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VARIABILITY IN DRAINAGE-INDUCED RESPONSE GROWTH AND ITS RELATION TO PRE-DRAINAGE GROWTH RATE OF PEATLAND BLACK SPRUCE AND TAMARACK

by ©

FENGYOU YIN

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirement for the degree of **MASTER OF SCIENCE**

DEPARTMENT OF FOREST SCIENCE

EDMONTON, ALBERTA

SPRING, 1993

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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 **VARIABILITY IN DRAINAGE-INDUCED RESPONSE GROWTH AND ITS RELATION TO PRE-DRAINAGE GROWTH RATE OF PEATLAND BLACK SPRUCE AND TAMARACK** submitted by **Fengyou Yin** in partial fulfilment of the requirements for the degree of **MASTER OF SCIENCE**.

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DEDICATION

I would like to dedicate this thesis to my wife Xiumei, our daughter Yin, and my parents in China. My family provided a constant source of support, love, and encouragement during the writing of this thesis.

Abstract

This study examined the relation between drainage -induced growth and tree growth rate prior to drainage as well as the effect of drainage on variability in the size of individuals in populations of peatland black spruce (*Picea mariana* (Mill) B. S. P.) and tamarack (*Larix laricina* (Du Roi). K. Koch). Drained black spruce and tamarack trees 38-42 years old were selected in 1991 on a peatland near the Saulteaux River in Alberta. The experimental plot area was drained in 1984 by ditching (25 m spacing). Undrained trees on a control plot were chosen at least 100 m from the drained area. Discs were cut from the trunks of all trees at 25 cm height above ground level and used for tree ring analysis. Stem radius data from undrained trees during the 12 years before drainage and during the 8 years after drainage were regressed on time separately to establish a relation between pre-drainage regression slopes and postdrainage regression slopes. This relation, together with the pre-drainage regression slope of drained tree, was used to estimate radial growth of each drained tree during post-drainage period as if drainage had not occurred. Two kinds of Response Indices (RI), Cumulative Response Index (CRI: the ratio of observed cumulative radial growth to estimated cumulative growth as if drainage had not occurred) and Annual Response Index (ARI: the ratio of observed annual growth to estimated annual growth as if drainage did

not occur), were calculated for each drained tree in the post-drainage period. CRIs for each tree in 1991 were then regressed on size (radius) at the time of drainage. RIs were also compared among three groups of trees which had different growth rate before drainage. The results showed that slow growing trees before drainage had larger RIs than faster growing trees, and that variability of stem radius among individuals in the drained population 8 years after drainage was significantly less than if the population had not been drained. This suggests that variability in tree growth rate in natural peatlands was mainly controlled by microenvironmental variation and that variability of stem radius in a population can be reduced by drainage. There was reduced growth (related to undrained trees) after drainage for both species. Release growth was declining 7 years after drainage. Tamarack showed greater release growth to drainage than black spruce.

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Background Information

Definitions of Peat and peatland.

Peat. Peat is an organic soil developed as a consequence of the incomplete decay and decomposition of wetland vegetation under high moisture conditions and a deficiency of oxygen (Päivänen, 1984). Basically, peat accumulation is controlled by production and decomposition (the ratio of production / decomposition). Peat accumulation is primarily due to slow decomposition and not to high productivity. Slow decomposition in peatlands can be attributed to either anaerobic conditions or to extreme nutrient-deficiency (Clymo, 1965). An adequate moisture supply is also critical. In fact, the water balance is probably the single most important factor influencing peat accumulation because a high water table decreases soil aeration, soil temperature, and activity of decomposing organisms, all of which reduce the speed of peat decomposition. Verry and Boelter (1978) found that the two most important conditions necessary for peat development are slow water movement and surplus water originating from precipitation, surface runoff, or the seepage of ground water to the surface.

Peatland. A peatland is defined as an unbalanced system where the production of organic material exceeds the rate of respiration and degradation (Moore & Bellamy, 1974). Peatland is usually defined as any type of peat-covered terrain, including bogs and fens. Zoltai and Pollett (1983), however, argue that peatlands should be defined as areas where peat depth is 40 cm or more.

Bogs are mineral-poor, acid peatlands raised above the ground water by an accumulation of peat (Crum, 1991). Such peat is usually formed _in situ_ under closed drainage, and oxygen saturation is very low. Bogs are dominated by a hummocky growth of _Sphagnum_ covered by a shrub layer. In North America, they are sometimes covered by black spruce (Crum, 1991; Zoltai & Pollett, 1983). Bogs develop under ombrotrophic conditions in which water and nutrients are supplied only by precipitation (atmosphere). The closed water drainage system and impermeable peat block mineral solutions from reaching the surface layers from outside the system or from the underlying mineral soil. Therefore, bogs are oligotrophic.

