent lack of pattern. Ammonium
extracted from clay, confounded with that extracted from
organic matter, is one possibility. Because ammonium
concentrations in the upland area were close to the detection
limits, analytical error may be of major importance. The
attempt to correlate changes in ammonium concentration with
vegetation pattern might have met with better success in
this association had the ammonium content of the litter been
measured. This conclusion is based on Ovington's (1956c)
report that he found variability in nutrient content of the

litter layers, formed on the same soil type by different tree species (Ovington 1958, 128). Challinor (1968) found that the variation in soil nitrogen under different species virtually disappeared below five centimetres (ibid. 289).

6. Nitrate

(a) Preliminary Remarks

The description and interpretation of the nitrate results must be accepted with reservation because of the error inherent in the data. For instance, both nitrate and nitrite were measured in the sample extracts. It was assumed that the concentrations of nitrite in the extracts would be negligible and if nitrite was present it would, under natural conditions, be rapidly converted to nitrate. The high per cent transmission readings of the unknown samples was fairly convincing evidence that nitrite was of negligible importance. Had nitrite been present it is unlikely that the readings for so many of the samples would have been close to the blank readings from the nitrate only standard curve. Although there exists the possibility that the nitrate data are confounded by nitrite, more serious inaccuracies than this are present in the data.

Since the concentration of nitrate in the extracts was close to and often below the limit of sensitivity of the autoanalyzer, an unknown and perhaps significant amount of instrument error is present in the results. When working with such low concentrations graph reading error assumes more significance than would otherwise be the case. Multiplying the concentration in the extract by the dilution ratio increases the magnitude of these inaccuracies.

Two such values were averaged to give the concentrations plotted in Figure 9, but an additional error resulted

because each of the replicate values were derived from different standard curves. Due to slight differences in the slopes and y-intercepts of each of these curves, the concentrations of the second replication are significantly lower than those of the first ($\bar{D} = 0.8$ ppm, $P < 0.05$).

(b) Discussion of Results

Nitrate levels all along the transect were low; the
large differences illustrated in Figure 8 result from vertical
exaggeration. The low concentrations, especially compared to
those of ammonium, suggest that the rates of nitrification
along the transect were slow. Fairly acid, wet, and probably
anaerobic conditions along much of the transect could account
for this.

Nitrate concentrations were highest in the larch -
black spruce and in the black spruce associations. Whether
this is due to a lack of uptake or whether it resulted from
high ammonium concentrations along this portion of the
transect is unknown. There was a small increase in the
nitrate levels from site 230 - 240E to the black spruce
association.

Except for the 0 - 15 cm sample of site 90 - 100E,
which showed a sharp drop in concentration (unlike ammonium),
nitrate levels among sites appeared fairly constant in that
community. It seemed that the nitrate in the black spruce
association has reached a steady state or equilibrium with
the tree cover. Generally there was less nitrate in the
15 - 30 cm than in the 0 - 15 cm samples, but sites 100 - 110E
and 90 - 100E were exceptions. Assuming a direct relation-
ship between ammonium and nitrate levels, higher nitrate
concentrations at 15 - 30 cm were anticipated at site 60 -
70E and possibly 70 - 80E.
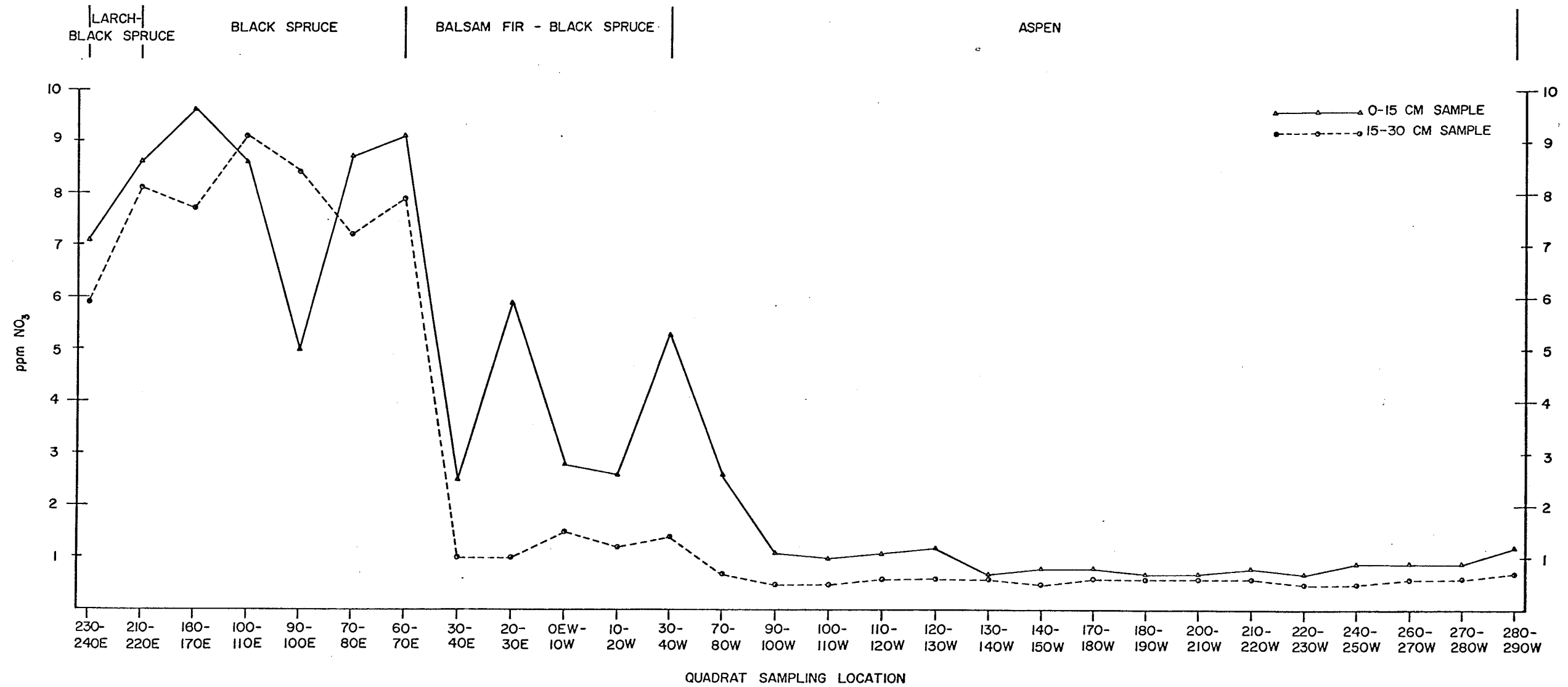
FIGURE 8

NITRATE CONCENTRATIONS ALONG THE TRANSECT

In the balsam fir – black spruce association there was a sharp and sizeable reduction in nitrate concentration from the previous community. While nitrate levels at sites 30 – 40E, 0EW – 10W and 10 – 20W were constant, there were comparatively large peaks in the upper stratum of sites 20 – 30E and 30 – 40W. These are not related to the basal area of the quadrats nor to species dominance; the lack of corresponding phenomena in the lower stratum suggests that understory vegetation may be responsible for the peaks. Nitrate concentrations in the 15 – 30 cm sample were less than those of the upper layer and varied little. Nitrate seemed to be at characteristic concentrations and the tree cover had little influence on them. One may be able to compare the relative rates of nitrate uptake by black spruce and by balsam fir. There was no variation in nitrate concentration among quadrats dominated by balsam fir or black spruce inferring that nitrate uptake is fastest by the fir. Further experimentation could prove this.

In the aspen community nitrate, unlike ammonium, did not peak in the 0 – 15 cm sample from 70 – 80W. The concentration was the same as in some quadrats of the balsam fir – black spruce association, even though the vegetation was very different. This suggests that the nature of the soil rather than the vegetation type or dominance may be responsible for the equilibrium previously mentioned. With the high ammonium concentration and good conditions for nitrogen mineralization, the low nitrate

values indicate that it was taken up rapidly. This can be expected from r-strategists (Wilson and Bossert 1971, 110) on a disturbed site. Nitrate may be leached away, but the fairly dense shrubbery (mostly willow) probably precluded this from occurring. The nitrate levels in the 15 - 30 cm stratum were intermediate between those to the immediate east and west of this site. The levels of nitrate were lowest in the aspen forest of the upland area. There was little variation in concentration although the levels from 90 - 130W in the 0 - 15 cm stratum appeared to be relatively higher. This corresponds with slightly higher ammonium concentrations from some quadrats. Similarly there was a small upward trend at the western extreme of the transect. There was no correlation with tree species composition or with the total basal areas of the trees at these sites. These trends may be disputed because of small differences in nutrient levels among quadrats. The nitrate concentrations in the 15 - 30 cm samples were lower than in the upper layer; in addition, there was little fluctuation. Equilibrial nitrate concentrations appeared to be more dependent on soil composition than on vegetation influence.

In summary, although a broad correspondence between nitrate concentration and the four major vegetation associations was recognized, no correlation with the total basal areas could be found. This suggests that some aspect of soil composition, rather than the influence of the vegetation, determines the nitrate concentrations that were observed

within these communities.

7. Organic Matter

(a) Preliminary Remarks

Samples dried at $60^{\circ}C$ were used in this study, but the loss of accuracy was assumed to be small. It is unlikely that increasing the drying temperatures of the inorganic soils to $110^{\circ}C$ would greatly increase the water loss, for sandy soils have low water retaining capacities. This point is especially significant since the precision of the balance (0.015 g) was low relative to the potential extra water loss. Although the proportion of water lost from the peat soils is potentially more, the relative increase in accuracy would not be great in view of the high percentages of organic matter.

(b) Discussion of Results

The percentages of organic matter were high in the peatland complex, while in the mixed aspen forest they were low (Figure 9). In the discussion that follows description of the percentages, their geneses, and the relationship of these fractions to the nutrient status in the four major associations along the transect will be presented.

