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Tree growth in relation to site characteristics on selected peatland sites in central Alberta

by

Antti Mäkitalo

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Tree growth in relation to site characteristics on selected peatland sites in central Alberta submitted by Antti Mäkitalo in partial fulfilment of the requirements for the degree of M.Sc.

A.K. Hellum
Supervisor

James Beck Jr.

Richard L. Rothwell

Robert T. Hardin

Date September 26, 1985

Abstract

The relationships between tree growth and site characteristics were examined on selected peatland sites in central Alberta. The study had a two-fold purpose. The first part deals with tree growth in relation to peat and water nutrients and the second part with possible relationships between lesser vegetation species and tree growth. The second part included tree growth comparisons among different vegetation classes established by Härkönen (1985). The possible relationship between basal area of black spruce and tamarack with lesser vegetation species was also investigated.

The study included two separate peatland areas which were systematically sampled for tree and vegetation data. The sample plots were later subsampled for stem analysis, and water and peat quality.

Tree growth was defined as being top height at the breast height age of 45 years. Mean site index curves were established for black spruce (*Picea mariana* (Mill.)) and tamarack (*Larix laricina* (L.)). These curves were used to adjust top height at 45 years.

Tamarack growth showed a stronger relationship both with site nutrients and lesser vegetation species than black spruce in the richer and wetter peatland area. In the drier and poorer peatland area, black spruce growth correlated with site nutrients but not with lesser vegetation species. No correlations could be established between the vegetation

classes by Härkönen (1985) and tree growth.

Basal area of black spruce correlated well with individual lesser vegetation species in both peatland areas.

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I. INTRODUCTION

The peatland area of the world is estimated to be about 422 million hectares (Kivinen, Pakarinen, 1981). Of this total peatland area approximately 150 million hectares are in the Soviet Union, 112 million hectares in Canada, 48 million hectares in USA and 10 million hectares in Finland. (Heikurainen, 1971a). These figures are somewhat different depending on the literature cited (e.g. Korpijaakko and Woolnough, 1977). In Alberta, peatlands are estimated to cover about 800,000 hectares of the surface area (Korpijaakko and Woolnough, 1977) and about one-fourth to one-third of the forested area of the province (Slack *et al.*, 1980).

A. Definition of Peat and Peatland

Peat is an organic type of soil which consists of incompletely decomposed organic material deposited *in situ* (Päivänen, 1980). Cajander (1913) defines peatland in two ways:

1. Geologically, peatlands are made up of layers of peat on mineral soil.
2. Biologically, peatlands support special plant communities characterized by mire vegetation such as:

    Sphagnum sp.
    Carex sp.
    Eriophorum sp.
    Trichophorum sp.

Mire shrubs (e.g. *Ledum* sp., *Betula* sp.)

Moore and Bellamy (1974) define peatland and peat as follows:

> "Peatland is an unbalanced system where the production of organic material exceeds the rate of respiration and degradation. The result is an accumulation of a proportion of this production as an organic deposit."

Conditions have to be favorable for the above mentioned situation to occur. This usually means a relatively high water table due to disturbance or impedance in the circulation of water and therefore only part of the precipitation cycles back to rivers and lakes. A major part accumulates in specific areas causing the rise of the water table. The high water table leads correspondingly to incomplete decomposition of organic material which results in the beginning of peat formation.

B. Different Types of Peatlands

Peatlands are usually divided into two broad categories:

1. Ombrotophic mires
2. Minerotrophic mires

The basic difference between these two types of peatlands is in the way water and nutrients are received (Heikurainen, 1971a). An ombrotrophic mire gets its water and nutrients mainly in precipitation whereas a minerotrophic mire receives nutrients and water from surrounding mineral soils in ground water and surface runoff. Ombrotrophic mires are usually very nutrient poor and relatively dry. Minerotrophic mires, on the other hand, are richer in nutrients but often considerably wetter.

The word bog usually implies an ombrotrophic peatland with a convex surface. Ruuhijärvi (1982) defines an ombrotrophic raised bog as follows:

> "Ombrotrophic raised bog develops where the peat deposit grows thick enough to insulate the surface vegetation from the effects of minerotrophic mire waters in which case the atmospheric input becomes the only source of additional nutrients."

According to Stanek (1977a) a bog is "all classes of wet, extremely nutrient poor, acid ombrotrophic mires with the vegetation in which Sphagnum species play a very important role usually supporting shrub and tree vegetation, and the remains of which make up a major part of the organic horizon".

The word fen is often used referring to minerotrophic mires. In addition to a continuous supply of nutrients, the water of a fen is rich in oxygen. Due to strong flooding in the spring and early summer and to relatively low evapotranspiration, many minerotrophic mires remain saturated for long periods, preventing significant accumulation of Sphagnum, especially *Sphagnum fuscum* peat (Ruuhijärvi, 1982). Usually a fen has a less acidic condition than an ombrotrophic bog because it forms in low-lying areas which receive external seepage and drainage waters. Fens are commonly sedge-rich areas with a substrate which has a high organic matter content and an alkaline reaction; Sphagnum species are usually rare or absent, whereas minerotrophic mosses, herbs and shrubs are abundant (Stanek, 1977a).

Little is known about peatlands in Alberta and only a few studies describing the mires in the province have been published (e.g. Lewis and Downing, 1926; Lewis, Downing and Moss, 1928; Moss, 1953; Vitt *et al.*, 1975; Slack *et al.*, 1980). Compared to Scandinavia, climatological conditions in Alberta are relatively dry for peat formation. Most of the precipitation falls during the summer months (Atlas of Alberta, 1969; Päivänen, 1980). Because peatlands collect water from the mineral soils surrounding them, the summer rains may explain why peat formation occurs in Alberta (Päivänen, 1980).

The continental climate and the calcareous nature of the mineral soils in most of the province have led to the extensive development of fen vegetation with truly ombrotrophic conditions being absent (Slack *et al.*, 1980). Therefore all of the patterned peatlands can be considered fens in the sense that minerotrophic conditions prevail (Vitt *et al.*, 1975). As a result a large proportion of these fens can be regarded as medium or rich fens. However, where precipitation is slightly higher and the parent material is not as minerotrophic, poor-fen vegetation may develop.

C. Factors Affecting Forest Growth on Peatlands

It is commonly known that trees show relatively poor growth performance on peatlands. On some peatlands no merchantable timber can be found and even totally treeless peatland areas exist. However, occasionally timber production on mires may exceed that of mineral soils. This great variation in tree growth on peatland sites is mainly due to two factors: the water table on site and the nutrient status of the substrate (Heikurainen, 1971a).

A high water table can inhibit forest growth even if a large amount of nutrients is available. The roots of trees cannot survive if the water table is too high, due to poor aeration. This leads to reduced growth or even death if the site is completely saturated for long periods (Fowells, 1965). High water tables also accelerate the growth of Sphagnum moss which may prevent germination of seeds or growth of young seedlings (Le Barron, 1945; Roe, 1949; McEwen, 1966; Stanek, 1968a).

High water tables affect the rooting pattern of trees. Generally, trees have two kinds of root systems. Some species tend to have a taproot, penetrating relatively deeply in the soil, thereby offering good support against heavy winds. Other species have a rather shallow, lateral root system making them susceptble to windthrow. Sometimes lateral roots may develop sinkers as the major support against winds (Fowells, 1965). However, species that typically grow a taproot (e.g. most pines) show a different kind of development when growing on sites with a high water table (Heikurainen, 1971a). Here they tend to grow a lateral root system existing in the surface layer of the soil where the aeration is better (Heikurainen, 1971a). Some other species like spruce, typically having a lateral root system, are able to grow adventitious roots which is an important factor on wet sites where older roots cannot survive because of high water table or fast growing Sphagnum moss (Fowells, 1965).

The chemical characteristics of peat soils differ considerably from the corresponding properties of mineral soils (Kurki 1982, Heikurainen, 1971a). The nature of the mineral soil and bedrock both underlying and adjoining the peatland and the degree to which the peat has undergone decomposition have an effect on peat properties (Kurki, 1982).

Peat soils are generally considered to be more acidic than mineral soils often having pH-values in the range of 3.5-5.0 (Heikurainen, 1971a). Some peat soils, rich in calcium, may however, have pH-values close to neutrality. (Heikurainen, 1971a).

The nitrogen content of peat soils is commonly higher than mineral soils (Heikurainen, 1971a). However, much of peat nitrogen is fixed in organic compounds and exists largely as poorly soluble proteins (Kurki, 1982). Some nitrate may be present in well drained peat soils (Walmsley, 1977). It is known that plants use nitrogen in the form of ammonium NH_4^+ but whether or not it is present in peat soil is hard to measure since it is utilized quickly by plants (Tamm, 1950). There are two factors influencing nitrogen release and its availability (Walmsley, 1977): the total content of nitrogen in the soil and microbial activity.

These two factors are both affected by pH (Walmsley, 1977). Due to the fact that the ratio of carbon to nitrogen decreases as peat decomposition advances, the nitrogen content of the peat substrate is higher than that of the peat material composing it (Kurki, 1982).

Most peats are relatively poor in calcium (Heikurainen, 1971a). Both total and exchangeable contents of calcium are, on the average, largest in Bryales-Carex peats and smallest in Sphagnum dominant peats (Kurki, 1982).

Magnesium contents of peat are usually low. However, plants need magnesium in only fairly small amounts and it is not usually the limiting factor for forest growth (Heikurainen, 1971a).

Organic soils tend to be low in potassium (Walmsley, 1977). This is probably because there is little mineral matter that is capable of releasing potassium over time or fixing applied potassium (Walmsley, 1977). Heikurainen (1971a), on the other hand, assumed that the low potassium contents in the peat soils resulted from potassium being in an easily soluble form in the peat and is thus often carried away by water. In some cases, potassium is considered the most limiting nutrient on peatlands for forest growth (Heikurainen 1971a).

Peat soils tend to be poor also in phosphorous (Stanek, 1977a; Heikurainen, 1971a). Of the total phosphorus content existing in the peat, the largest proportion (approximately 75%), occurs in an organic form (Kaila, 1956). Many investigators have found an increase in phosphorus solubility as pH increases (Urvas, Sillanpää, Erviö, 1979).

D. Means to Improve Forest Growth on Peatlands

Because forest growth on peatlands is inhibited by a high water table and deficiency of available nutrients, and because organic soils are colder than adjacent uplands, tree growth is hampered. To improve forest growth on peatlands the water table has to be lowered considerably and sometimes fertilizers have to be applied to supplement or balance the nutrient status.