Fens are peatlands characterized by surface layers of poorly to moderately decomposed peat (Zoltai & Pollett, 1983). The water and peat are less acid than in bogs of the same area, and sometimes show alkaline reactions. They are characterized by grasses, and sedges. _Sphagnum_ is usually subordinate or absent on fens. Often there is much shrub cover, and sometimes a sparse layer of trees (Crum, 1991), often tamarack. Fens are minerotrophic (rich in nutrients) because they develop under the influence of precipitation as well as mineral-rich ground or surface water (Crum, 1991).

Silvics of Black Spruce and Tamarack

Black spruce. Black spruce is a usually slow-growing and small to medium sized tree. It usually grows to 10 m in height, 25 cm in diameter under regular conditions. Under favourable conditions it can reach 30 m in height, 90 cm in diameter (Elias, 1989). The range of black spruce extends from Alaska, across Canada, to Newfoundland and into the northeastern United States. It is one of the most abundant coniferous species in northern forests (Elias, 1989). The southern limit corresponds roughly with the 21^{0}C July isotherm while the northern limit closely follows the 10^{0}C July isotherm (Vincent, 1965). It occurs from about 100-850 m elevation (Elias, 1989) and 1142 mm to less than 253 mm precipitation. Half or more of this falls as rain during the growing season.

Black spruce forests occur on sites across a large ecological amplitude ranging from dry upland sites to water saturated peatlands (Heinselman, 1957). It is most common in swamp areas or muskegs throughout central and northern Alberta (Blackmore et al., 1985).

Even though black spruce occurs on soils ranging from very wet peat bogs to deep sandy soils or gravel tills, it grows best in the main range in Canada on well-drained loamy and clay loam soils. However, because black spruce is less competitive than other species, it is more often a minor component on these sites compared with other species (Fowells, 1965). Black spruce occurs in pure stands or mixed with tamarack, white spruce, balsam fir, jack pine, and aspen (Elias, 1985).

Sphagnum mosses provide a very common seedbed type for black spruce. On moderately moist to somewhat wet sites, elevated hummocks somewhat above the water table level provide good seed germination conditions, especially when Sphagnum grows slowly. On very moist and very wet sites, seed germination tends to occur on the drier and warmer parts (tops) of hummocks because the moisture retaining capacity and good aeration of Sphagnum make them almost ideal (Vincent, 1965).

The root system is platelike and averages six meters in diameter for mature trees and is rarely more than 60 cm deep, usually being confined to the upper 15 to 30 cm (Stanek, 1961 in Vincent, 1965). On peatlands, black spruce usually has a shallow root system (Lieffers & Rothwell, 1987b) because of high water tables. Roots of black spruce are generally restricted to the upper 10 - 20 cm (Mannerkoski, 1985; Lieffers & Rothwell, 1986), and more often to the 7-10 cm below ground level just above the water table (Strong & La Roi, 1983).

Tamarack. Tamarack is a small- to medium-sized tree, usually 15-22 m tall and 35 cm -50 cm in diameter. If exposed to full sunlight, tamarack is one of the fastest growing conifers on uplands and lowlands (William & Carpenter, 1985).

Tamarack is a northern tree with a natural range larger than most North American conifers (Elias, 1989). In the United States, its range extends from Maine to Minnesota. The tree also grows throughout much of Canada and in Alaska to the northern limit of tree growth, and at altitudes of up to 365.7 m (Welch, 1979). Over its range annual precipitation varies from 180 mm to 1400 mm (Roe, 1957) and the average frost-free period ranges from about 80 to 180 days (Fowells, 1965).

Tamarack is a characteristic tree of bogs and swamps (Fowells, 1965). In Alberta, it is found in muskeg or swamp areas in central and northern Alberta where it receives plenty of sunlight. In northern Alberta, it can also be found on better drained sites such as valley slopes (Blackmore et al., 1985). It is the only larch that tolerates swamp conditions and the only coniferous tree in Alberta that sheds its leaves each fall (Welch, 1979; Blackmore et al., 1985).

The tree grows on the full range of organic-soil sites from rich swamp to raised bog and is also found on mineral soils ranging from heavy clay to coarse sand. It grows best on moist but well-drained loamy soil on beaches and uplands (Richard & Preston, 1989). However, it is mainly found on poorly drained sites, especially on wet lowland where the organic soil is more than 30 cm thick.