The greatest fraction of organic matter was found in the larch – black spruce association, suggesting that the decomposition of organic matter was comparatively slow. The only nutrient present in low concentrations was calcium. Lack of uptake by the vegetation may explain the high concentrations of the rest of the nutrients. There was slightly more organic matter in the 0 – 15 cm than in the 15 – 30 cm stratum resulting from greater decomposition in the lower
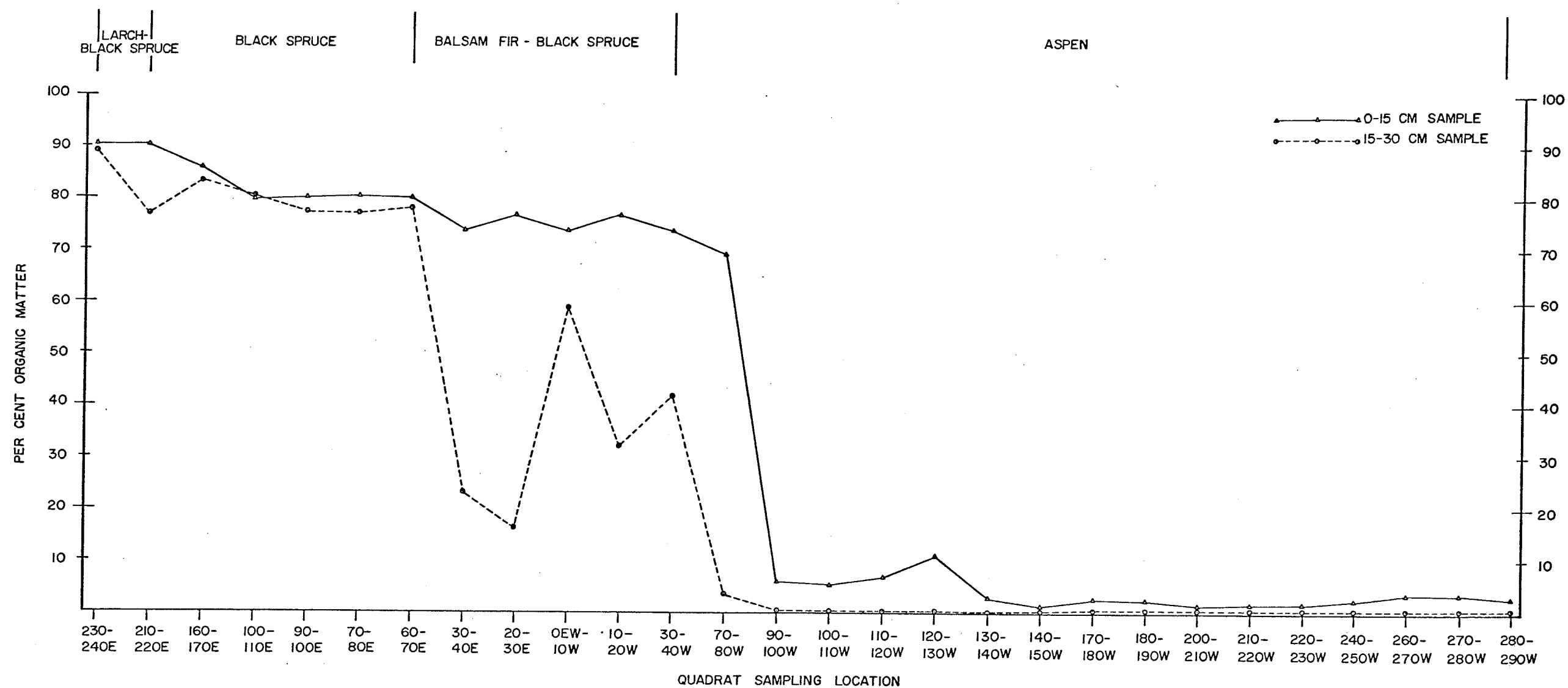
FIGURE 9

PER CENT ORGANIC MATTER ALONG THE TRANSECT

sample. The particularly low percentage at site 210 - 220E was due to experimental error.

The percentages of organic matter in the black spruce community were approximately ten per cent lower than those in the larch - black spruce association and indicate faster decomposition. Calcium, was more highly concentrated in the black spruce community. Relating the levels of the other nutrients to the increased rate of decomposition per se is impossible. The percentages of organic matter at site 160 - 170E were intermediate and suggest a gradual change in soil conditions progressing westward. The percentages of organic matter in the rest of the samples, especially those at the 0 - 15 cm sample depth, were stable. With the exception of site 100 to 110E the upper samples had slightly more organic matter than the lower samples.

Large differences in the amount of organic matter between sample depths are characteristic of the balsam fir - black spruce association. The average in the 0 - 15 cm samples was approximately five per cent lower than at the same depth in the black spruce community, probably because decomposition was more rapid under fir than under spruce (Dammon 1971, 265). The percentages in the lower stratum were much lower and fluctuated more than in the upper layer. Reduced levels resulted because the sample included the underlying clay moreso than because of better decomposition. The fluctuation is probably the consequence of different proportions of clay within the sample. The concentrations of

calcium resemble those of organic matter at both sample depths.
Faster decomposition rates may explain the slightly higher
concentrations in the upper sample of the balsam fir - black
spruce association when compared with the black spruce as-
sociation. Ammonium and nitrate exhibit levels similar to
that of organic matter at the 15 - 30 cm depth, but no
similarities between organic matter and the rest of the
nutrients was apparent.

Small accumulations of organic matter distinguish the
soils of the aspen forest. Site 70 - 80W was an exception.
The percentage in the upper layer was similar to those in
the upper layer of balsam fir - black spruce association,
probably because this site represents the former boundary
of the balsam fir - black spruce community; low basal areas
of the trees suggests recent disturbance. The low fraction
of organic matter in the lower stratum illustrates the
shallow nature of the organic layer at this site. In all
quadrats within the mixed forest more organic matter was
found in the upper than in the lower sample. The levels
from 90 - 130W were relatively high and showed considerable
fluctuation; thereafter the percentages dropped and showed
little variation. In the 15 - 30 cm samples the percentages
of organic matter were nearly constant at 0.5 per cent.
Within this association the concentration of all nutrient
parameters except phosphorus and pH exhibit a trend similar
to that of organic matter and suggest that the amount of
nutrient extracted is a function of the amount of organic

matter present.

It was apparent that along the transect the amount of organic matter and the rates of decomposition exerted a strong influence on the nutrient levels in the soil, and that the differences in these parameters between the peatland and sandy soils were large. In the peat complex the nutrient levels were comparatively high due to the large amounts stored and complexed by the organic matter. Although the organic matter in the balsam fir - black spruce zone decomposed more rapidly than in the black spruce community, the lower nutrient levels in the former association are probably explained by more favourable environmental conditions allowing greater uptake of nutrients by the vegetation. One possible explanation for the high concentrations in the eastern section of the peatlands is that some soil conditions such as pH may prevent nutrient uptake by causing physiological harm to the vegetation.

Probably the quantity of organic matter deposited yearly in the mixed forest exceeds that in the peatland communities, but the relatively low percentages indicate that decomposition is rapid. The levels of most nutrients were low, suggesting rapid uptake of nutrients once they were mineralized. This may result from the immaturity of the mixed forest. In the early stages of secondary succession humus decomposition is rapid. The growth rate of the vegetation is also rapid so that most of the nutrient is immobilized within the biomass and only small

amounts remain in the soil. Unlike the peat soils, no association between nutrient levels and tree species were perceptible.

C. Analysis of Mensuration Data in Relation to Nutrient Status of Soils along the Transect

1. Introduction

In the larch – black spruce association the total basal area per quadrat was low, but it rose to a maximum in the black spruce and balsam fir – black spruce associations. In the aspen forest the total basal areas were considerably lower. The patterns in basal area are similar to those of many of the nutrients.

Because of the variation in the total basal area of the quadrats and the significant ($r = 0.46$, $P < 0.05$) contribution of tree density to total basal area, the average basal area per tree was calculated. These data are found in Table III and are plotted in Figure 10.

The total and average basal areas per species per quadrat were calculated in order to evaluate species dominance (Table III). The total basal areas of each species are plotted in Figure 11; the arrangement of species from right to left in each quadrat is in order of contribution to the total basal area of the quadrat.

Analysis of the relationship between nutrient status and the total and average basal areas was conducted using multiple regression analysis. Regression equations were calculated for 1) the complete transect and 2) the evergreen and the aspen forests because the low numbers of samples from the peatland would not permit proper evaluation of the statistical significance of the equations for each community. Discussion of the equations is deferred to a later section.

TABLE III

MENSURATION DATA ALONG THE TRANSECT

SITE	SPECIES	TOTAL BASAL AREA (cm^2)	NUMBER OF TREES	AVERAGE BASAL AREA PER TREE (cm^2) $\pm$ S.D.
230E – 240E	Larix laricina	380.8	12	31.7 $\pm$ 21.5
	Picea mariana	54.3	4	13.6 $\pm$ 13.0
Total	2	435.1	16	27.2 $\pm$ 20.9
220E – 230E	Larix laricina	307.4	14	22.0 $\pm$ 21.3
	Picea mariana	39.5	6	6.6 $\pm$ 8.2
Total	2	346.9	20	17.3 $\pm$ 19.5
210E – 220E	Larix laricina	633.0	16	39.6 $\pm$ 23.7
	Picea mariana	156.5	7	22.4 $\pm$ 21.7
Total	2	789.5	23	34.3 $\pm$ 24.0
160E – 170E	Picea mariana	980.6	35	28.0 $\pm$ 12.7
Total	1	980.6	35	28.0 $\pm$ 12.7
110E – 120E	Picea mariana	2786.3	47	59.3 $\pm$ 40.6
Total	1	2786.3	47	59.3 $\pm$ 40.6
90E – 100E	Picea mariana	2906.6	58	50.1 $\pm$ 36.0
Total	1	2906.6	58	50.1 $\pm$ 36.0

TABLE III (continued)