The water table can be lowered by drainage leading the excess water away from the area to a local water system. As a result, hydrological conditions become closer to those of mineral soils.

The lower water table offers better aeration for tree roots and this has a great impact on growth.

Better aeration in the peat also causes mobilization of nutrients. This is due to increase of available oxygen in the substrate. After drainage there are considerably more nutrients available for vegetation than before (Heikurainen, 1971a).

The influence of drainage on soil temperature is complex. Drainage decreases the heat capacity of the peat which means that after drainage, soils warm up faster but also cool down quicker than before (Heikurainen, 1971a). This can be detrimental because the possibility of damaging frosts in the late spring increases with decreasing heat capacity. On the other hand, if cold temperatures do not exist, decreased heat capacity may prolong the growing season and have a positive effect on tree growth.

The conductance of heat in the peat is smaller than that of mineral soils (Heikurainen, 1971a). This means that it takes a longer time for energy to penetrate and warm organic soils than mineral soils. The drier the peat the smaller the conductance of heat (Heikurainen, 1971a).

However, not all the effects of drainage on soil temperature are negative. Drainage causes compaction of peat layers which increases both the heat capacity and the conductance of heat, thus decreasing the negative effects of drainage mentioned above. Drainage also decreases evapotranspiration which can improve temperature conditions. Improved forest growth due to drainage has a positive influence on temperature. With development of a forest stand temperature extremes are reduced. Maximum temperatures decrease but minimum temperatures increase correspondingly

(Heikurainen, 1971a).

E. Forest Growth After Drainage

Several experiments and large scale programs have shown that drainage can have considerable effect on forest growth and yield. In North America, where drainage has not been used in forest management, most of the information about improved forest growth is based on individual experiments of fairly small scale. Averell and McGrew (1929) found that drainage significantly increased the volume growth of trees. The study also paid attention to the responses of different tree species and the effects of different peat and ditch spacings on growth. Le Barron and Neetzel (1942) observed the growth rate of young saplings accelerated two to four times that of controls between the drainage ditches. Satterlund and Graham (1957) found an immediate beneficial effect on leader growth of black spruce (*Picea mariana* Mill. B.S.P.) due to removal of excess water from a Sphagnum bog. Payandeh (1973 a,b) analyzed a forest drainage experiment in northern Ontario and concluded that both the volume and value growth of submarginal peatland black spruce can be improved significantly by drainage. Similar results are also described by Zon and Averell (1930), Lundberg (1952), Stanek (1968b) and McEwen (1969).

In Finland, where forest drainage was started as early as the nineteenth century, extensive drainage programs have been carried out and the results have generally been positive. Drainage have been found to bring the volume growth of peatlands up to the level of mineral soils in most cases (Heikurainen, 1971a). About 55% (i.e. 5.5 x 10^6 ha) of the total peatland area of Finland has already been drained (the goal being 6.5 x 10^6 ha). According to the National Forest Inventory of Finland the total increment of forests in Finland increased about 2.2 million m^3/year during the ten year period between 1948 and 1958 because of drainage (Heikurainen, 1961). In 1982 the increased forest growth due to drainage was estimated to be roughly 8 million m^3/year and it is estimated to reach approximately 17 million m^3/year by year 2000 (Heikurainen, 1982b).

The increases in harvestable wood are usually obtained between 15 and 20 years after drainage. In 1982 the increase in the allowable cut for Finland was estimated to be 2 million m^3/year due to drainage work in the 1960's and before. The increase in the allowable cut is expected to reach 8-9 million m^3/year by the end of the century and the maximum of 15 million m^3/year approximately 40 years from now (Heikurainen, 1982b). The allowable cut in Finland is presently around 50 million m^3/year so the figures describing the increase are significant both in annual increment and annual cut due to drainage.

F. Criteria to Use When Considering Drainage

If drainage is decided upon as a method to increase the productive forest land base, there are several factors to consider when determining which peatland areas to drain.

There should be a classification system of one sort or another so that one would be able to predict post-drainage growth of peatland forests with the help of some easily recognizable parameters found on virgin peatlands. These parameters should indicate the nutrient status of the peatland, as a basis for prediction of future growth subsequent to drainage.

Drainage costs should be considered so that the money spent on draining a site yields returns as quickly as possible in terms of tree growth. This requires some consideration of ditch espacement and initial growing stock.

In Finland several studies of post-drainage timber production of peatlands have focused on the potential tree growth on sites of varying quality and fertility. The major factor influencing the growth and development of trees has been found to be macroclimate, especially temperature (Heikurainen, 1982a).

Finnish peatlands have been classified into site types (Cajander, 1949; Heikurainen, 1972). The classification is based on the theory of forest types by Cajander (1909; 1913; 1926; 1949). This theory states that different ground vegetation communities reflect the overall ecological environment indicating the growth potential of the site. In the peatland classification system, the vegetation simultaneously indicates both the level of fertility and the wetness.

In Finland all types of mires which are drainable have been inventoried and ranked according to their potential post drainage timber production. Site fertility has been defined by the type of lesser ground vegetation on site. Fertility combined with macroclimatic parameters gives a site quality index for all peatlands. This site quality index is then used to estimate the post drainage forest growth for the whole country within all the site types.

Even though the system has been used extensively and successfully to determine drainable peatland areas, only a few research projects have been carried out to compare tree growth on different peatland site types. Westman (1981) found a correlation between the fertility and the site type (i.e. forest growth potential) but the study did not include comparisons of tree growth among the sites. The tree growth aspect has been studied by Lukkala (1929), Heikurainen (1959), Seppälä (1968, 1969) Keltikangas (1945) and Huikari (1974). These studies mainly confirmed the positive effects of drainage on tree growth. A recent study was conducted by Laine and Starr (1979) on the nature of stand growth from four different main site types.

Laine and Starr (1979) studied sites drained 20-30 years before stand measurements and concluded that the post drainage increment of the stand was dependent upon the site type. This confirmed the efficacy of using the site type classification for evaluating the suitability for forest drainage.

Whether or not different peatland site types exhibit different characteristics in terms of tree growth in virgin conditions is not known. Only one study has been conducted on this matter in Finland (Heikurainen 1971b) and no clear correlation between stand volume or increment, and site type was found.

Canadian wetlands have been classified by Jeglum, Boissonneau and Haavisto (1974), and Zoltai, Pollett, Jeglum and Adams (1975). These classifications are of general nature and do not focus attention specificly on forest drainage. Forest drainage aspects in Canada have been studied by Heikurainen (1968) and Stanek (1977 b).

Some pilot studies have been carried out in Alberta on certain peatland areas and their suitability for forest drainage (Päivänen, 1980). According to Päivänen (1980) there are good possibilities in Alberta to increase the growth of trees suffering from excess water in virgin peatlands. Päivänen's opinion is based on the climatological data of Alberta, and the actual response of black spruce and tamarack to drainage in many areas along highways where drainage channels have been dug at the time of road construction.

To start a drainage program in Alberta would require definite criteria to identify peatlands that are drainable, i.e. whose post-drainage timber production would give the greatest return as quickly as possible. These criteria should include parameters that are easily recognizable by practical foresters. In trying to develop a system similar to that in Finland one faces certain problems. In Finland the classification for forestry purposes was derived from drained peatlands by observing the development of these particular areas after drainage. In Alberta this is not possible since no peatland drainage programs or even individual experiments have existed in the province until recently.

Secondly, most of Alberta's peatlands are considered fens with fairly high pH values and these kinds of peatlands are usually not recommended for drainage because of the sensitivity of their nutrient balance (Heikurainen, 1983).[1] For this reason the nutrient relationships in areas suggested for drainage should be determined to monitor possible detrimental changes in the nutrient regime.

Only limited literature exists about the nutrient regime of peat soils and its relation to tree growth. Most of the authors have studied the relationship between the foliar concentrations of selected nutrients and the productivity, i.e. site index of peat soils (Gagnon (1964), Leyton and Armson (1965), Watt and Heinselman (1965), Lowry and Avard (1967), Tilton (1978)).

---

[1] Personal communication, May 15, 1983.

Paarlahti (1971) studied the relationship between height growth of Scots pine (*Pinus sylvestris* L.) and the nutrient concentrations in the foliage and in the peat after N-K-P fertilization. Most studies pay attention to fertilization effects (Dickson, 1971; van Nostran, 1979; Morrison *et al.*, 1979) or seedling nutrition and seedling growth characteristics on different peat types (McEwan, 1966; Swan, 1970; Richardson, 1979; Jeglum, 1981) rather than paying attention to the relationship between peat nutrients and tree growth directly.

The same situation exists in research on virgin peatlands and their vegetation in relation to tree growth. Vallee and Lowry (1970) found that lesser vegetation species native to black spruce stands can be used to estimate site fertility with a reasonable degree of accuracy. The authors studied the relationship between Plonski's (1956) site index for black spruce and forest vegetation. However, peatland sites in this study formed only one stratum and no comparison within peatland sites could therefore be carried out.

G. Objectives

Recognizing the need of research in the area of virgin peatlands in Alberta and the rest of the world, especially as applied to forestry, the objectives of this study were formulated.

The primary objective of this study was to test for relationships between tree growth and site characteristics of selected peatlands in central Alberta.

Two questions emerged from this which led to the formulation of two null hypotheses.

1. By assuming that the hydrological conditions in the study area were fairly constant, it was expected that differences in nutrient regimes would lead to differences in tree growth. This was the basis for creating the first null hypothesis:

Ho: There is no correlation between tree growth and site nutrients in the study area.

2. Cajander's (1913) theory of forest types was used to formulate the second hypothesis. This theory assumes a strong correlation between different ground vegetation types and ecological environment. Vegetation is believed to indicate the true growth potential of the site.

The second null hypothesis was therefore:

Ho: There is no correlation between tree growth and lesser vegetation communities within selected peatland ecosystems.

II. STUDY AREA

A. Location and General Characteristics

The study area consisted of two separate peatland areas: 1. Saulteaux River Area - a part of a large peatland area adjacent to the Saulteaux River and, 2. Athabasca Highway Area - a part of a 'forested bog' area east of the junction of Highways 2 and 44 south of Hondo. Both areas are located in the Slave Lake Forest District of the Alberta Forest Service (Figure 1).

Experience and knowledge about Finnish peatlands affected the decision to use only two peatland areas in the study. In Finland a peatland area often consists of several different site types; a gradient from poor to fertile sites exists on many peatlands (Heikurainen, 1971a). This was anticipated also in this study.