Seed germination and seedling establishment of tamarack are best on warm, moist mineral or organic soil with a light cover of herbaceous vegetation and are generally favoured by slash-burned seedbed and hummocks of slow-growing *Sphagnum* moss (William & Carpenter, 1985)

Tamarack typically has a shallow, compact root system. In wet sites, however, this species develops a shallow and spreading root system (Green, 1933). In soft deep mud and in silted-up ponds and streams, the roots become somewhat deeper (Green, 1933).

In low, wet areas the tree may occur in pure stands, but in other areas tamarack is found in association with several species, including black spruce, balsam fir, aspen, birch, and jack pine (Richard & Preston, 1989).

Annual Rings and Dendrochronology.

Annual Rings. Trees in the temperate zone have prominent annual rings of wood (xylem) which result from different cell sizes, different cell wall thickness, and different proportions of various cell types formed in different seasons (Paul et al., 1979).

The formation of annual growth rings means that an individual tree can be aged and the characteristics of the growth rings can sometimes reveal more detail about the past history of the individual such as when it was suppressed by or released from the influence of certain environmental factors (Thomas et al., 1985).

The width of an annual ring is often changed by environmental factors in the year it was formed and this fact has been used extensively to study climatic conditions in the past (Fritts, 1976).

Dendrochronology. Dendrochronology is defined as tree -ring studies where the annual growth layers are assigned to or are assumed to be associated with specific calender years (Fitts, 1976). Dendrochronology may be divided into a number of subfields. Two subfields of dendrochronology closely associated with this study are: dendroclimatology and dendrohydrology. Dendroclimatology refers to dendrochronological investigations of past and present climates. Dendrohydrology refers to the application of dendrochronology to the study of past river flow and flooding history. Although I used similar methods and procedures in my study, they did not completely follow these two definitions (Fitts, 1976). These two definitions refer to the use of tree-ring growth to date past (climatic and hydrological) events, while the objectives of my study were to identify the effects of a past event (drainage) on the tree ring growth.

Population Size Structure

Krebs (1978) defines a population as "a group of organisms of the same species occupying a particular space at a particular time". The ultimate constituents of the population are individual organisms that can potentially interbreed. The boundaries of a population both in space and in time are vague and in practice are usually fixed by the investigator arbitrarily (Krebs, 1978). From a practical point of view, a population should be a unit of study.

One important characteristic of a population of trees is the size structure. Generally, this refers to size distribution, i.e., identifying size relationships of diameter and volume among trees. If the size structure can be predicted and reconstructed successfully, the dynamics of the population can be traced in the past and in the future.

An important concept for describing population size structure is variability of tree size within the population. Variability describes whether or not tree size values in the distribution cluster closely about the mean (Byrkit, 1987).

Variance and standard deviation are often used to investigate the variability of data about the mean. However, these should not be used in population ecology when two data sets with different means are compared. In this situation, it is strongly recommended that the Coefficient of Variation be used, because it expresses the standard deviation of a sample as a percentage of the mean (CV =

(std./mean)* 100) and is a pure number without units. In my opinion, this method might be best way to compare variability between two populations even though it is not used much in population ecology.

To illustrate the variability of tree size in a population, graphs of frequency distribution are often used instead of calculating the size variance or standard deviation of the population. This provides a good visual representation.

In my study, variability in tree size was not assessed directly. I inferred the significance of changes in size variability following drainage by comparing postdrainage Cumulative Response Indices of trees that were growing at different rates prior to drainage. The frequency distributions of drained black spruce and tamarack tree size and Coefficients of Variation were also used.

Previous Research

Black spruce and tamarack are dominant trees of many peatlands of the boreal forest in Canada. Black spruce and tamarack grow on peatlands, which are characterized by high water tables, poor soil aeration, cold substrate, and low nutrient availability (Lieffers & Rothwell, 1986, 1987a; Payandeh, 1973), and are low in productivity (Macdonald & Lieffers, 1990). For these reasons natural peatlands are not exploited for timber harvesting in Alberta. Besides very low productivity, black spruce populations on peatlands also have wide variability in growth rate (Jeglum, 1972; Lieffers, 1986). No data on variability in growth rate of tamarack are available. Casual observation suggests that growth variability for both peatland black spruce and tamarack may be greater than for most upland species.

Factors Influencing Variability in Growth Rate.