SITE	SPECIES	TOTAL BASAL AREA (cm^2)	NUMBER OF TREES	AVERAGE BASAL AREA PER TREE (cm^2) $\pm$ S.D.
70E – 80E	_Picea mariana_	2968.7	39	76.1 $\pm$ 47.7
Total	1	2968.7	39	76.1 $\pm$ 47.7
60E – 70E	_Picea mariana_	2812.8	24	117.2 $\pm$ 89.6
Total	1	2812.8	24	117.2 $\pm$ 89.6
30E – 40E	_Picea mariana_	1857.6	10	185.8 $\pm$ 122.6
	Abies balsamea	1174.4	14	83.9 $\pm$ 82.4
	Picea sp.	392.0	2	196.0 $\pm$ 85.8
Total	3	3424.0	26	131.7 $\pm$ 109.8
20E – 30E	_Picea mariana_	1713.9	11	155.8 $\pm$ 101.9
	Abies balsamea	315.8	8	39.5 $\pm$ 32.8
	Picea sp.	28.2	1	28.2 $\pm$ 0.0
Total	3	2057.9	20	102.8 – 97.3
0 – 10W	_Abies balsamea_	1245.9	13	95.8 $\pm$ 151.4
Total	1	1245.9	13	95.8 $\pm$ 151.4

TABLE III (continued)

SITE	SPECIES	TOTAL BASAL AREA (cm^2)	NUMBER OF TREES	AVERAGE BASAL AREA PER TREE (cm^2) $\pm$ S.D.
1OW - 2OW	Abies balsamea	1453.2	17	85.5 $\pm$ 99.7
	Picea mariana	1410.4	6	235.1 $\pm$ 106.2
Total	2	2863.5	23	124.5 $\pm$ 114.8
2OW - 3OW	Abies balsamea	1923.3	14	137.4 $\pm$ 163.0
	Picea mariana	494.0	3	164.7 $\pm$ 169.5
Total	2	2417.3	17	142.2 $\pm$ 159.0
3OW - 4OW	Abies balsamea	1849.9	22	84.1 $\pm$ 124.6
	Picea mariana	1302.6	3	434.2 $\pm$ 69.6
Total	2	3152.5	25	126.1 $\pm$ 165.8
7OW - 8OW	Betula papyifera	64.2	5	12.8 $\pm$ 4.4
	Abies balsamea	48.3	6	8.0 $\pm$ 3.6
	Fraxinus nigra	39.2	1	39.2 $\pm$ 0.0
	Populus balsamifera	19.8	1	19.8 $\pm$ 0.0
	Picea mariana	7.4	1	7.4 $\pm$ 0.0
Total	5	178.9	14	12.8 $\pm$ 9.0

TABLE III (continued)

SITE	SPECIES	TOTAL BASAL AREA (cm^2)	NUMBER OF TREES	AVERAGE BASAL AREA PER TREE (cm^2) $\pm$ S.D.
90W – 100W	Populus tremuloides	758.9	8	94.9 $\pm$ 71.0
	Betula papyrifera	401.7	18	22.3 $\pm$ 22.5
	Abies balsamea	70.4	3	23.5 $\pm$ 15.2
	Picea mariana	21.3	1	21.3 $\pm$ 0.0
Total	4	1252.4	30	41.7 $\pm$ 51.0
100W – 110W	Populus tremuloides	532.3	12	44.4 $\pm$ 42.9
	Abies balsamea	115.9	14	8.3 $\pm$ 4.9
	Picea mariana	71.0	9	7.9 $\pm$ 4.9
	Betula papyrifera	51.8	6	6.6 $\pm$ 6.5
	Populus balsamifera	9.6	2	4.8 $\pm$ 3.6
Total	5	780.6	43	18.1 $\pm$ 27.8
110W – 120W	Populus tremuloides	645.8	17	38.0 $\pm$ 38.5
	P. balsamifera	324.6	3	108.2 $\pm$ 99.0
	Betula papyrifera	174.8	10	17.5 $\pm$ 18.0
	Ulmus americana	46.8	1	46.8 $\pm$ 0.0
	Abies balsamea	45.4	7	6.5 $\pm$ 2.1
	Picea mariana	17.7	4	4.4 $\pm$ 1.0
	Picea glauca	8.8	1	8.8 $\pm$ 0.0
Total	7	1263.9	43	29.4 $\pm$ 42.1

TABLE III (continued)

SITE	SPECIES	TOTAL BASAL AREA (cm^2)	NUMBER OF TREES	AVERAGE BASAL AREA PER TREE (cm^2) $\pm$ S.D.
120W - 130W	Populus tremuloides	1496.5	25	58.7 $\pm$ 43.0
	Betula papyrifera	264.6	12	22.0 $\pm$ 12.5
	Pinus banksiana	51.2	1	51.2 $\pm$ 0.0
	Abies balsamea	7.5	1	7.5 $\pm$ 0.0
	Populus balsamifera	4.4	1	4.4 $\pm$ 0.0
Total	5	1824.3	40	45.6 $\pm$ 39.5
130W - 140W	Populus tremuloides	1996.8	38	48.7 $\pm$ 52.5
	Betula papyrifera	291.0	8	36.4 $\pm$ 37.2
	Abies balsamea	6.2	1	6.2 $\pm$ 0.0
Total	3	2294.0	47	48.8 $\pm$ 46.9
140W - 150W	Populus tremuloides	376.0	5	75.2 $\pm$ 94.2
	Picea sp.	29.3	2	14.7 $\pm$ 1.7
	Picea glauca	20.8	1	20.8 $\pm$ 0.0
	Betula papyrifera	11.2	1	11.2 $\pm$ 0.0
	Abies balsamea	10.6	1	10.6 $\pm$ 0.0
Total	5	447.9	10	44.8 $\pm$ 70.6

TABLE III (continued)

SITE	SPECIES	TOTAL BASAL AREA (cm^2)	NUMBER OF TREES	AVERAGE BASAL AREA PER TREE (cm^2) $\pm$ S.D.
170W – 180W	Populus tremuolides	1547.5	18	85.9 $\pm$ 57.5
	Betula papyrifera	771.3	20	38.6 $\pm$ 34.2
	Abies balsamea	117.4	10	11.7 $\pm$ 8.2
	Pinus banksiana	17.9	2	8.8 $\pm$ 4.5
	Picea sp.	13.0	1	13.0 $\pm$ 0.0
	Picea mariana	6.7	1	6.7 $\pm$ 0.0
Total	6	2473.9	52	47.6 $\pm$ 50.0
180W – 190W	Populus tremuloides	1108.3	20	55.4 $\pm$ 48.1
	Pinus banksiana	74.0	1	74.0 $\pm$ 0.0
	Abies balsamea	25.5	4	6.4 $\pm$ 2.6
	Picea mariana	12.4	1	12.4 $\pm$ 0.0
	Picea sp.	2.8	1	2.8 $\pm$ 0.0
Total	5	1223.0	27	45.3 $\pm$ 46.3
200W – 210W	Populus tremuloides	389.4	14	27.8 $\pm$ 18.9
	Pinus banksiana	254.9	2	127.5 $\pm$ 8.3
	Betula papyrifera	36.2	3	12.1 $\pm$ 8.0
	Abies balsamea	5.7	1	5.7 $\pm$ 0.0
	Picea mariana	4.3	1	4.3 $\pm$ 0.0
Total	5	690.6	21	32.8 $\pm$ 36.0

TABLE III (continued)

SITE	SPECIES	TOTAL BASAL AREA (cm^2)	NUMBER OF TREES	AVERAGE BASAL AREA PER TREE (cm^2) ± S.D.
210W – 220W	Populus tremuloides	608.4	18	33.8 ± 25.6
	Betula papyrifera	214.7	11	19.5 ± 19.5
	Populus balsamifera	128.5	4	32.1 ± 27.9
	Abies balsamea	16.9	3	5.6 ± 3.3
Total	4	968.5	36	26.9 ± 24.0
220W – 230W	Populus tremuloides	1083.8	17	63.7 ± 40.1
	Betula papyrifera	132.9	6	22.1 ± 9.9
	Populus balsamifera	88.9	7	12.7 ± 9.1
	Abies balsamea	25.0	2	12.5 ± 5.4
	Picea mariana	5.3	1	5.3 ± 0.0
Total	5	1335.9	33	40.5 ± 38.2
240W – 250W	Populus tremuloides	229.7	6	38.3 ± 12.2
Total	1	229.7	6	38.3 ± 12.2
260W – 270W	Populus tremuloides	1875.9	32	58.6 ± 41.9
	Populus balsamifera	34.3	3	11.4 ± 4.9
	Betula papyrifera	30.4	1	30.4 ± 0.0
Total	3	1940.6	36	53.9 ± 41.8

TABLE III (continued)