Mean temperature in the study area varied between -17 C and -15 C in January, and between 16 C and 17 C in July during the thirty-year period of 1931-1960 (Atlas of Alberta, 1969). The mean annual precipitation during the same period was 457-508 mm and more than 50% of the annual precipitation in this area fell during the growing season (Atlas of Alberta, 1969).

The two areas were different in terms of their ecology. The Saulteaux River area was very heterogeneous in terms of tree cover, and could be considered 'real' peatland having peat depths from 30 cm up to 150 cm and more.

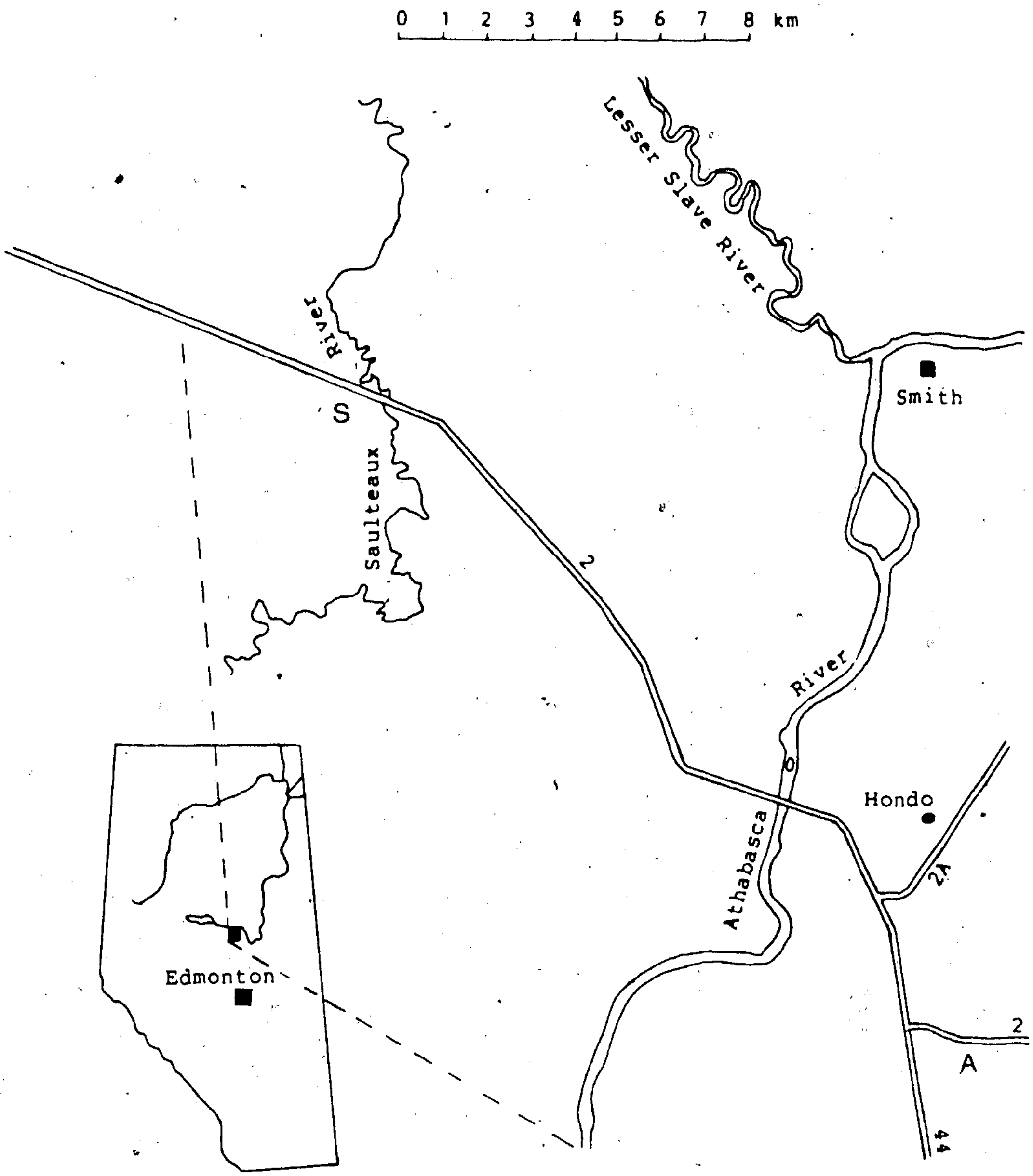

Figure 1 - Map showing the locations of the two study areas in Alberta. S = Saulteaux River Area, A = Athabasca Highway Area.

The Athabasca Highway area was a fairly homogeneous, bog looking peatland area where the peat depth rarely exceeded 50 cm. These two areas were analyzed separately due to their differences.

B. Growing Stock in the Study Area

Mensurational parameters of the growing stock can be seen in the appendix in tables A.1 and A.2. As the tables indicate the variability in basal area within both areas was great. The two areas were not significantly different in basal area. The mean basal area in the Saulteaux River area was 13.1 m^2/ha with the standard deviation of 8.4 m^2. The corresponding values in the Athabasca Highway area were 11.6 m^2 with the standard deviation of 6.8 m^2. Maximum basal area in both areas was close to 30 m^2/ha and some plots were treeless. Other parameters such as height and dbh (diameter at breast height) showed less variation.

With the exception of a few scattered older trees which escaped past fires, both areas were even-aged. The mean age at breast height in the Salteaux River area was 54.8 years with a standard deviation of 21.9. In the Athabasca Highway area the mean age at breast height was 42.5 years having a standard deviation of 7.2. The difference in age between the two areas was statistically significant.

The two main tree species growing in the study area were black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (L.)). Some white spruce (*Picea* *glauca* (Moench.) Voss.) and paper birch (*Betula papyrifera* Marsh.) were also found but since the occurrence of these species was scattered and infrequent they were ignored in the analysis.

C. Some Silvical Characteristics of the Tree Species in the Study Area

Black spruce

Black spruce is one of the most important commercial tree species in Canada. In eastern Canada it is the most common species used by forest industry (Ketcheson and Jeglum ,1972; Hearnden, 1975). In western Canada black spruce is of less importance. Species like lodgepole pine (*Pinus contorta* Dougl.), white spruce and Douglas fir (*Pseudotsuga menziesii* (Mirbel.) Franco) are more important here.

Black spruce shows great variation in dimensions within the range of habitats it occupies. On better sites it may reach the height of 30 m and a diameter of 80 to 90 cm (Heinselman, 1957, Fowells, 1965). On poor sites its maximum height may be less than 6 m and diameter less than 5 cm (Fowells, 1965). The crown form of black spruce is usually irregular.

Root development of black spruce is characteristically shallow and it has no taproot (Fowells, 1965). Black spruce is able to develop adventitious roots, particularly in peatlands due to the high water table and rapidly growing Sphagnum moss (Fowells, 1965). Sinker roots may develop on older trees.

Black spruce has a large ecological amplitude. It grows from sea level to elevations of 2,000 m, and from dry, shallow, or deep sands to wet, completely saturated peatland areas (Heinselman, 1957).

On moist loams or well-drained uplands black spruce is usually accompanied by balsam fir (*Abies balsamea* (Mills)), white spruce, white birch and trembling aspen (*Populus tremuloides* (Michx.)) (Fowells, 1965). Sometimes pure black spruce stands can be found on these sites and according to Fowells (1965), it is most productive on these particular sites.

Although on very moist sites black spruce can form pure stands, it often grows with balsam fir, white spruce, white birch, and balsam poplar (*Populus balsamifera*, L.) (Fowells, 1965).

On peatlands sites where the organic layer does not exceed 1 m or on wet clay soils, black spruce grows either in pure stands or accompanied by white spruce, balsam fir, trembling aspen, balsam poplar and tamarack (Fowells, 1965). On these sites feather mosses or Sphagnum mosses or sometimes both form the ground vegetation with shrubs such as *Ledum* sp. and *Alnus* sp. (Heinselman, 1957).

On peatlands with a thick peat layer and very wet conditions, black spruce forms pure stands or grows sometimes with tamarack (Heinselman, 1957). Sphagnum species are dominant in the ground vegetation (Heinselman, 1957; Vincent, 1965; Jeglum, 1971a). As mentioned before, black spruce grows best on well-drained loamy soils, but being less competitive than other species it cannot occupy these sites (Fowells, 1965). It has been suggested that one of the reasons black spruce survives on extremely wet sites is because of its ability to grow adventitious roots. This is, however, questionable because all spruce species have the same characteristics and few of them can grow on wet sites. In Finland the most common tree species on peatlands is Scots pine (*Pinus sylvestris*) which does not possess the ability to grow adventitious roots. It is obvious that a certain advantage exists with the characteristic of being able to grow adventitious roots on wet sites, but other factors like the ability to grow in cold soils with nutrient deficiencies are important.

In the study areas black spruce was found to associate especially with the two feather mosses *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens*(Hedw.) BSG. *Ledum groenlandicum* Oeder was also common in the vegetation under black spruce. Sphagnum species were not dominant which is probably due to the fen-like conditions prevailing in both of the areas under study.

Most black spruce stands are said to be of fire origin and have an even-aged structure (Fowells, 1965). In spite of often being the first species after a fire, black spruce is not a typical pioneer species. It usually forms climax stands (Stanek, 1968a).

In both of the study areas, black spruce formed pure stands or mixed stands with tamarack. The mean height of black spruce in the Saulteaux River area for the trees of 5 cm or more at breast height was 6.8 m having a standard deviation of 1.6 m. The estimated mean age of black spruce in this area was 51.1 years at breast height with a standard deviation of 12.5 years.

In the Athabasca Highway area the mean height of black spruce was 6.7 m for the trees of 5 cm or more at breast height with a standard deviation of 1.8 m. Corresponding estimates for age at breast height were 44.6 years with a standard deviation of 7.2 years. It was estimated that black spruce reached breast height of 1.3 m on the average in 16 years in both of the study areas.

Tamarack

Tamarack has one of the widest ranges of all American conifers and it grows in extremely varied conditions (Roe, 1957). Precipitation over its range varies from 180 mm to 1400 mm and both the length of the growing season and the temperature during the growing season have a great variation in different geographical areas (Fowells, 1965).

The height of tamarack varies from 15 m to 25 m and according to Fowells (1965), in Alberta tamarack reaches its maximum height (15 m) and diameter (30 cm) in 80-95 years.