On peatlands, growth of conifers is quite variable (Jeglum, 1972; Lieffers, 1986), even in stands originating from fire in which seedlings recruit at about the same time and in the period prior to canopy closure when above-ground competition is not likely significant. Lieffers (1986) found that high variability in growth rates among individual trees was the main source of variability in tree size (mean annual increment in height of trees is associated with their height at 10 years). The result is consistent with results from some nursery studies (Morgenstern, 1978; Pollard & Logan, 1974). Such variability may be a function of: a) genetic differences in growth rate among trees (Morgenstern, 1978; Pollard & Logan, 1974); b) environmental heterogeneity in space (Hartgerink & Bazzaz, 1984; Van Cleve et al., 1981); and c) possibly below-ground competition.

Genetic. It is unknown whether growth variability in field conditions is correlated with tree genotype because no studies have been done to examine the relation in natural populations. However, some findings from nursery studies can be consulted.

Some studies show that there is significant genetic variability in growth rates (Morgenstern, 1978) during the period of free growth (fast growing period) of black spruce (Pollard & Logan, 1974) and of tamarack seedlings (Park & Fowler, 1982).

A provenance study of black spruce by Hall (1987) showed good correlation between heights at ages two and four years in the nursery. This relationship often disappeared after outplanting. Correlations in height between ages 10 and 15 were found to be very high in some experimental plantations while, in some other plantations, correlations were low because the trees were under stress and genetic effects were masked (Hall, 1987).

A progeny trial with black spruce by Williams et al. (1987) showed the phenotypic correlation between early growth (6-month) and field growth rate (height, volume) for families was generally high, positive and statistically significant from 6-months to 7-13 years.

It should be noted, however, that these results came from range-wide provenance trials in nursery beds and prepared stands. Therefore results may differ from those for populations in natural peatlands. Stress caused by high water table, poor nutrient availability and cold soils may severely limit growth of peatland trees, and therefore mask genetic differences among individuals.

Environment. Many abiotic factors (soil aeration, soil temperature, peat decomposition, depth to water table, nutrient availability, etc.) may influence growth rates of peatland trees. It is hard to separate the combined effects of these factors in the field. Uneven distribution of these factors in space and different positions of tree roots might account for highly variable tree growth rate.

Several factors which affect tree growth change along the hollow to hummock gradient: 1) Depth to water table increases (Karlin & Bliss, 1983); 2) pH values decrease from the hollow to hummock (Karlin & Bliss, 1983; Vitt et al., 1974; Crum, 1991); 3) Substrate chemistry changes (Karlin & Bliss, 1983); 4) Bulk density decreases from hollow to hummock (Karlin & Bliss, 1983); 5) Moisture declines from hollow to hummock (Karlin & Bliss, 1983; Vitt et al., 1974; Crum, 1991); and 6) Within the hollow to hummock gradient there is a definite order of moss species which indicates that the microenvironment changes with position (Karlin & Bliss, 1983; Vitt et al., 1974; Crum, 1991). This type of spatial heterogeneity may produce variability in tree growth rate within a population.

Below-ground competition could also cause variability in growth rate. However, no studies on this aspect have been done.

The relation between drainage-induced tree growth and tree growth rate prior to drainage is helpful to explain the factors affecting tree growth rate on natural peatlands. If slowly growing trees show more release after drainage, environmental heterogeneity may be the primary factor affecting growth. This would be true if slow growing trees were under more severe stress before drainage. If faster growing trees show more release, below-ground competition may be the controlling or limiting factor in growth. This would be true if fast growing trees had larger root systems.

Tree Release by Drainage and Relation to Tree Growth Rate Prior to Drainage.

Drainage of peatlands has the potential to improve tree productivity (Hillman, 1987). Large increases in tree diameter and height growth after drainage are reported for black spruce and tamarack (Richardson, 1981; Trottier 1986; Dang & Leiffers, 1989). These increases may be due to increased substrate temperatures and improved aeration (Lieffers & Rothwell, 1987a; Lieffers, 1988), and/or increased nutrient availability and uptake leading to higher rates of photosynthesis (Macdonald & Lieffers, 1990).

Some studies with other woody species showed drainage -induced growth was variable among trees which differed in size at the time of drainage (Heikurainen & Kuusela, 1962; Payandeh, 1973). A detailed study of Scotch pine and Norway spruce in Finland (Heikurainen and Kuusela, 1962) yielded the following results: a) small trees (of variable age) had greater response to drainage; b) at a certain size (12 m in height) Scotch pine and Norway spruce trees lose their capacity to release (i.e., their annual increment decreased despite drainage). This study did not consider the effect of tree age on release growth responses.

Payandeh (1973) found that the response of peatland black spruce to drainage was greater for younger trees with larger crowns growing on better sites. Also, younger stands with lower stocking tended to show more release. Older trees with short narrow crowns showed no positive response to drainage (Stanek, 1968). Thus, tree age, tree form and site quality should all be taken into account when studying the relationship between release of individual trees and growth rate prior to drainage.