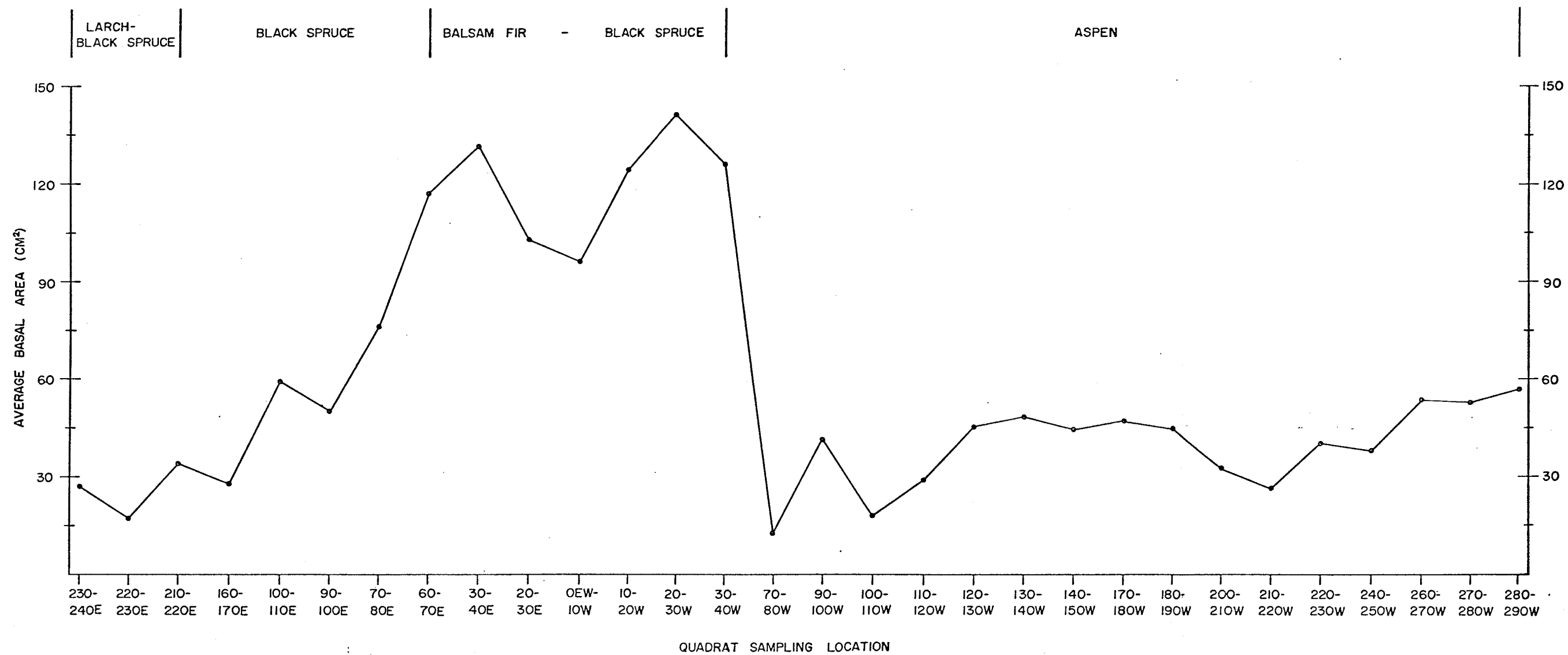| SITE	SPECIES	TOTAL BASAL AREA (cm^2)	NUMBER OF TREES	AVERAGE BASAL AREA PER TREE (cm^2) $\pm$ S.D.
270W – 280W	Populus tremuloides	876.6	18	48.7 $\pm$ 43.2
	Betula papyrifera	342.5	5	68.5 $\pm$ 66.9
Total	2	1219.1	23	53.0 $\pm$ 48.2
280W – 290W	Populus tremuloides	1290.0	21	61.4 $\pm$ 50.0
	Betula papyrifera	82.2	3	27.4 $\pm$ 13.3
Total	2	1372.3	24	57.2 $\pm$ 48.2

QUADRAT SAMPLING LOCATION

FIGURE 10

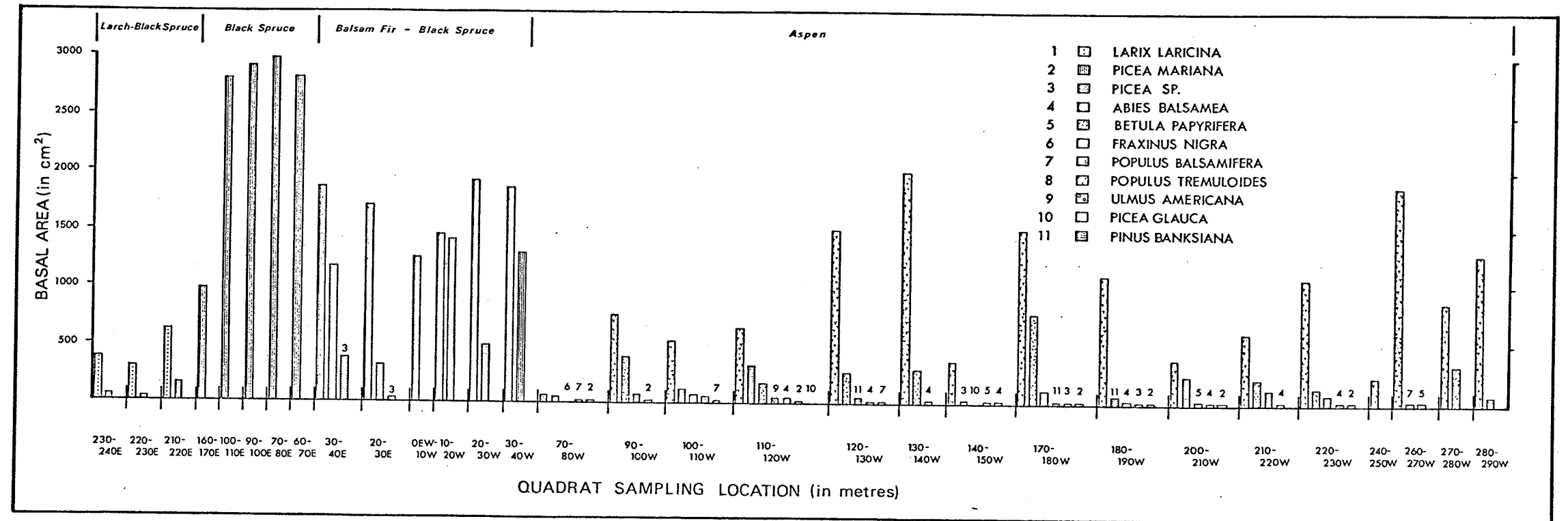AVERAGE BASAL AREA PER TREE ALONG THE TRANSECT

FIGURE 11

TREE SPECIES COMPOSITION AND DOMINANCE ALONG THE TRANSECT

2. Qualitative Analysis of the Relationship between
   Tree Cover and Nutrients in each Association

(a) Larch - black spruce association

The nutrient levels of this association were quite
high but the low per tree basal areas (Figure 10) and the
slow growth rates (Dugle et al. 1974) indicate that normal
tree growth is impossible. The high acidity probably prevents
this by directly injuring the trees, by keeping the nutrients
in chemical forms unavailable to the plant, and/or by retard-
ing decomposition of organic matter.

Larch was clearly dominant over black spruce in this
association (Figure 11). Large differences in the total
basal areas of each species were accounted for by the greater
tree densities. The average basal areas per tree of larch
greatly exceeded those of black spruce.

Towards the western extreme of this association the
average size for both species increased although larch was
still dominant. This increase probably resulted from greater
availability of nutrients. No larch was found in the samples
west of 190E. The absence of larch even though it was a
strong competitor up to that point, plus the fact that
larch exhibits better growth under more ameliorative
conditions (Forbes 1961, 17), suggest that this species is
subject to competitive exclusion by black spruce.

(b) Black spruce association

The total basal area per quadrat generally increased
from east to west in the black spruce association (Table III).
The high tree density primarily accounted for the large

total basal areas of the quadrats since the values for
average basal area per tree, although rising towards the
western extreme of this association, were not large and the
trees were distributed within relatively few size classes.
The concentrations of all nutrients were very high in this
community.

The evidence, suggests that tree growth was probably
not optimal and that the increase in tree size was not a
simple response to the higher nutrient levels. The total
basal areas per quadrat were comparable to, and the per tree
basal areas much greater in the balsam fir - black spruce
association, than in the black spruce association even though
the nutrient status was relatively low. If growth were
optimal in the black spruce community, then larger trees as
in 60 - 70E would be expected. The change in basal area
increased approximately linearly, while the nutrient
concentrations might be described as uniform (eg. phosphate
and potassium) or sigmoid (eg. calcium) between the two
extremes.

One interpretation of the restricted tree growth
might be that the levels of nutrients are optimal and that
other environmental variables limit tree growth. Dammon's
(1971) paper suggested that the high nutrient levels indicate
low rates of mineralization and that the vegetation in the
black spruce association is nutrient limited. Calcium,
phosphate, and nitrate appear to be the primary limiting
nutrients. The levels of potassium were similar in the

black spruce and the balsam fir - black spruce associations and, while the ammonium levels were lower from OEW to 40W, high ammonium concentrations from 60E to OEW associated with high basal areas suggest that it was not in short supply.

Using the data from site 60 - 70E it is proposed that nitrate and phosphate are of greater consequence than calcium. This site had fewer trees per quadrat and high basal areas per tree, both characteristic of the balsam fir - black spruce associations. Calcium was present in high concentrations, but unlike the other spruce sites the levels of nitrate and phosphate were low and would appear to be most restrictive to tree growth in the black spruce community.

It is not known what limits mineralization along this portion of the transect. Unlike the larch - black spruce association, acidity was apparently not critical; the pH range of the soil was virtually ideal for the growth (Wilde 1958, 215 - 216) and for the mineralization of nitrogen and phosphorus. It is hypothesized that growth in the black spruce association is related to peat depth, since there was better tree growth on shallow peats than on deep peats. Differences in oxidation-reduction levels may account for the differences in mineralization between the two communities.

(c) Balsam fir - black spruce association

Few trees and large basal areas per tree were characteristic of this section of the transect although there was considerable variability among quadrats. The relative contribution of black spruce to the total basal

area decreased progressively from east to west. From OEW to 40W balsam fir was dominant, although in many cases the differences between it and black spruce were not large. The average basal area per fir tree (Table III) remained comparatively constant over the community, but that of black spruce increased, especially at the western extreme of this association.

Dugle et al. (1974, 5) found that the growth rate of balsam fir was fairly high on sites similar to those under discussion, although slower than expected. Probably black spruce exhibited similarly high growth rates. In view of the short life span of balsam fir (Forbes 1961, 17; Rowe 1956, 69 - 70) it is conceivable that black spruce may eventually become dominant.

As outlined in 2 (b) good growth is probably due to improved mineralization of nutrients, especially phosphate and nitrate, and perhaps calcium. The concentrations of calcium were the same in the 0 - 15 cm depths in this and in the black spruce associations; the much reduced concentrations in the 15 - 30 cm stratum may be due to improved mineralization, but the substrate may also explain the lower concentrations.

(d) Aspen association

With few exceptions the total basal areas of quadrats in this association (Table III) were less than those two previously discussed. Uniformity of average basal area per tree is characteristic of this association.

This results from the similarity in the age of the trees (Dugle et al. 1974) because of recolonization following a fire. Competition is of minor importance in governing tree size in this association since the uniformity occurs despite wide fluctuations in tree density in each quadrat. Whether intrinsic growth rates or environmental conditions are responsible is unknown. Depressions in Figure 10 from 70 - 290W probably represent sites that were colonized later than the others. The average basal area per tree was not large. Tree species diversity was highest in the aspen association. Aspen poplar was dominant, except at 70 - 80W. The average basal area per aspen tree was generally greatest. Paper birch was the primary subdominant species. Other species rarely significantly contributed to the total basal area.