Tamarack typically has a shallow, compact root system and does not grow a taproot on peatlands whereas adventitous roots are common on wet sites (Roe, 1957).

According to Roe (1957), tamarack is one of the fastest growing of the conifers of the boreal forest when growing on fertile well-drained sites and by far the fastest growing of the species growing on peatlands. Roe (1957) stated that in Alberta tamarack easily outgrows black spruce on peatland sites if enough growing space is available.

According to the tree data from the study area, the top height - mean height of the tallest stems - of tamarack at the breast height age of 45 years was 8.3 m. The corresponding height for black spruce was 7.5 m. Mead (1978), has described a similar difference between the two species on peatlands in Ontario.

The best growth of tamarack is achieved on rich, moist, well-drained loamy soils along streams, lakes, and mires but most often tamarack is found on extremely wet, organic soils (Fowells, 1965). Tamarack is able to tolerate high soil moisture, acidity and low soil temperatures better than many other local tree species, but long periods of heavy flooding will kill it (Denyer and Riley, 1964).

Tamarack can form pure even-aged stands of considerable extent but is often associated with black spruce and white spruce (Fowells, 1965).

Tamarack is a very shade intolerant species. It has to become dominant after the first 3 to 4 years of its development or it will not survive (Roe, 1957).

Tamarack is normally the first pioneer tree species invading peatland areas (Fowells, 1965). It is not able to reproduce under its own shade like some other species so it is usually succeeded by black spruce on poorly drained, acid peat or by black spruce, white spruce, and balsam fir (*Abies* *balsamea*) on better organic soils.

In the study area the mean height of tamarack for trees 5 cm or more at breast height was 8.4 m with a standard deviation of 2.5 m. The estimated mean age for tamarack was 64.2 years at breast height having a standard deviation of 39.5 years. In some of the plots there were a few extremely old tamaracks that had obviously survived disturbance for a long time. These old trees contributed significantly to the higher mean age and standard error values. For tamarack it took on the average of 14 years to reach breast height.

D. Chemical Characteristics of the Study Area

The pH values for peat and water in both areas were relatively high (see Table A.3). The average pH of the water in the Saulteaux River area was 6.4 with a standard deviation of .7. In the Athabasca Highway area the corresponding figures were 7.0 and .3. The pH values for peat for both areas were respectively 6.2 with a standard deviation of .6 in the Saulteaux River area and 7.0 with a standard deviation of .4 in the Athabasca Highway area. These peat pH values exceed the recommended optimal range of 5.0-5.8 for nutrient availability (Lucas and Davis, 1961).

The physiognomy and the pH values of the study areas can be used to classify these peatlands as fens. The Saulteaux River area is an intermediate fen (pH=5.2-6.4) and the Athabasca Highway area a transitional rich fen (pH=5.8-7.0) (Sjörs, 1952).

III. METHODS AND ANALYSIS

A. Experimental Design

The areas were systematically sampled using a random starting point. First a grid of points was laid out on an aerial photograph (see Plates 1 and 2). By using this grid sampling was done along parallel transects. The distance between the transects was 300 m and the distance between plots was 150 m.

Circular plots of 0.01 ha were used and in each plot the following parameters of trees above 5 cm in diameter at breast height were recorded:

tree species
diameter at breast height (cm) to the nearest cm
height of the tree (m) to the nearest .5 m
age of every third tree
radial growth of every third tree

Both the age and the radial growth were determined at breast height.

The vegetation of each plot was analyzed on two to four smaller plots (0.25 m²) inside the main plot in addition to all the tree measurements. A total of 71 sample plots were established in the Saulteaux River area and 39 in the Athabasca Highway area.

The sample plots were subsampled for stem analysis and for water and peat quality. In the Saulteaux River area the subsample was distributed in such a way that it covered the

Plate 1 - Aerial photograph with the grid of sample plots in the Saulteaux River Area.

Plate 2 - Aerial photograph with the grid of sample plots in the Athabasca Highway Area.

maximum number of different site types. This was done by stratifying the initial data into four groups:

black spruce 76 - 100% of basal area
black spruce 51 - 75% of basal area
black spruce 26 - 50% of basal area
black spruce 0 - 25% of basal area

Within each stratum the plots were subsampled randomly. In the Athabasca Highway area this procedure was not followed because black spruce was practically the only species in the area. The total number of subsample plots in the Saulteaux River area was 37 and in the Athabasca Highway area 15. These figures were based on the estimated required sample size for the chemical analysis of the peat and water.

An attempt was made to measure the water table depth in each subsample plot to assess its effect on tree growth. This was done by using two different reference points: estimated average ground level between hummocks and hollows, and the level where most of the trees were growing on each sample plot.

B. Analysis

Stepwise multiple regression analyses were used in combination with analyses of variance to evaluate tree growth. Water and peat nutrients were used as independent variables in the multiple regression analyses. The same procedure was utilized when trying to establish a relationship between tree growth and species of ground vegetation. Analyses of variance were used to test for differences in tree growth among Härkönen's (1[illegible]85) vegetation classes.

Selecting the Dependent Variable for the Multiple Regression

For the multiple regression analysis, the following models were created:

1. Tree Growth = $A + B_1X_1 + B_2X_2 + \ldots B_n\ X_n$

$X_1 \ldots X_n$ = peat and water variables

2. Tree Growth = $A + B_1Y_1 + B_2Y_2 + \ldots B_n\ Y_n$

$Y_1 \ldots Y_n$ = plant species

In both of the models tree growth was used as the dependent variable. At this point it was necessary to determine what mensurational parameter should be used to describe tree growth. It was considered important that the tree growth variable shoul[illegible] express the actual growth potential of the site adequately. Several parameters were considered.

The stand volume, stand basal area, as well as the basal area increment were all rejected as the history of each plot was not known. It is impossible to tell whether the reasons for differences in these parameters are due to differences in site productivity or some other factors such as circumstances at the time of seed fall.

The mean basal area, mean dbh and mean basal area increment were also rejected. All of these parameters are very dependent on stand density on the site (Assmann, 1970).

Because tree height depends very much on site and relatively less on density (Loetsch, Zöhrer and Haller, 1973) top height at a certain age was chosen as the dependent variable in the models. It was assumed that top height was an index of site quality in the study area.

There are many definitions for top height (see Loetsch, Zöhrer and Haller, 1973). Most often it is the mean height of a fixed or relative number of tallest or largest trees in the area. In this study top height for each plot was derived by averaging the height of the tallest stems - each having an age observation - on the plot, in such a way that 10% of the total number of trees per plot were included. However, no suppressed trees were selected. This was done by acquiring frequency distributions of height for each plot and studying these distributions. Top height was determined for both tree species separately.

Because height of each particular tree is a function of age, the age has to be taken into account to be able to compare plots of different age. This was done by creating site index curves for black spruce and tamarack growing on the study area. First an attempt was made to prepare the site index curves by using the temporary sample plot data. However, the range of age classes was so narrow that this was impossible. Top height of each plot for both species can be seen in Figures A.1 and A.2 in the appendix.

To overcome this problem of the narrow age range, stem analysis (Herman *et al.*, 1975) was done for both species. In the case of black spruce 22 trees were analyzed and for tamarack the analysis consisted of 16 trees. The sample trees were selected randomly but only dominant and codominant trees were chosen.

The stem analysis data were used to prepare site index curves for both species. These curves were created applying the guide curve technique by Bruce and Schumacher (1950) with the help of linear regression.

This technique produces an average site index curve and all the other curves above or below the mean curve are harmonized with it. In other words, all the possible curves are proportional to the mean curve i.e. differences between sites result in similar differences in the rate of height growth at all ages (Bruce and Schumacher, 1950). The reference age in this study was 45 years in both species of trees.

The guide curve technique is sound only if no correlation exists between age and site quality (Curtis, 1964). This problem was partly avoided by setting the reference age at 45 years at breast height and including only data points lesser than or equal to 45 years in the analysis. In the black spruce stem analysis only two trees out of 22 were younger than 45 years at breast height. In the case of tamarack the number of stems in the analysis was 16 of which 14 were at least 45 years old. The possible age-site correlation was checked in both cases by comparing the mean height of all the stem analysis trees at their highest common age against the mean height of those trees at least 45 years old (20 black spruce, 14 tamarack) at the same age. The highest common age was 35 years for black spruce stem analysis trees and 30 for tamarack stem analysis trees at breast height. This comparison showed that no correlation existed between age and site in either species if only the data points having age lesser than or equal to 45 years were used. The reference age of 45 years was justifed also because it was close to the average breast height age of both species.

A straight line gave a better fit for both species than any curvilinear relationship. The mean site index curve for each species can be seen in Figures 2 and 3 on pages 36 and 37. The top height of 9.5 m at 45 years represented an average tamarack site. An average black spruce site had correspondingly a top height of 8.6 m.

By adjusting the top height of each plot to 45 years using the proportionality assumption of the guide curve technique as a basis, a site index was assigned for each plot. This made it possible to compare plots of different age.

Theoretically, curves describing the development of height as a function of age would not be straight lines but rather asymptotic parabolic curves. Smith (1984), however found that black spruce growing on a great variety of sites

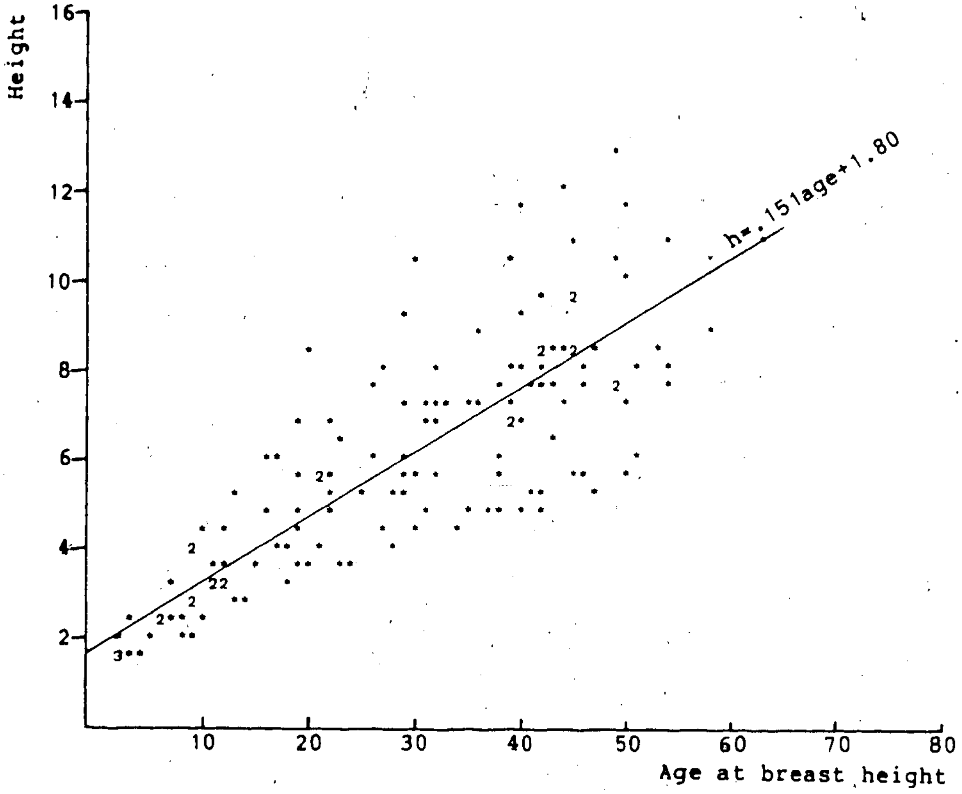

Figure 2 - Black spruce stem analysis data and the site index curve used to adjust top heights at 45 years.

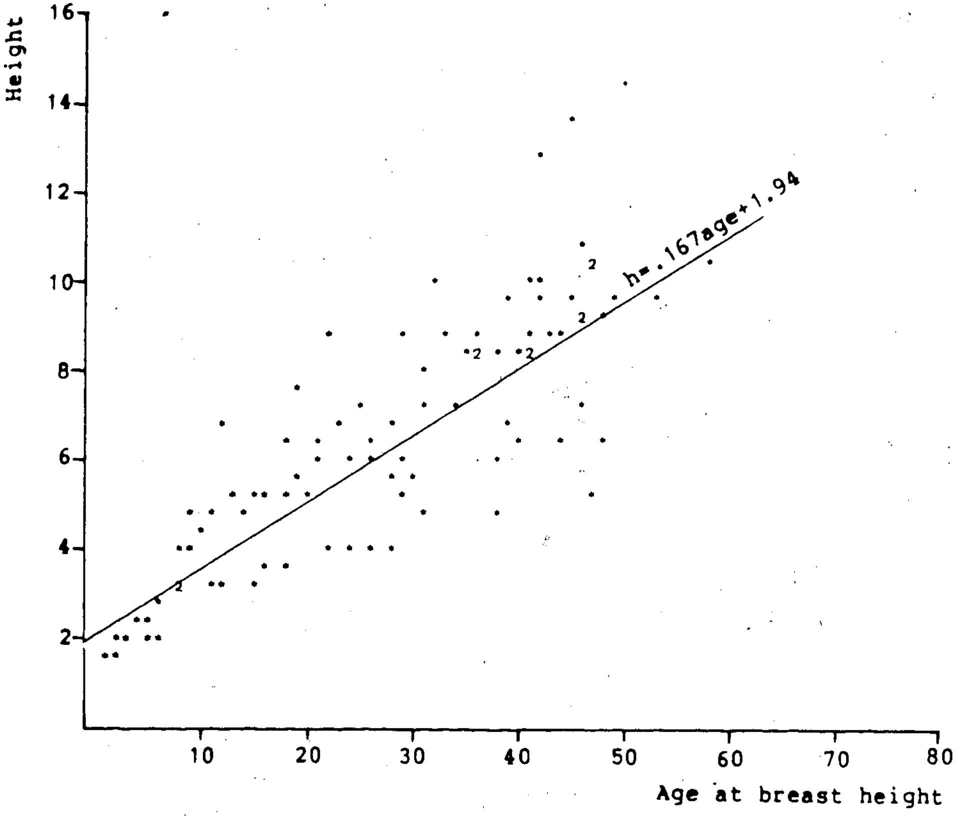

Figure 3 - Tamarack stem analysis data and the site index curve used to adjust top heights at 45 years.

did not exhibit any strong asymptotic height properties for stands up to 180 years old. Instead a linear relationship existed between the stand age and stand height.

Heger (1968) established site index curves for several tree species in eastern Canada using stem analysis data. For all the species in the study a straight line gave the best fit. Similar results have been reported by Heger and Lowry (1971) who tested applicability of Plonski's (1956) yield tables for black spruce in central and eastern Canada.

The trees used for preparing the site index curves for the study areas in this study were relatively young which probably contributed to the form of a straight line.

The adjustment of the top heights of individual plots using a straight line can be justified only if the trees to be adjusted do not represent older trees whose development could not be considered following a straight line. Fortunately, only 8 out of 70 black spruce and 4 out of 40 tamarack plots were represented by trees older than 60 years and thus the bias due to using a straight line as an indicator of site index was ignored.

In some plots both tamarack and black spruce formed the canopy and thus were selected separately to determine the top height for both species. In these plots there were two different site indices, one for black spruce and the other for tamarack. The relationship of these two site indices can be seen in Figure 4 on page 39.

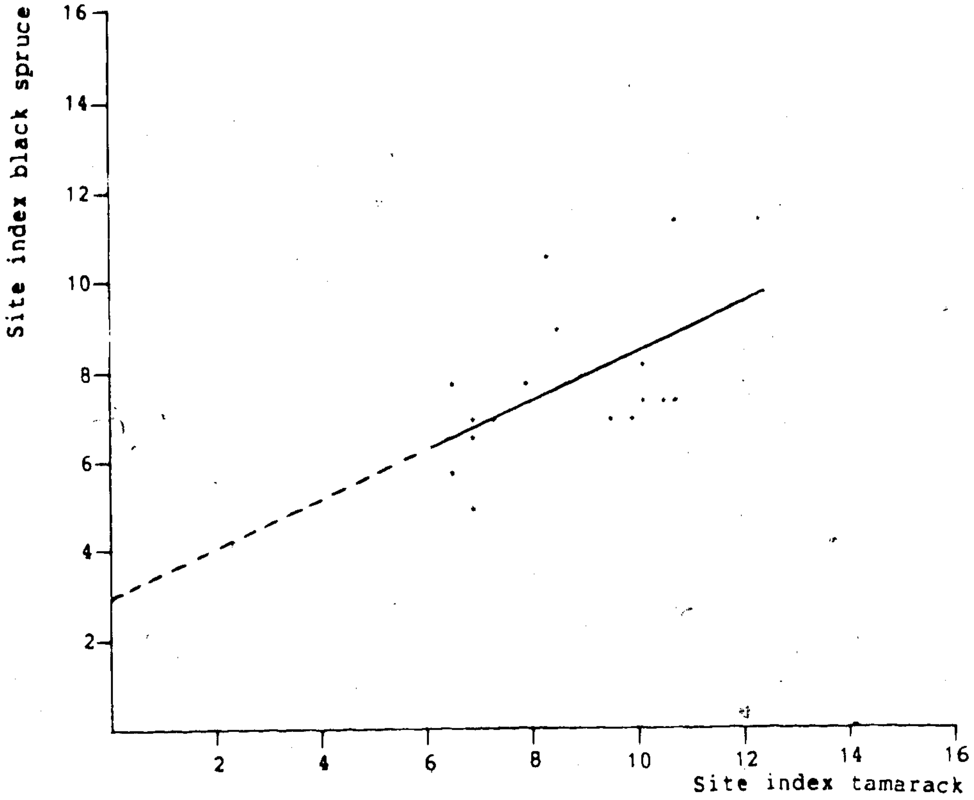

Figure 4 - Relationship of black spruce and tamarack site indices in the Saulteaux River Area.

The site index for black spruce at 45 years in the Saulteaux River area varied from 4.5 m to 11.5 m. The mean value was 7.5 m and the standard deviation 1.7 m. In the same area the tamarack site index at 45 years had a range from 4.0 m to 13.5 m with the mean of 8.3 m. The standard deviation was 2.2 m. In the Athabasca Highway area, the black spruce site index varied between 6.1 m and 12.0 m having the mean of 7.8 m and the standard deviation of 1.3 m at 45 years.

The site index variable was then used as a dependent variable in the analysis separately for both species and areas.

Peat and Water Chemistry

The peat samples were taken with a peat core sampler and were generally 30 cm deep. The water was sampled in natural depressions or other open water holes on the study sites.

Independent variables in the nutrient analysis were as follows:

Water

pH

Mg^{++}, mg/l

Ca^{++}, mg/l

Na^{+}, mg/l

K^{+}, mg/l

Peat

pH
C, total, %
C/N - ratio
NO_3-N, Ng/g
PO_4-P, Ng/g
TEC, meq/100 g
Ca^{++}, mg/l
N, total, %
NH_4-N, Ng/g
P, total, %
CEC, meq/100 g
depth, cm

All these variables were used in the stepwise multiple regression analyses to determine whether or not a relationship existed between tree growth and chemical characteristics of the peat and water.

Vegetation Analysis

Average cover percentages of different mosses and vascular plants were used in the second part of the analysis as independent variables to explain differences in tree growth. Average cover percentages of plants on smaller vegetation plots were used to represent .01 ha sample plots in the analysis.

A total of 124 different plant species were found of which 56 were mosses and 68 vascular plants. Sixty-five of these 124 plants were selected using their frequencies as criteria. At least ten observations of each species was required for getting selected. These 65 plants were then used in the stepwise multiple regression analyses in the attempt to explain differences in tree growth.

Basal area of each tree species was also regressed against plant cover to see whether or not any lesser vegetation species showed any correlation with stocking of trees.

In the last part of the analysis, the vegetation classes established by Härkönen (1985) were compared with the tree growth data.