The concentrations of calcium, potassium (Wilde 1958, 224 - 226), nitrate, and ammonium were low and may be inadequate for best forest growth. The mineralization and uptake rates for these nutrients are probably high. Phosphorus levels were high in the 15 - 30 cm stratum of samples 140 - 290W, suggesting that the trees are not phosphorus demanding. The visual similarity between total basal area and phosphate concentration suggested that tree growth is dependent upon phosphorus concentration.

3. Mathematical Relationships between the Basal Areas of
   Trees and Soil Nutrients

(a) Introduction

Because the original variables were measured in differ-
ent units, the data were standardized by expressing each
datum in units of one standard deviation from the mean
(Davies 1971, 275). The resulting regression equations do
not require an intercept. The beta weights, or standard
partial regression coefficients, measure the contribution
of each independent variable to the predicted value of the
dependent variable (ibid. 275). The interpretation is
complicated when the independent variates are highly
correlated (Snedecor and Cochran 1967, 398).

(b) Regression Equations without Regard to Species

1. Using the Total Basal Area as the Dependent Variable

Only regressions using twenty-eight quadrats were
significant, moreso when variables from the 0 - 15 cm
samples were used (Table IV). Calcium and organic matter
appeared most important in that equation. No nutrients were
as prominent in the second equation, although calcium and
potassium seemed to be most important. The importance of
phosphorus in the 15 - 30 cm equations, especially those of
the aspen forest, may result from the high concentrations
of phosphorus from samples between 140 and 290W.

Of the remaining regression equations, those using
data from the lower sample depth accounted for slightly

TABLE IV

MULTIPLE REGRESSION EQUATIONS OF TOTAL BASAL AREA ON NUTRIENT LEVELS

INDEPENDENT VARIABLES: 0 - 15 cm Sample

240E - 290W (whole transect)

$\hat{y} = -0.23$ pH $+ 1.89$ ppm Ca $- 0.14$ ppm K $+ 0.33$ ppm P
$+ 0.20$ ppm NO_3 $- 0.03$ ppm NH_4 $- 1.41$ % o.m.

F = 3.77 with 7,20 d.f.; $R^2 = 0.57$**

240E - 40W (evergreen association)

$\hat{y} = 0.09$ pH $+ 0.54$ ppm Ca $- 0.64$ ppm K $+ 0.29$ ppm P
$+ 0.10$ ppm NO_3 $+ 0.10$ ppm NH_4 $- 0.03$ % o.m.

F = 2.06 with 7,4 d.f.; $R^2 = 0.78$

70W - 290W (aspen association)

$\hat{y} = -0.03$ pH $- 3.31$ ppm Ca $+ 1.13$ ppm K $- 0.55$ ppm P
$+ 0.42$ ppm NO_3 $- 3.14$ ppm NH_4 $+ 4.88$ % o.m.

F = 2.17 with 7,8 d.f.; $R^2 = 0.65$

INDEPENDENT VARIABLES: 15 - 30 cm Sample

240E - 290W (whole transect)

$\hat{y} = 0.35$ pH $+ 0.52$ ppm Ca $- 0.52$ ppm K $+ 0.29$ ppm P
$- 0.09$ ppm NO_3 $- 0.08$ ppm NH_4 $+ 0.22$ % o.m.

F = 3.09 with 7,20 d.f.; $R^2 = 0.52$*

240E - 40W (evergreen association)

$\hat{y} = 0.39$ pH $+ 0.17$ ppm Ca $- 0.69$ ppm K $+ 0.50$ ppm P
$+ 0.81$ ppm NO_3 $- 0.22$ ppm NH_4 $- 0.85$ % o.m.

F = 2.48 with 7,4 d.f.; $R^2 = 0.81$

70W - 290W (aspen association)

$\hat{y} = + 0.53$ pH $+ 0.44$ ppm Ca $- 0.61$ ppm K $+ 0.93$ ppm P
$+ 0.45$ ppm NO_3 $+ 0.26$ ppm NH_4 $- 0.79$ % o.m.

F = 2.32 with 7,8 d.f.; $R^2 = 0.69$

**significant at 1 per cent level

more of the total sum of squares that did those from the upper sample depth. The equations for the evergreen forest have large R-squared values, but few variables were as important at those in the equations 0 - 15 cm for the samples of the aspen forest. There organic matter, calcium, ammonium, and potassium were prominent. Some of these variables were important in the equation for the 15 - 30 cm sample but the beta weights were less pronounced.

2. Using the Average Basal Area per Tree as the Dependent Variable

Equations using the average basal area per tree were calculated to determine whether any deviations from the previous trends would result from differences in tree density between quadrats (Table V). Only the regressions using twenty-eight quadrats were significant. Calcium, organic matter, potassium and ammonium continued as the most important parameters. Organic matter was more important in the equation for the lower sample than in the corresponding equation using total basal area. Nitrate was also important in this regression equation. Only minor changes in the predominance of nutrients were observed after accounting for differences in tree density. By comparing R-squared values, it was concluded that both total and average basal area are predicted equally well by the nutrient parameters and was probably due to the significant correlation between tree density and total basal area ($r = 0.46$, $P < 0.01$).

TABLE V

MULTIPLE REGRESSION EQUATIONS OF AVERAGE BASAL AREA PER TREE ON NUTRIENT LEVELS

INDEPENDENT VARIABLES: 0 – 15 cm Sample

240E – 290W (whole transect)

$\hat{y}$ = – 0.27 pH + 1.34 ppm Ca – 0.03 ppm K – 0.10 ppm P – 0.16 ppm NO_3 – 0.22 ppm NH_4 – 0.16 % o.m.

F = 4.14 with 7,20 d.f.; R^2 = 0.59**

240E – 40W (evergreen association)

$\hat{y}$ = + 0.03 pH – 0.25 ppm Ca – 0.63 ppm K – 0.40 ppm P – 0.07 ppm NO_3 + 0.06 ppm NH_4 – 0.22 % o.m.

F = 3.72 with 7,4 d.f.; R^2 = 0.87

70W – 290W (aspen association)

$\hat{y}$ = – 0.28 pH – 1.29 ppm Ca + 1.13 ppm K – 0.12 ppm P + 0.01 ppm NO_3 – 0.78 ppm NH_4 + 0.82 % o.m.

F = 2.15 with 7,8 d.f.; R^2 = 0.65

INDEPENDENT VARIABLES: 15 – 30 cm Sample

240E – 290W (whole transect)

$\hat{y}$ = – 0.02 pH + 0.99 ppm Ca – 0.22 ppm K – 0.02 ppm P – 1.69 ppm NO_3 – 0.01 ppm NH_4 + 1.14 % o.m.

F = 4.35 with 7,20 d.f.; R^2 = 0.52**

240E – 40W (evergreen association)

$\hat{y}$ = – 0.15 pH + 0.32 ppm Ca = 0.45 ppm K – 0.17 ppm P – 0.44 ppm NO_3 – 0.08 ppm NH_4 – 0.15 % o.m.

F = 2.54 with 7,4 d.f.; R^2 = 0.82

70W – 290W (aspen association)

$\hat{y}$ = + 0.34 pH – 0.35 ppm Ca + 0.37 ppm K + 0.17 ppm P + 0.31 ppm NO_3 – 0.16 ppm NH_4 – 0.43 % o.m.

F = 1.48 with 7,8 d.f.; R^2 = 0.56

** significant at 1 per cent level

3. Interpretation

The nutrients of the upper stratum were more easily interpreted than those from the lower stratum because of their greater beta weights. Two explanations for this are offered. The first is the erratic fluctuations in nutrient concentrations from 15 - 30 cm relative to those at 0 - 15 cm of the aspen forest. The second is that differences in the nutrient levels are greatest in the upper soil layer because deposition occurs there. When there are large changes in basal area better correlations can be anticipated if the nutrient concentrations also change considerably.

The most important nutrients were described as a cation complex with organic matter being the exchange medium. Good correlation of this complex to the basal area was expected since the mass of organic matter deposited is related to the degree of forest cover, at least up to the point of canopy closure (Challinor 1968, 287). Sampling only the litter layers may further emphasize the statistical importance of these variables.

Except for potassium, there were no clearly dominant nutrient variables in the organic soils while the cation complex was clearly dominant in the mineral soils. Differences in decomposition rates may account for the dissimilarity. In the aspen forest decomposition was rapid with all but the most abundant (Lousier and Parkinson 1976) and relatively immobile nutrients being quickly released from the organic matter complex. Thereafter the mobile nutrients

are leached, absorbed by the plants, or are otherwise
immobilized. The net result was that only organic matter
and some cations remained to show a relationship to the
vegetation. In the evergreen associations the decomposition
rate was slow and no nutrients showed similar importance.

The rapid loss of some nutrients may also account
for the lower R-squared values of the equations for the
aspen forest. The lower multiple correlation coefficient
may result from a difference in maturity of the two forest
types. The forest on the organic soils was more mature and a
stable relationship between the vegetation and the soil had
developed. In contrast, the mixed forest was immature and
less clearly dominated by few species; the differential
uptake of nutrients, growth rates, etc., of these species
could result in less efficient regression.

(c) Regression Equations on Species

(1) Black spruce

Both regression equations using total basal area as
the independent variable were highly significant and
explained much of the error variation (Table VI). Calcium
and organic matter had the largest beta weights in both
equations. Nitrate was also important, moreso in the equa-
tion on nutrients from the 15 - 30 cm stratum.

When average basal area was regressed the equations
were less efficient. The R-squared value for the 0 - 15 cm

TABLE VI

MULTIPLE REGRESSION EQUATIONS OF BASAL AREAS OF BLACK SPRUCE ON NUTRIENT LEVELS

0 - 15 cm - Total Basal Area

$\hat{y}$ = - 0.19 pH + 1.60 ppm Ca - 0.35 ppm K + 0.55 ppm P
    + 0.55 ppm NO_3 - 0.06 ppm NH_4 - 1.06 % o.m.

F = 32.75 with 7,11 d.f.; R^2 = 0.95**

15 - 30 cm - Total Basal Area

$\hat{y}$ = - 0.31 pH + 1.01 ppm Ca - 0.55 ppm K - 0.26 ppm P
    - 0.73 ppm NO_3 + 0.16 ppm NH_4 + 0.93 % o.m.