Härkönen's classes were derived by using a FORTRAN program called TWINSPAN (Hill, 1979). TWINSPAN, a two-way indicator species analysis, is a polythetic divisive method of classification. It produces an ordination that is based on a few of the most preferential species. TWINSPAN offers a variety of options for the user, making it possible to modify the program according to the specifics of the data

The outcome of Härkönen's TWINSPAN analysis for the Saulteaux River area can be summarized as follows:

Class 1: feather moss - *Ledum* - *Sphagnum fuscum* (Schimp.) Klingg. - group

Class 2: feather moss - *Ledum* - *Sphagnum angustifolium* (Russ.) C. Jens. - *Salix* - group

Class 3: feather moss - *Ledum* - *Sphagnum warnstorfii* Russ. - group

Class 4: brown moss - *Calamagrostis* - *Sphagnum teres* (Schimp.) Angstr. ex Hartm. - group

Class 5: brown moss - *Calamagrostis* - *Betula pumila* L. - group

Class 6: brown moss - *Calamagrostis - Sphagnum magellanicum* Brid. - group

Class 7: brown moss - *Tomenthypnum - Sphagnum warnstorfii* Russ. - group

Class 8: brown moss - *Tomenthypnum - Caltha palustris* L. - group

Feather mosses here are referred as being *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) BSG. The group 'brown mosses' consists of mosses such as: *Plagiomnium ellipticum* (Brid.) Kop., *Brachytecium turgidum* (C.J. Hartm.) Kindb., *Drepanocladus* spp., *Calliergon* sp. and *Bryum pseudotriquetrum* (Hedw.) Gaertn. *et al.*. The first two, *Plagiomnium ellipticum* and *Brachytecium turgidum*, were the most important indicator species of the brown mosses in the classification (Härkönen, 1985).

For the Athabasca Highway area three vegetation classes were established:

Class 1: *Sphagnum fuscum - Betula pumila* - group

Class 2: *Sphagnum fuscum - Carex capillaris* L. - group

Class 3: non - *Sphagnum fuscum* - group

Although the number of classes in this area was three, the main division in the classification was between the sample plots with *Sphagnum fuscum* and those without it (Härkönen, 1985).

In both of the study areas a significant relationship was found between the vegetation classes, and peat and water nutrients.

Analysis of variance was used to test whether or not the site index variable was significantly different in different vegetation classes.

IV. RESULTS

A. Nutrients

Abbreviations of the statistical terms used in this chapter are as follows:

N = number of observations
M = mean value of the dependent variable
Std = standard deviation of the dependent variable
$S_{y.x}$ = sample standard deviation about regression
r^2 = coefficient of determination

In the Saulteaux River area only available ammonium (NH_4^+) and extractable calcium (Ca^{++}) had statistically significant correlations with the growth of tamarack. The regression equation computed and the contribution of each variable to the total r^2 were:

$$\text{Site Index} = 1.67089 + .01783NH_4^+ + .06057Ca^{++}$$

N=17, M=9.2 m, Std=±2.1 m
$S_{y.x}$=±1.5 m, r^2=.56

VARIABLE	r^2
NH_4^+	.48216
Ca^{++}	.08221
total	.56437

The model was statistically significant at the .01 level of probability.

Black spruce in the Saulteaux River area did not have any significant correlations with any of the independent variables. The subsample in this case consisted of 20 plots. The mean site index was 7.5 m with a standard deviation of 2.3 m.

In the Athabasca Highway area the total amount of phosphorous (P) had the highest correlation with the growth of black spruce. Phosphorus alone had an r^2 of .72 and the model was significant at the .01 level. When the total nitrogen (N) was added in the model, the r^2 went up to .87 and the model was again significant at the .01 level of probability. The regression equation and the contribution of each variable to the total r^2 were as follows:

Site Index = 2.1972 + 156.63394P + 6.34777N

N=9, M=7.5 m, Std=±1.7 m

$S_{y.x}=\pm.7$ m, $r^2=.87$

VARIABLE	r^2
P	.72095
N	.14698
total	.86793

B. Vegetation

Abbreviations of the lesser vegetation species used are as follows:

Bepu = *Betula pumila* L.

Casp = *Calamagrostis* sp.

Cadi = *Carex diandra* Schrank.

Cagy = *Carex gynocrates* Wormsk.

Smtr = *Smilacina trifolia* (L.) Desf.

Legr = *Ledum groenlandicum* Oeder

Vaox = *Vaccinium oxycoccos* L.

Vavi = *Vaccinium vitis-idaea* L.

Drve = *Drepanocladus vernicosus* (Lindb. ex C.J. Hartm.) Warnst.

Aupa = *Aulacomnium palustre* (Hedw.) Schwaegr.

Hysp = *Hylocomium splendens* (Hedw.) BSG

Plel = *Plagiomnium ellipticum* (Brid.) Kop.

Plsc = *Pleurozium schreberi* (Brid.) Mitt.

Toni = *Tomentypnum nitens*(Hedw.) Loeske

In the Saulteaux River area the following regression equation was computed to explain differences in the growth of tamarack:

$$\text{Site Index} = 9.66880 + .65926\text{Plel} - 1.12205\text{Cagy} - 2.47853\text{Smtr} - .50677\text{Toni} - .38319\text{Drve} - 1.53477\text{Plsc} + .46775\text{Casp}$$

$N=36$, $M=8.3$ m, Std=±2.2 m

$S_{y.x}=\pm 1.3$ m, $r^2=.79$

The model was statistically significant at the .01 level of probability. The contribution of each species in the model to the total r^2 was as follows:

SPECIES	r^2
Plagiomnium ellipticum	.28373
Carex gynocrates	.12010
Smilacina trifolia	.09748
Tomenthypnum nitens	.09632
Drepanocladus vernicosus	.09371
Pleurozium schreberi	.06885
Calamagrostis sp.	.03406
total	.79425

Black spruce in the same area showed weaker relationships than tamarack. The following species were selected in the model:

SPECIES	r^2
Betula pumila	.16277
Vaccinium oxycoccos	.14725
total	.31002

Both of these species were negatively correlated with tree growth of black spruce. The regression equation was as follows:

Site index = $8.00624 - 1.30038\text{Bepu} - .91899\text{Vaox}$

$N=46$, $M= 7.5$ m, $Std=\pm 1.7$ m

$S_{y.x}=\pm 2.3$ m, $r^2=.31$

The model was statistically significant at the .01 level of probability.

In the Athabasca Highway area the model consisted only of *Carex gynocrates*:

Site Index = $6.95172 + .53681\text{Cagy}$

$N=30$, $M=7.6$ m, $Std=\pm 1.3$ m

$S_{y.x}=\pm 1.3$ m, $r^2=.29$

This model was statistically significant at the .01 level of probability

When the basal area of each tree species was used as a dependent variable in the model, the results were quite different. In the Saulteaux River area the following equation was computed for tamarack:

Basal Area = $6.54179 - 1.32291\text{Cadi} + 1.76156\text{Plel} - 1.14359\text{Plsc}$

$N=71$, $M=5.9\ \text{m}^2$, $Std=\pm 6.2\ \text{m}^2$

$S_{y.x}=\pm 27.2\ \text{m}^2$, $r^2=.32$

Each species contributed to the total r^2 in the following way:

SPECIES	r^2
Plagiomnium ellipticum	.16149
Pleurozium schreberi	.09105
Carex diandra	.06268
total	.31522

Plagiomnium ellipticum was positively correlated with basal area while the other two species correlated negatively with the basal area of tamarack. The model was statistically significant at the probability level of .01.

Black spruce in the Saulteaux River area showed stronger evidence of more faithful associate species than tamarack. The regression equation was as follows:

Basal Area = 3.15524 + 1.68214Plsc + 2.72921Hysp + 1.49815Casp + 1.26203Legr - 1.37672Aupa - 3.20609Vavi

$N=71$, $M=7.5\ m^2$, $Std=\pm7.7\ m^2$

$S_{y.x}=\pm21.0\ m^2$, $r^2=.68$

The first four species were positively correlated with the basal area of black spruce. The model was significant at the .01 level and the r^2 was .68. The contribution of each species to the total r^2 was as follows:

SPECIES	r^2
Pleurozium schreberi	.34262
Hylocomium splendens	.18327
Calamagrostis sp.	.06612
Ledum groenlandicum	.03654
Aulacomnium palustre	.02646
Vaccinium vitis-idaea	.02331
total	.67832

In the Athabasca Highway area the relationship between cover percentages of some plants and black spruce basal area was also found significant. The model consisted of the following plants, all of them having a positive correlation:

SPECIES	r^2
Hylocomium splendens	.36414
Pleurozium schreberi	.13592
Tomenthypnum nitens	.20650
Carex gynocrates	.05650
total	.76306

The following regression equation was computed for the basal area of black spruce:

$$\text{Basal Area} = -1.20551 + 1.89356\text{Hysp} + 2.28461\text{Plsc} + 1.49084\text{Toni} + 1.39320\text{Cagy}$$

$N=38$, $M=10.8\ m^2$, $Std=\pm 7.1\ m^2$

$S_{y.x}=\pm 3.6\ m^2$, $r^2=.76$

This model was statistically significant at the .01 level of probability.

C. Comparison between Härkönen's (1985) Vegetation Classes and the Tree Data

An analysis of variance was used to compare Härkönen's (1985) vegetation classes using the site index as a response variable. Mean site index values of each vegetation class for both tree species can be seen in Table 1. As the table indicates some of the means of tamarack site index differed considerably among vegetation classes. These differences were, however, not significant at the .05 level of probability. In the case of black spruce the relationship between the site index variable and the vegetation classes was even weaker and no significant differences could be found.

The same analysis was run in the Athabasca Highway area for black spruce but no correlations could be established here between plant associations and tree growth.

Table 1 - Tamarack and black spruce site index (top height (m) at 45 years breast height) within Härkönen's (1985) vegetation classes in the Saulteaux River Area and Athabasca Highway Area.

Saulteaux River Area

	Black Spruce			Tamarack		
Class	Mean	Std	N	Mean	Std	N
1	7.1	2.5	3	6.6	2.0	7
2	6.1	1.7	6	7.6	1.2	8
3	7.5	2.0	4	10.4	.1	2
4	7.6	1.2	7	9.6	2.3	11
5	8.1	1.9	5	10.6	.0	1
6	7.9	2.1	8	9.1	2.5	4
7	7.7	1.7	9	6.8	.1	2
8	7.7	1.4	5	6.4	.0	1
Whole Area	7.5	1.7	47	8.3	2.2	36

Athabasca Highway Area

	Black Spruce		
Class	Mean	Std	N
1	8.6	1.7	3
2	7.3	1.0	14
3	8.2	1.5	13
Whole Area	7.8	1.3	30

D. Water Table Level

Initially it was assumed that, because of the fen-like conditions, the water table level would be constant. That is, differences in the water table level between sample plots in the study areas were expected to be small. However, the variation in the water table level was found to be large, even within individual sample plots, and a decision was made to include the water table observation in the study.