F = 22.55 with 7,11 d.f.; R^2 = 0.93**

0 - 15 cm - Average Basal Area

$\hat{y}$ = - 0.07 pH + 0.63 ppm Ca + 0.13 ppm K - 0.27 ppm P
    - 0.35 ppm NO_3 - 0.34 ppm NH_4 + 0.54 % o.m.

F = 1.99 with 7,11 d.f.; R^2 = 0.56

15 - 30 cm - Average Basal Area

$\hat{y}$ = + 0.21 pH + 0.41 ppm Ca - 0.13 ppm K - 0.06 ppm P
    - 2.62 ppm NO_3 + 0.32 ppm NH_4 + 2.13 % o.m.

F = 5.37 with 7,11 d.f.; R^2 = 0.54**

**Significant at 1 per cent level

stratum was 0.56 and insignificant. The R-squared value
of the equation on nutrients from the 15 - 30 cm stratum
was 0.54 and highly significant. In view of the high
correlation between density and the total basal area of
black spruce (r = 0.81, P< 0.01) no explanations for the
lower coefficients of determination of these equations
are offered. Calcium, organic matter, and nitrate had the
greatest beta weights, but the latter two were especially
prominent in the second equation.

The good correlation between the basal area of
black spruce and the soil nutrient concentrations, the
high total basal areas of black spruce (and fir) on the
peatlands, and the relatively high nitrate levels found in
the black spruce association (when Dammon (1971, 260) found
no mineralization of nitrate under balsam fir or black spruce)
indicated that a good supply of nutrients was available. Even
though the rate of mineralization was slower in the organic
than in the mineral soils, the amount of available nutrient
may be greater in the peatlands because of the larger quan-
tities of organic matter and nutrients there. A corollary to
this hypothesis is that the response of black spruce to avail-
able nutrients depends on the severity of interspecific
competition, which increases with the rate of nutrient
mineralization. In the black spruce association mineraliza-
tion was slow, but black spruce was free from competition

by other tree species and showed high basal areas.
In the balsam fir - black spruce association it was also
successful. Competition, however, by fir for the more
readily available nutrients hindered the growth of black
spruce. Mineralization in the aspen forest was rapid.
The basal areas of black spruce were low because this
species has only recently invaded the aspen association
and severe competition allows only small quantities of
nutrient to filter to the spruce.

(2.) **Balsam fir**

All regression equations for balsam fir were highly
significant and had large and nearly identical R - squared
values (Table VII). The even size of the fir trees between
quadrats in the balsam fir - black spruce community may
explain the similar efficiencies of the regressions on total
and average basal areas. Calcium and organic matter dis-
played high beta weights, especially in the equations for
the 0 - 15 cm sample. Ammonium and potassium were of
secondary importance. While the beta weights of calcium were
reduced in the equations for the 15 - 30 cm samples, those of
organic matter increased. Ammonium and nitrate had relatively
high beta weights.

The large overlap in the ranges of balsam fir and
black spruce and the similarity in prominence of certain
nutrients in the equations for these species suggested a

TABLE VII

MULTIPLE REGRESSION EQUATIONS OF BASAL AREAS OF BALSAM FIR ON NUTRIENT LEVELS

0 - 15 cm - Total Basal Area

$\hat{y} = -0.23$ pH $+ 3.59$ ppm Ca $- 0.26$ ppm K $+ 0.21$ ppm P $+ 0.05$ ppm $NO_3 - 0.77$ ppm $NH_4 - 1.91$ % o.m.

F = 16.69 with 7,9 d.f.; $R^2 = 0.93$**

15 - 30 cm - Total Basal Area

$\hat{y} = +0.24$ pH $+ 0.42$ ppm Ca $- 0.18$ ppm K $+ 0.22$ ppm P $- 0.82$ ppm $NO_3 - 1.03$ ppm $NH_4 + 2.34$ % o.m.

F = 40.40 with 7,9 d.f.; $R^2 = 0.97$**

0 - 15 cm - Average Basal Area

$\hat{y} = -0.20$ pH $+ 2.55$ ppm Ca $+ 0.43$ ppm K $+ 0.07$ ppm P $- 0.21$ ppm $NO_3 - 0.43$ ppm $NH_4 - 1.46$ % o.m.

F 38.83 with 7,9 d.f.; $R^2 = 0.97$**

15 - 30 cm - Average Basal Area

$\hat{y} = +0.06$ pH $+ 0.82$ ppm Ca $+ 0.33$ ppm K $+ 0.05$ ppm P $- 1.20$ ppm $NO_3 - 0.54$ ppm $NH_4 + 1.48$ % o.m.

F 35.56 with 7,9 d.f.; $R^2 = 0.97$**

**Significant at 1 per cent level

similarity in their ecological relationship to the seven nutrient variables that were measured. Another variable such as wetness or redox potential was probably responsible for the failure of balsam fir to co-exist with black spruce along the whole peatland transect.

3. <u>Aspen</u>

No equations for this species were statistically significant (Table VIII). The R-squared values were low, although highest when total basal area was the dependent variable.

The strong contribution of calcium and organic matter was illustrated again. The cation complex was prominent in the equations of total basal area on upper stratum nutrients. Phosphorus had the greatest beta weight in the equation of total basal area on variates from 15 - 30 cm. The cation complex, however, was of negligible importance in this equation. Very low and relatively constant organic matter percentages in the 15 - 30 cm sample with little correlation to basal area is one explanation for its decreased importance. Damping the fluctuation by using the average basal area as the independent variable increased the beta weights of calcium and organic matter. Phosphorus and pH appeared to be of some importance in these equations for average basal area.

The organic matter complex was most important because the quantity of organic matter deposited depended

TABLE VIII

MULTIPLE REGRESSION EQUATIONS OF BASAL AREAS OF ASPEN ON NUTRIENT LEVELS

0 - 15 cm - Total Basal Area

$\hat{y}$ = + 0.20 pH - 1.79 ppm Ca + 1.06 ppm K - 0.55 ppm P - 0.04 ppm NO_3 - 0.56 ppm NH_4 + 1.34 % o.m.

F = 2.28 with 7,7 d.f.; R^2 = 0.69

15 - 30 cm - Total Basal Area

$\hat{y}$ = + 0.53 pH + 0.05 ppm Ca - 0.46 ppm K + 0.94 ppm P + 0.43 ppm NO_3 + 0.06 ppm NH_4 - 0.12 % o.m.

F = 1.00 with 7,7 d.f.; R^2 = 0.50

0 - 15 cm - Average Basal Area

$\hat{y}$ = - 0.53 pH + 1.04 ppm Ca + 0.35 ppm K - 0.46 ppm P + 0.42 ppm NO_3 + 0.20 NH_4 - 1.34 % o.m.

F = .38 with 7,7 d.f.; R^2 = 0.27

15 - 30 cm - Average Basal Area

$\hat{y}$ = + 0.74 pH - 0.51 ppm Ca + 0.00 ppm K - 0.05 ppm P + 0.03 ppm NO_3 + 0.04 ppm NH_4 + 0.82 % o.m.

F = .56 with 7,7 d.f.; R^2 = 0.36

on the degree of vegetation cover and (the cations) were
chemically bound to the organic matter. Soil pH and
orthosphosphate made stronger contributions to the predicted
value of the dependent variable in these equations than in
those of Tables III and IV. The reduction in basal area
of the quadrat that resulted from considering only aspen
did not account for all of the organic matter deposited.
Therefore, the relationship to the organic matter complex
was weaker and a better numerical relationship resulted
between aspen and the other nutrients. The dominance of
trembling aspen, however, suggested that pH and soil
phosphate may be critical to the welfare of trembling aspen.

(4. Paper birch

No regression equations for this species were
statistically significant (Table IX). The coefficients of
determination were low, possibly because aspen exerted
the greatest influence on the nutrient budget of the aspen
association. Also, since birch was subdominant competition
may be of greater influence than nutrients on paper birch.
Contrary to aspen, the R-squared values of the equations
using average basal area were larger than those using total
basal area. The 'damping effect' of using average values
in the aspen forest may explain this. The higher R-squared
values of the equations for average basal area appeared to
indicate that paper birch successfully competes with aspen

TABLE IX
MULTIPLE REGRESSION EQUATIONS OF BASAL AREAS OF PAPER BIRCH ON NUTRIENT LEVELS

0 - 15 cm - Total Basal Area

$\hat{y} = -0.76$ pH $+ 2.73$ ppm Ca $+ 0.30$ ppm K $- 0.09$ ppm P
$+ 0.03$ ppm $NO_3 - 1.16$ ppm $NH_4 - 1.47$ % o.m.

$F = .24$ with 7,6 d.f.; $R^2 = 0.22$

15 - 30 cm - Total Basal Area

$\hat{y} = +0.80$ pH $- 1.89$ ppm Ca $- 0.43$ ppm K $+ 0.67$ ppm P
$+ 0.16$ ppm $NO_3 - 0.12$ ppm $NH_4 + 1.54$ % o.m.

$F = .34$ with 7,6 d.f.; $R^2 = 0.29$

0 - 15 cm - Average Basal Area

$\hat{y} = +0.30$ pH $- 2.97$ ppm Ca $+ 1.05$ ppm K $+ 0.01$ ppm P
$- 0.74$ ppm $NO_3 - 1.86$ ppm $NH_4 + 4.28$ % o.m.

$F = .72$ with 7,6 d.f.; $R^2 = 0.46$

15 - 30 cm - Average Basal Area

$\hat{y} = +1.59$ pH $- 4.16$ ppm Ca $- 0.55$ ppm K $+ 0.10$ ppm P
$+ 0.34$ ppm $NO_3 - 0.65$ ppm $NH_4 + 3.23$ % o.m.

$F = .80$ with 7,6 d.f.; $R^2 = 0.48$

for nutrients and may be considered a stable component of
the aspen forest.

Calcium and organic matter had the highest beta
weights in all the regression equations and their compara-
tively high values suggested that these nutrients were more
important to birch than trembling aspen. In the 0 - 15 cm
samples ammonium appeared to be an important secondary
nutrient. Its homology in the lower samples was pH. Low and
stable percentages of organic matter in the 15 - 30 cm
stratum may explain the decreased importance of ammonium.
Although the cation complex was more strongly related to
birch than to aspen, the similarities in their habitats and
regression equations suggested that the ecological require-
ments of these two species were similar. Theoretically,
however, there was one important difference between the two
resulting from the smaller litter mass contributed by paper
birch. Since aspen deposited the greatest quantities of
litter, a stronger mathematical relationship between it and
the organic matter complex must exist, even if these nutrients
are not quantitatively important to the well-being of this
species. A strong relationship of birch to the cation
complex would suggest that the association was ecologically
important.

4. Mathematical Relationships between Simpson's Index of Diversity (inverse) and Soil Nutrients

Not Simpson's index per se, but rather its inverse was used to measure diversity (Appendix E). Expressing diversity this way was more intuitively appealing than expression in a probablilistic sense. This liberty would not have been taken if tree species diversity along the transect was high because disproportionately large values would have resulted. The index was regressed on the same independent variates as basal area (Table X).

All equations except for those of the 15 - 30 cm strata of the evergreen and aspen association were insignificant. The R-squared values indicate that "Simpson's" index of diversity was best predicted on nutrients from the lower depth. For twenty-eight quadrats, from 0 - 15 cm organic matter, potassium, and calcium had the highest beta weights. Phosphorus, organic matter and calcium were most important in the lower sample, but the beta weights were smaller. Calcium, phosphorus, and soil pH were most prominent in the 0 - 15 cm equation for the evergreen forest. From 15 - 30 cm pH and organic matter had relatively high beta weights; the very high R-squared value indicated that it was a good predictor of diversity. In the aspen forest all beta weights, except those of pH and phosphate, from 0 - 15 cm were pronounced, although that of organic

TABLE X
MULTIPLE REGRESSION EQUATIONS OF AN INDEX OF DIVERSITY ON NUTRIENT LEVELS

INDEPENDENT VARIABLES: 0 – 15 cm Sample

240E – 290W (whole transect)

$\hat{y} = -0.08$ pH $- 0.78$ ppm Ca $- 0.88$ ppm K $- 0.42$ ppm P $- 0.24$ ppm NO_3 $+ 0.45$ NH_4 $+ 1.23$ % o.m.

F = 1.91 with 7,20 d.f.; $R^2 = 0.40$

240E – 40W (evergreen association)

$\hat{y} = -1.23$ pH $+ 3.12$ ppm Ca $- 0.38$ ppm K $- 0.72$ ppm P $- 0.38$ ppm NO_3 $+ 0.58$ ppm NH_4 $- 0.12$ % o.m.

F = 1.72 with 7,4 d.f.; $R^2 = 0.75$

70W – 290W (aspen association)

$\hat{y} = +0.55$ pH $- 1.68$ ppm Ca $- 1.12$ K $- 0.33$ ppm P $+ 1.55$ ppm NO_3 $- 1.47$ ppm NH_4 $+ 2.46$ % o.m.

F = 0.88 with 7,8 d.f.; $R^2 = 0.44$

INDEPENDENT VARIABLES: 15 – 30 Sample

240E – 290W (whole transect)

$\hat{y} = -0.34$ pH $- 0.34$ ppm Ca $+ 0.03$ ppm K $- 0.53$ ppm P $+ 0.24$ ppm NO_3 $+ 0.16$ ppm NH_4 $- 0.40$ % o.m.

F = 2.22 with 7,20 d.f.; $R^2 = 0.44$

240E – 40W (evergreen association)

$\hat{y} = -1.23$ pH $+ 0.29$ ppm Ca $+ 0.04$ ppm K $- 0.34$ ppm P $- 0.22$ ppm NO_3 $+ 0.17$ ppm NH_4 $- 1.15$ % o.m.

F = 39.96 with 7,4 d.f.; $R^2 = 0.99$

70W – 290W (aspen association)

$\hat{y} = -0.72$ pH $- 0.02$ ppm Ca $- 0.37$ ppm K $- 0.51$ ppm P $- 0.33$ ppm NO_3 $+ 0.94$ ppm NH_4 $+ 0.02$ % o.m.

F = 3.59 with 7,8 d.f.; $R^2 = 0.76$*

* significant at 5 per cent level

matter was the largest. Especially interesting was the
newly assumed importance of nitrate and ammonium. Ammonium,
pH, and phosphorus were important in the equation for the
15 - 30 cm samples. Tree species diversity was largely
related to organic matter and calcium because these two
nutrients are probably a good index of the ecological
maturity of an ecosystem. The relative importance, however,
of the variates changed with the nature of the ecosystem
and sample depth. The extra importance of nitrogen in
the equations for the aspen forest may indicate that
nitrogen has a strong effect on tree species diversity
during the earlier stages of succession.

CHAPTER VI

CONCLUSIONS

The concentrations of all nutrients except phosphate are much higher in the organic than in the mineral soils. Hypotheses for the high concentrations were base flow of nutrients from the upland soils, greater amounts of nutrients adsorbed or immobilized because there is more organic matter, retardation of nutrient mineralization, and inhibition of nutrient uptake. Rapid decomposition of organic matter with rapid nutrient uptake, immobilization within the vegetation, and leaching may explain the low nutrient levels in the sandy soils.

There are characteristic relationships between the soil nutrient status and tree species composition along the 200N transect of FIG. The levels of organic matter, phosphate, ammonium, and nitrate under larch and black spruce were comparable to those under black spruce. Potassium concentrations were highest under the former community, but pH and calcium levels were low. Most nutrients were highly concentrated in the soils of the black spruce community. The lowest nutrient levels in the peatlands were generally found below the balsam fir – black spruce association. Better mineralization resulting from ameliorated environmental conditions, rapid uptake of nutrients, and differences in substrate composition appeared to explain the lower concentrations. A diverse aspen forest was found on mineral soils with low nutrient levels.

Relationships between tree basal area and soil
nutrient levels were described by multiple regression
equations. Basal area appears to be strongly related to
a cation complex composed of organic matter, calcium, and
to lesser extent potassium and ammonium. The prominence of
these parameters decreased with soil depth and with a shift
to the evergreen communities. The inclusion of the litter
layer explained the importance of these variables in the
upper sample and their prominence in the aspen forest may
be explained by the immaturity of this association. Growth
of the forest during early succession is accompanied by a
build-up in organic matter and nutrient levels.

The basal area of black spruce, balsam fir, trembling
aspen, and paper birch was also related to the cation complex.
There was little difference between species in the relative
prominence of the components of the cation complex. The
lower multiple correlation coefficients of the equations for
species dominant in the aspen forest may have resulted from
the immaturity of the aspen forest. Because the nutrient
levels were so low there was poor correlation with basal
area which fluctuated considerably between quadrats. The
differential uptake of nutrients and growth rates of the
many species in the aspen forest may obscure correlations
between any one species and the soil nutrients.

A better understanding of tree and soil nutrient

associations within FIG would result after studies on:

(1) the differences in rates of nutrient mineralization between communities,

(2) the yearly nutrient flux within each community and the contribution of ground-water flow to the flux,

(3) the relative rates of nutrient uptake of each species and its relation to species growth rate,

(4) the fraction of extractable nutrients available to trees, and

(5) the importance of soil aeration upon tree growth and nutrient mineralization along the topographic gradient

were completed.

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APPENDICES

APPENDIX A. Procedure used in drying, sieving, and storing the soil sample.

1. A composite soil sample was spread on an enameled drying tray.

2. The trays were placed in a Napco Model 430 drying oven at 60°C because the soils were very wet. The samples were left in the oven until dry, the minimum being 8 h.

After removal from the drying oven, the mineral soil was deposited in an Endecotts (Test Sieves) Limited 2mm sieve and shaken for 10 min on a sieve shaker. Smaller pieces of organic matter that remained on the sieve were removed, ground with a mullite mortar and pestle, and added to the material passing through the sieve. The sieved sample was then placed in either twist-tie or "ziploc" plastic bags, and after the addition of 2 or 3 drops of toluene, was then stored in a freezer at 0°C.

APPENDIX B. Procedures used in measuring soil pH

The following procedure used for the measurement of soil pH in 0.01M $CaCl_2$ solution is derived from Peech (1965, 923).

To 10g of 2mm soil in a 50ml beaker were added 20ml of 0.01M $CaCl_2$ solution. Due to the low specific gravity of peat soils 2 rather than 10g of partially decomposed peat were used, while raw peat was packed to the 15ml graduation mark of the beaker before adding the $CaCl_2$ solution. The sample was stirred vigourously for a few seconds with a glass stirring rod. The suspension was allowed to stand for at least 15 min. The glass electrode of a Radiometer 21 pH meter was lowered into the partly settled suspension and the calomel electrode was immersed in the clear supernatant solution.

Between measurements the electrode was rinsed with distilled water. After each tenth measurement the performance of the meter was checked and standardized against standard buffer solutions. After each 100 measurements the calomel electrode was flushed and refilled with fresh solution saturated with KCl.

APPENDIX C. <u>Procedure used in measuring calcium and potassium</u>

1. 10g of mineral soil, 1g of raw peat or 2g of partially decomposed peat were placed in a 250 ml Erlenmeyer flask.

2. To this was added 75 ml of neutral 1N NH_4OAc.

3. The flask was stoppered and shaken for 10 min (Pratt 1965, 1026) on a modified Soiltest Model Cl-392-B shaker.

4. Using water suction the extract was filtered through Whatman no. 40 filter paper into a 250 ml filter flask. The Erlenmeyer flask was rinsed with another 25 ml of extraction solution which was subsequently filtered.

5. To 95 ml of filtrate was added 5 ml of neutral 1N NH_4OAc in which strontium was dissolved at a concentration of 30,000 ppm. If 95 ml of filtrate could not be obtained, it was brought to volume with neutral 1N NH_4OAc.

6. The filtrate was then stored in firmly sealed 125 ml plastic vials at temperatures near $0^{o}C$ until analysis.

7. The standard solutions for calcium and potassium were prepared in concentrations of 0 - 25 and 0 - 30 ppm respectively with 1500 ppm strontium.

8. Calcium was analyzed by absorption and potassium by flame emission on a Unicam SP 90A Series 2 Atomic Absorption Spectrophotometer. Acetylene was used for fuel and compressed air was the oxidant. The instrument was adjusted as

to the instructions given in the technical manual supplied with the spectrophotometer.