Because a water table well-network was lacking in the study areas and the schedule of this project did not allow establishment of such a network, measuring the water table level on a long term basis was not possible. It was decided to measure the water table level on a one-time basis, but a difficulty arose in defining a consistent reference point for measurements. Often a typical peatland surface consists of hummocks and hollows and intermediate surfaces, and their cover percentages vary greatly. Two separate water table measurements were made on each sub-sample plot at different reference points. Because no correlation could be established between the results of these two measurements ($r^2=.11$) it was concluded that the reference point for water table measurements could not be determined accurately enough to justify their use in the analysis.

V. DISCUSSION

According to the results site index for tamarack showed some significant correlations with NH_4^+ and extractable Ca^{++} in the peat in the Saulteaux River area. No relationships were detected between black spruce growth, peat and water nutrients.

The poor correlation for tree growth in the Saulteaux River area may be explained by high nutrient levels of the site. The Saulteaux River area was rich in all the major peat and water nutrients. On fertile sites little variation would be expected in tree growth due to variations in the nutrient regime. This is particularly true for trees growing on their natural sites (Spurr and Barnes, 1980).

The variation in the soil-water relationships, even within individual plots, seemed to be large. The growth of trees is probably influenced more by the hydrological conditions than the nutrient regime (Heikurainen, 1971b). As a result, nutrients probably were not the major factor limiting tree growth on the study sites.

The same applies even more to black spruce than tamarack because this species is fairly non-demanding. The nutrient contents in the area were probably more than adequate for black spruce growth. Generally speaking, the black spruce sites in the Saulteaux were a little poorer than tamarack sites in the Saulteaux River area. This can be seen in Table A.4, where the mean values for all the peat and water nutrients are presented separately for both tree species strata.

The fact that Ca^{++} correlated positively with tamarack growth is somewhat puzzling. Ca^{++} contents of a substrate are usually correlated with pH (Heikurainen, 1971a; Puustjärvi, 1967), but in this study this was not the case. Whether or not this was because of the overall high pH and lack of variability is not known.

Even though it is common knowledge that plants use nitrogen in the form of ammonium (NH_4^+), it is not agreed how much of all the nitrogen is extracted in this form. Ammonium is said to be utilized immediately by plants and its content is hard to measure (Tamm, 1950). The analysis method in this study included drying of the peat samples before the chemical analysis. This method itself causes some ammonium to be lost[2], which has to be born in mind when interpreting the results.

In the Athabasca Highway area black spruce growth showed a fairly strong relationship with the total amounts of phosphorous (P) and nitrogen (N). These elements were in considerable lesser supply here than in the Saulteaux River area (see Table A.3). The total nitrogen contents were so low that, by the Finnish standards (Heikurainen, 1971a), the area should not be drained.

Even though total amounts of these nutrients do not indicate actual amounts of P and N available for trees, the results suggest a relationship between tree growth and these

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[2] Pluth D., personal communication, December 5, 1984.

nutrients.

The rather low water table in the Athabasca Highway area probably inhibited tree growth less than the higher water table in the Saulteaux River area. Should this be the case, other factors such as peat nutrients could be expected to affect tree growth to a considerable degree in the Athabasca Highway area.

In both of the areas one has to interpret the results with caution. Without tissue analysis of the foliage one cannot be certain, whether or not the nutrients detected in the soil are fully utilized by the trees[3]. Paarlahti (1971) found that a foliar analysis was useful in determining some nutrient deficiencies in a fertilization experiment but no evidence was provided in favour of peat analysis.

In the Saulteaux River area the percent cover of different plant species correlated well, statistically, with the growth of tamarack. The growth of black spruce was poorly correlated with different ground vegetation species in both areas.

It seems that the species in the model for tamarack partly reflect the nutritional conditions of the sites. The less demanding ground vegetation species formed the majority of the plants in the model and had a negative partial correlation with tamarack growth. The less demanding species in the model were *Carex gynocrates*, *Smilacina trifolia* and *Pleurozium schreberi* (Heikurainen 1971a; Jeglum, 1971b). The

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[3] Pluth D., personal communication, December 5, 1984.

two positively correlated species *Plagiomnium ellipticum* and *Calamagrostis* sp. can both be considered more demanding species in terms of their nutrient requirements (Heikurainen, 1971a). *Plagiomnium ellipticum* had an r^2 of .28 by itself [illegible] thus was by far the most important species in the model.

A more demanding moss species with a negative correlation - *Drepanocladus vernicosus* described the hydrological condition of the site, because the moss usually grows on rich, completely saturated sites where tree growth would be poor or even impossible (Heikurainen, 1971a).

The fifth negatively correlated species *Tomenthypnum nitens* is another demanding moss species growing on drier peatland surfaces, i.e. hummocks. The reason why *Tomenthypnum nitens* significantly and negatively correlated with the growth of tamarack is hard to explain ecologically. The sampling for vegetation was carried out using a small sample plot size. This, according to discussions with Zoltai[4], could lead to great variation and randomness in the results of the vegetation analysis and thus make it difficult to use the vegetation data for further analysis.

Nutrient rich sites can support a great variety of different plant species including those that normally grow on nutrient poor sites. The sites occupied by tamarack were both nutrient rich and wetter. These sites exhibited great variation in their lesser vegetation but little variation in

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[4] Zoltai S, personal communication, December 5, 1984.

the peat and water quality. This may have influenced the results of the analysis.

In the Saulteaux River area the same reasoning can be used to explain why black spruce growth did not show any practical significant relationships with any of the lesser vegetation species. The fact that tamarack did and black spruce did not can be related to different site requirements. In this nutritionally rich area more demanding tree species like tamarack (Chapin, 1983) can be expected to have a stronger relationship with most of the site parameters than a less demanding species like black spruce (Chapin, 1983) growing on very nutrient rich sites.

Even though there were differences in some macro nutrients between sample plots these differences did not show up in the vegetation analysis in the Athabasca Highway area. The reason why these differences affected tree growth but not the lesser vegetation is unclear.

Using the basal area of both tree species separately as a dependent variable it was the black spruce that showed a distinct relationship with the percent cover of certain lesser vegetation species in both areas. The relationship of the tamarack basal area with the lesser vegetation was weak. This might reflect the different ecological ranges these two tree species cover. Black spruce grows normally on poorer and drier sites than tamarack where ground vegetation is less variable and represented by a few dominant species. Tamarack, on the other hand, tends to grow on richer, wetter sites where the ground vegetation varies greatly supporting a great number of species with fairly small individual percent cover.

Some lesser vegetation species correlated well with the basal area of black spruce. The associate species for black spruce in both areas were especially the two feather mosses *Pleurozium schreberi* and *Hylocomium splendens*. In the Saulteaux River area they had a major contribution to the total r^2 of .68 in the regression model and had an r^2 of .52. In the Athabasca Highway area the same species had an r^2 of .50 while the total r^2 of the model was .76. These two mosses are generally described to be common under black spruce (Fowells, 1965).

Because of the great heterogeneity in the vegetation and the fairly small variability in the nutrients among plots and sites, it was not surprising that Härkönen's (1985) vegetation classes did not correlate well with tree growth. Although many of her classes had a distinct relationship with the nutrient status in the areas, the small differences in nutrients between different sites did not show up in the tree data.

In Härkönen's (1985) vegetation classification a total of eleven different classes were established. Eight of these classes were in the Saulteaux River area and three in the Athabasca Highway area. Because the number of vegetation classes was relatively high, many of them were represented by a only few sample plots. All the eight vegetation classes in the Saulteaux River area were used in the analysis for both species. Five of these classes consisted of less than five sample plots. The small sample size in many of the classes resulted in great variability in site index and thus probably contributed to the results of the analysis.

A larger variation in terms of the chemical characteristics in the peat and water would probably be needed to detect differences in tree growth between different classes of lesser vegetation based on selected chemical properties of the growing substrate.

One has to remember that the classification developed by Härkönen (1985) is only one approach to categorize the vegetation of a peatland ecosystem. A TWINSPAN analysis was used to classify the vegetation and in the interpretation of such an analysis subjectivity is hard to avoid. The classification as it stands at the moment is very botanical and could not be used e.g. by field foresters for any practical decisions. Since some individual lesser vegetation species correlated with tree growth in this study, maybe an autecological approach could be used to classify peatland vegetation in the province. Such an approach should result in , easily recognizeable indicator species that would correlate with tree growth. This kind of classification would be handy in terms of finding the most economical peatland utilization projects.

VI. CONCLUSIONS AND SUGGESTIONS FOR FURTHER STUDY

The results show that chemical characteristics of the peat can be used only in limited cases to explain tree growth on virgin peatlands judging from the data of this study. Tissue analysis of the foliage should be included in future analyses to determine the correlation between the foliage nutrients and the nutrients in the growing substrate of the peatland.

In the case of the lesser vegetation, individual plants and their combinations did not satisfactorily explain tree growth in the study areas. Broad groups of lesser vegetation gave rise to poorer relationship with tree growth than did individual species of lesser vegetation.

The water table and its variation should be included in the analysis. Without measuring this variable on a long term basis the experiments on virgin peatlands lack control and the results are hard to interpret.

In Alberta, where most of the peatlands are reportly fens, (Vitt *et al.* 1975), further research should be focused on drainage effects on nutrient mobilization and possible disturbances in the nutrient balance of these peatlands. If the peatlands in the province are nutrient rich, as suggested, the differences in tree growth due to differences in the nutrient regimes of Alberta's organic soils would be marginal. A disturbance in the peat nutrients due to drainage could, however, endanger the results of large drainage projects and its importance in peatland studies must be emphasized.

A new approach to classify the peatland vegetation in the province should also be considered. Efforts should continue to develop a classification system that would include tree growth aspects along with easily recognizeable individual indicator plants.

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VIII. APPENDIX

Table A.1 - Means and standard deviations of height, diameter at breast height, age at breast height, and basal area for black spruce, tamarack and white spruce combined in the Saulteaux River Area and Athabasca Highway Area.

Saulteaux River Area

	Mean	Std	N
Height	7.3 m	±2.2	67
DBH	8.8 cm	±3.4	67
Age	54.8 years	±21.5	67
Basal Area	13.1 m²	±8.4	71

Athabasca Highway Area

	Mean	Std	N
Height	6.7 m	±1.6	37
DBH	7.8 cm	±2.7	37
Age	42.5 years	±7.2	36
Basal Area	11.6 m²	±6.8	39

Table A.2 - Means and standard deviations of hei[illegible] at breast height, age at breast height, and basal area for black [illegible]k and white spruce separately in the Saulteaux River Area and Athabasca [illegible] Area.