9. The standard curve for calcium was checked after every ten samples, and if necessary the instrument was adjusted to its previous readings (Cooke 1969, 11). Three standards were atomized with each check, the two extreme solutions followed by one of intermediate concentration. Due to the greater instability of the instrument during potassium analysis, the standards were verified after every six samples of unknown concentration were analyzed.

10. Extracts giving weak signals were reanalyzed using a standard curve with a lower concentration range than the first; extracts having elemental concentrations beyond that of the standard curve were diluted.

By oversight the strontium concentrations in the filtrate were not made up to 1500 ppm when the extracts were diluted.

As a quick test for calcium depression extracts from four sites that required maximum dilution (dilution by 50, bringing the concentration of strontium down to 30 ppm) were selected. From each site two aliquots, the first containing 30 ppm and the second 1500 ppm strontium, were analyzed. The results in ppm, based on one reading, were:

SITE		EXTRACT WITH 30 ppm	EXTRACT WITH 1500 ppm
30 – 40E 15 – 30 cm		9700	10000
20 – 30E 15 – 30 cm		7200	7500
0 – 10W 15 – 30 cm		13000	12000
10 – 20W 15 – 30 cm		14000	11000

Since the data show no clear relationship between calcium concentration and level of strontium the uncorrected data were accepted.

Low strontium concentrations were no source of concern when potassium was analyzed because no dilution of the extracts was necessry.

APPENDIX D. Procedure used in measuring organic matter

The method used to estimate the amounts of organic matter is a simple loss on ignition test, with slight modifications as described by Jackson (1958, 225).

1) Approximately 10g of inorganic soil or 2gm of peat soil dried at 60°C were placed in weighed crucibles and the total weight of crucible and sample was recorded.

2) Samples were placed in a furnace at 400°C for 8 h.

3) Crucibles were removed from the oven and allowed to cool for approximately 10 min. The crucible and sample were then reweighed.

4) The percentage organic matter in the sample was calculated using the formula

$$\frac{a - b}{a} \times 100 \%, \quad \text{where}$$

a = weight of the soil sample before ignition, and

b = weight of the soil sample after ignition.

Appendix E. Data on Trees and Nutrient Levels along the Transect

Quadrat Sampling Location	Total Basal Area (cm^2)	Density	Simpson's index of diversity (inverse)	pH	ppm Ca	ppm K	ppm P	ppm NO$_3$	ppm NH$_4$	per cent o.m.
230 - 240E										
0 - 15 cm	435	16	1.67	3.5	3500	820	590	7.1	236	90.2
15 - 30 cm		$\bar{x}^a = 27.2$		3.5	3400	700	320	5.9	24	89.1
220 - 230E										
0 - 15 cm	347	20	1.79							
15 - 30 cm		$\bar{x} = 17.4$		nutrient data not available						
210 - 220E										
0 - 15 cm	790	23	1.79	5.4	13000	1000	340	8.6	456	90.1
15 - 30 cm		$\bar{x} = 34.3$		4.6	11000	840	220	8.1	154	76.8
160 - 170E										
0 - 15 cm	981	35	1.00	6.1	19000	950	160	9.6	120	85.8
15 - 30 cm		$\bar{x} = 28.0$		6.1	22000	800	160	7.7	44	83.3
100 - 110E										
0 - 15 cm	2790	47	1.00	6.6	21000	460	380	8.6	196	79.6
15 - 30 cm		$\bar{x} = 59.4$		6.4	25000	220	110	9.1	100	80.5
90 - 100E										
0 - 15 cm	2910	58	1.00	6.5	25000	590	380	5.0	262	80.1
15 - 30 cm		$\bar{x} = 50.2$		6.6	27000	180	220	8.4	192	77.4

Appendix E. (continued)

Quadrat Sampling Location	Total Basal Area (cm²)	Density	Simpson's index of diversity (inverse)	pH	ppm Ca	ppm K	ppm P	ppm NO₃	ppm NH₄	per cent o.m.
70 - 80E										
0 - 15 cm	2970	39	1.00	6.5	23000	600	440	8.7	134	80.4
15 - 30 cm		$\bar{x} = 76.2$		6.6	28000	240	160	7.2	130	77.2
60 - 70E										
0 - 15 cm	2810	24	1.00	6.6	21000	430	150	9.1	82	80.1
15 - 30 cm		$\bar{x} = 117.1$	1.00	6.6	27000	200	160	7.9	106	78.2
30 - 40E										
0 - 15 cm	3420	26	2.37	6.4	23000	470	190	2.5	172	73.9
15 - 30 cm		$\bar{x} = 131.5$		6.6	7200	72	33	1.0	10	23.2
20 - 30E										
0 - 15 cm	2060	20	2.29	6.0	23000	420	140	5.9	194	76.7
15 - 30 cm		$\bar{x} = 103.0$		6.6	7200	48	30	1.0	11	16.4
0EW - 10W										
0 - 15 cm	1250	13	1.00	7.2	23000	510	120	2.8	56	73.9
15 - 30 cm		$\bar{x} = 96.2$		7.6	12000	120	31	1.5	55	59.1
10 - 20W										
0 - 15 cm	2860	23	1.68	7.4	24000	390	120	2.6	54	76.8
15 - 30 cm		$\bar{x} = 124.4$		7.4	11000	72	20	1.2	22	32.4

Appendix E. (continued)

Quadrat Sampling Location	Total Basal Area (cm^2)	Density	Simpson's index of diversity (inverse)	pH	ppm Ca	ppm K	ppm P	ppm NO_3	ppm NH_4	per cent o.m.
20 - 30W										
0 - 15 cm	2420	17	1.45	nutrient data not available						
15 - 30 cm		$\bar{x} = 142.4$								
30 - 40W										
0 - 15 cm	3150	25	1.28	7.2	23000	390	78	5.3	48	73.8
15 - 30 cm		$\bar{x} = 126.0$		7.5	11000	90	44	1.4	18	42.0
70 - 80W										
0 - 15 cm	179	14	3.64	6.5	15000	170	100	2.6	74	69.4
15 - 30 cm		$\bar{x} = 12.8$		7.0	3600	28	12	0.7	8	3.8
90 - 100W										
0 - 15 cm	1250	30	2.36	5.5	2700	74	40	1.1	7	6.2
15 - 30 cm		$\bar{x} = 41.7$		6.0	730	12	14	0.5	1	0.7
100 - 110W										
0 - 15 cm	781	43	4.32	5.2	1300	64	76	1.0	11	5.6
15 - 30 cm		$\bar{x} = 18.2$		5.6	440	10	32	0.5	2	0.5
110 - 120W										
0 - 15 cm	1260	43	4.28	5.8	2800	80	90	1.1	4	7.1
15 - 30 cm		$\bar{x} = 29.3$		6.2	550	14	10	0.6	5	0.5

Appendix E. (continued)

Quadrat Sampling Location	Total Basal Area (cm²)	Density	Simpson's index of diversity (inverse)	pH	ppm Ca	ppm K	ppm P	ppm NO$_3$	ppm NH$_4$	per cent o.m.
120 - 130W										
0 - 15 cm	1820	40	2.13	5.8	4000	130	50	1.2	14	11.2
15 - 30 cm		$\bar{x}$ = 45.5		6.6	1000	16	10	0.6	2	0.6
130 - 140W										
0 - 15 cm	2290	47	1.48	5.3	1200	69	34	0.7	2	3.0
15 - 30 cm		$\bar{x}$ = 48.7		5.6	380	10	18	0.6	2	0.4
140 - 150W										
0 - 15 cm	448	10	4.09	4.6	550	40	53	0.8	3	1.5
15 - 30 cm		$\bar{x}$ = 44.8		4.4	240	22	76	0.5	2	0.6
170 - 180W										
0 - 15 cm	2470	52	3.41	3.8	330	53	78	0.8	2	2.8
15 - 30 cm		$\bar{x}$ = 47.5		3.9	230	25	320	0.6	4	0.8
180 - 190W										
0 - 15 cm	1220	27	1.79	4.0	440	40	70	0.7	2	2.6
15 - 30 cm		$\bar{x}$ = 45.2		4.3	520	24	180	0.6	2	0.8
200 - 210W										
0 - 15 cm	691	21	2.21	4.0	340	34	63	0.7	1	1.6
15 - 30 cm		$\bar{x}$ = 32.9		4.4	630	25	120	0.6	1	0.6

Appendix E. (continued)

Quadrat Sampling Location	Total Basal Area (cm^2)	Density	Simpson's index of diversity (inverse)	pH	ppm Ca	ppm K	ppm P	ppm NO$_3$	ppm NH$_4$	per cent o.m.
210 - 220W										
0 - 15 cm	969	36	2.90	4.2	300	34	68	0.8	2	1.9
15 - 30 cm		$\bar{x} = 26.9$		4.0	95	18	180	0.6	1	0.6
220 - 230W										
0 - 15 cm	1340	33	3.05	5.1	620	48	86	0.7	2	1.9
15 - 30 cm		$\bar{x} = 40.6$		4.9	340	28	140	0.5	4	0.6
240 - 250W										
0 - 15 cm	230	6	1.00	5.3	1000	68	145	0.9	4	2.5
15 - 30 cm		$\bar{x} = 38.3$		4.8	280	37	230	0.5	1	0.6
260 - 270W										
0 - 15 cm	1940	36	1.26	4.8	1000	110	90	0.9	2	3.8
15 - 30 cm		$\bar{x} = 53.9$		4.5	320	30	300	0.6	2	0.6
270 - 280W										
0 - 15 cm	1220	23	1.55	5.5	1400	100	89	0.9	4	3.6
15 - 30 cm		$\bar{x} = 53.0$		4.9	380	31	100	0.6	1	0.6
280 - 290W										
0 - 15 cm	1370	24	1.30	5.0	700	89	110	1.2	8	2.8
15 - 30 cm		$\bar{x} = 57.1$		4.8	380	36	180	0.7	2	0.5

Each chemical result is the average of two readings (G. Paul pers. comm.). One complete set of measurements was taken in random order before the second measurement was made. A new standard curve was prepared for the second sample reading.

a. average tree size