Saulteaux River Area

	Black Spruce			Tamarack			White Spruce		
	Mean	Std	N	Mean	Std	N	Mea[illegible]	[illegible]	N
Height	6.8 m	1.6	61	8.4 m	2.5	52	7.0 [illegible]	[illegible]	2
DBH	8.3 cm	1.6	61	11.4 cm	4.3	52	9.0 c[illegible]	[illegible]	2
Age	51.1 yr	12.5	56	64.2 yr	39.5	48	24.0 yr	[illegible]	[illegible]
Basal Area	7.6 m²	7.8	71	5.8 m²	6.1	71	--	--	71

Athabasca Highway Area

	Black Spruce			Tamarack			White Spruce		
	Mean	Std	N	Mean	Std	N	Mean	Std	N
Height	6.7 m	1.8	37	6.8 m	1.2	4	10.9 m	1.3	2
DBH	8.2 cm	3.6	37	7.3 cm	2.0	4	15.3 cm	3.3	2
Age	44.6 yr	7.2	35	28.6 yr	4.0	4	33.0 yr	--	1
Basal Area	11.3 m²	6.5	39	--	--	39	--	--	39

Table A.3 - Means and standard deviations of peat and water parameters in the Saulteaux River Area and Athabasca Highway Area.

	Saulteaux River Area			Athabasca Highway Area		
	Mean	Std	N	Mean	Std	N
pH, water	6.4	.7	38	7.0	.3	13
Spec. cond., US	111.0	38.4	36	200.0	38.9	13
Ca, water, mg/l	20.0	7.7	42	57.0	11.4	13
Mg, water, mg/l	5.2	1.8	42	12.8	2.5	13
Na, water, mg/l	5.5	3.5	42	.1	.0	13
K, water, mg/l	.7	1.1	42	.1	.0	13
pH, peat	6.2	.6	37	7.0	.4	15
total C, %, peat	45.0	2.9	37	38.0	6.2	15
total N, %, peat	1.7	.5	37	1.3	.5	
NH4-N, Ng/g, peat	113.0	67.0	37	145.0	121.0	15
NO2-N, Ng/g, peat	6.2	3.0	37	6.5	6.4	15
C/N-ratio, peat	30.0	12.0	37	32.0	10.0	15
total P, %, peat	.1	.04	37	.09	.03	15
Ca, ml/l, peat	81.0	21.0	37	117.0	30.0	15
CEC, meq/100 g	100.0	23.0	37	136.0	35.0	15
TEC, m[illegible]100 g	129.0	25.0	37	159.0	35.0	15
depth, cm	121.0	38.0	30	56.0	22.0	14

Table A.4 - Means and standard deviations of peat and water parameters in the Saulteaux River Area by tree stratum (black spruce, tamarack).

	Black Spruce			Tamarack		
	MEAN	Std	N	MEAN	Std	N
pH, water	6.3	0.94	12	6.8	0.15	10
Spec. cond., US	97.2	45.0	12	113.9	39.4	10
Ca, water, mg/l	18.8	8.6	12	19.5	6.0	10
Mg, water, mg/l	4.5	1.9	12	5.2	1.7	10
Na, water, mg/l	5.0	2.5	12	5.4	2.2	10
K, water, mg/l	0.81	0.8	12	0.42	0.45	10
pH, peat	6.0	0.9	12	6.2	0.3	9
total C, %, peat	44.3	4.4	12	45.3	1.4	9
total N, %, peat	1.4	0.5	12	1.9	0.4	9
NH4-N, Ng/g, peat	84.9	53.9	12	131.1	43.2	9
NO2-N, Ng/g, peat	5.4	1.5	12	8.2	5.1	9
C/N-ratio, peat	36.7	19.1	12	24.3	5.7	9
total P, %, peat	0.1	0.04	12	0.15	0.04	9
Ca, ml/l, peat	78.0	30.3	12	82.9	20.8	9
CEC, meq/100 g	96.5	33.6	12	102.3	21.4	9
TEC, meq/100 g	125.4	26.0	12	129.3	24.3	9
depth, cm	109.0	47.0	12	128.0	33.0	9

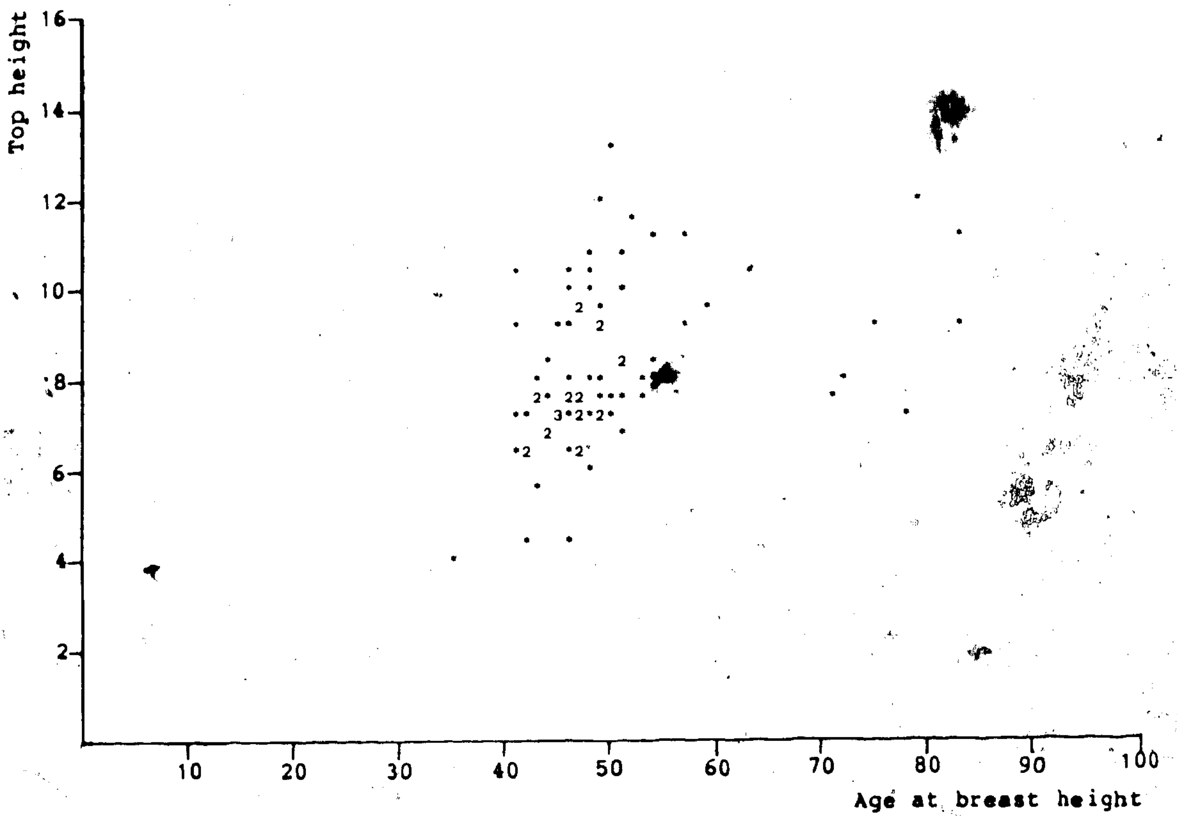

Figure A.2 - Top height of tamarack in relation to age at breast height in the Saulteaux River Area.

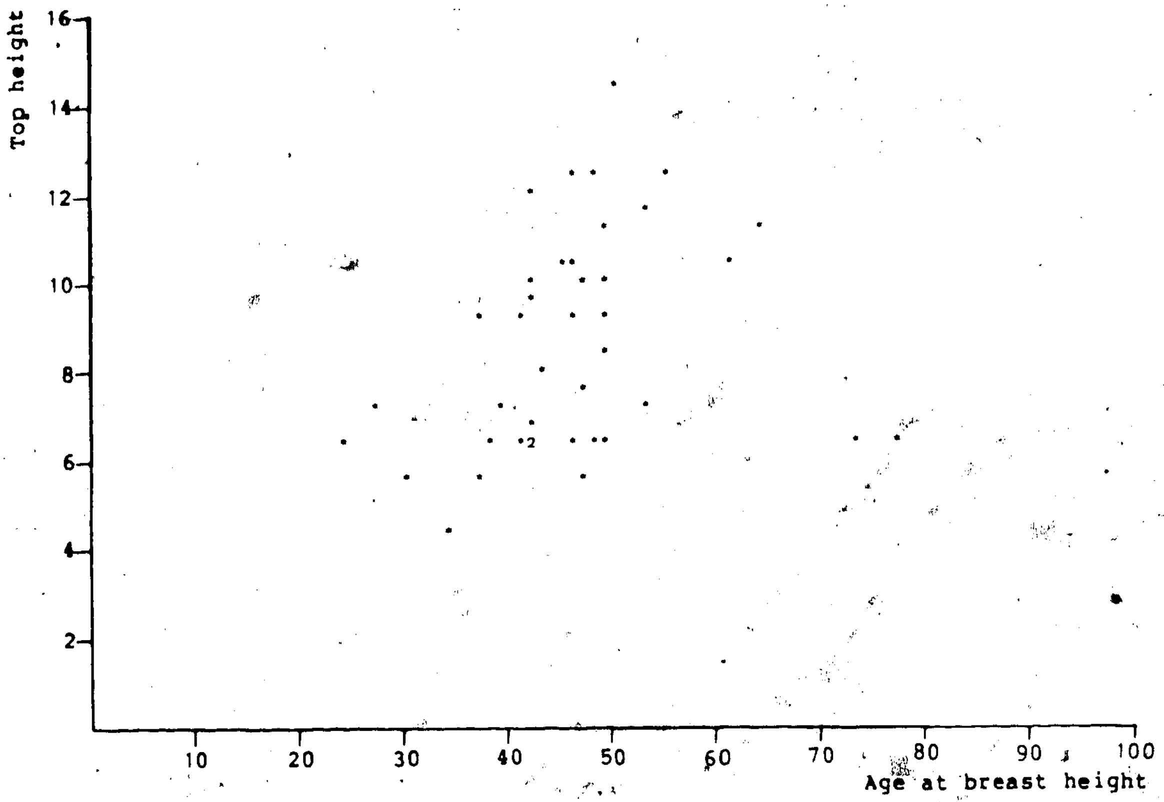

Figure A.2 - Top height of tamarack in relation to age at breast height in the Saulteaux River Area.