According to the above information, trees with different growth rates may have different growth responses to drainage. As a result of drainage, substrate conditions for tree growth may improve and may be less variable. My hypothesis is: If slow growing trees are primarily limited by poor microsite conditions, they stand to derive a greater benefit from improved conditions accompanying drainage and so should show more release growth. If this is the case, the variability in size among individuals in the drained population will decrease over time after drainage. Alternatively, if below-ground root competition is limiting growth of trees, faster growing (larger) trees with larger root systems should have a greater ability to take advantage of improved edaphic conditions after drainage and so would show more release growth than slower growing trees. In this case size variability among individuals will increase over time after drainage.

It is still unknown if variation in drainage-induced growth among trees of different size can result in changes in variability in size of individuals in the population (Hillman et al., 1990). Yet, identifying the effect of tree growth rate prior to drainage on tree release growth is critical because of its role in making decisions on stands to be drained and in predicting the effects of drainage on stand size structure.

Calculation of Drainage-Induced Growth.

In order to estimate the response of trees to drainage, it is important to calculate the amount of drainage-induced growth accurately. Several methods have been used to evaluate the effects of peatland drainage on tree growth (Dang & Lieffers, 1989; Heikurainen & Kuiesela, 1962; Richardson, 1981; Wang & Micko, 1985). However, these methods all have drawbacks and limitations.

Heikurainen and Kuiesela (1962) compared average radial increment values over the 10 years period (10-20 years after drainage) to the average increment for the 10 years prior to drainage to examine drainage effects on tree growth. This method ignored different growth rates of trees with different age, different absolute amounts of growth among trees of different size, and possible effects of other environmental changes in the post-drainage period because it had no undrained control. This method can be used to compare average periodic increment before and after drainage, but is not suitable if tree age and size are not the same or if there environmental changes occur following drainage (i.e. post-, pre-drainage environmental factors such as precipitation and temperature are different).

Wang and Micko (1985) described a relative growth rate method to estimate the effects of drainage on tree growth. Two expressions were used in this method: 1, (total tree volume at the time of measurement - pre-treatment tree volume) / pre-treatment volume; 2, Total tree volume at the time of measurement / hypothetical volume at the time of measurement if no drainage occurred. There are two major drawbacks to this method. The first expression underestimates the effect of drainage on larger trees because larger trees have larger pre-drainage tree volume (larger denominator in the expression). The second expression assumes that, if there was no drainage, average radial and height growth of individuals in the post-drainage period would be the same as in the pre-drainage period. Generally, this assumption does not hold.

In his study on the effects of drainage on tree growth, Richardson (1981) directly compared height growth of black spruce and eastern larch before and after drainage and between drained and undrained sites. It was very difficult to separate the drainage-induced growth from the growth if drainage had not occurred. This is because a) there was no information on the expected growth trend of drained trees after drainage if they were not drained, and b) the drained site and undrained site might not have the same site quality (the height was different between sites before drainage). The tree growth differences between drained sites and undrained sites may be caused not only by drainage, but also by different site quality and different tree growth trends.

More recently, Dang and Lieffers (1989) developed a method using the curve of annual tree ring width vs time to estimate post-drainage tree ring growth for each tree as if no drainage occurred. They used regression procedures to fit a negative exponential function to the observed tree ring data for the period from the growth peak (the curve peak of annual radial growth over time) to the time of drainage for each tree. The regression function was extrapolated for the post-drainage period to calculate expected tree ring growth in this period. Further, drainage-induced tree ring growth was calculated by subtracting extrapolated tree ring growth from observed tree ring growth. However, this method did not work well for my data because (1) the population had different growth trends which did not all fit the negative exponential function, (2) the population was too young so that the period from the growth peak to the time of drainage was not long enough to build a reliable regression function, (3) there was a high degree of variability in ring growth data.

Drainage-Induced Size Structure Change.

There is limited information on effects of drainage on variability in size among individuals in a population. Hillman et al. (1990) compared tree size (height) frequency distributions on a drained site with that on an undrained site. They found that the average tree height on the drained site was much larger than that on the undrained site. They did not look at changes in size variability, but their frequency distributions reveal a skewed distribution in the undrained area and a more normal distribution in the drained area. The trees in this study had different ages so the changes in tree size distribution might be due to different growth rate for trees of different age.

The above concerns regarding existing methods call for the development of new methods to calculate the amount of drainage-induced growth and to estimate changes in population size structure.

Objectives

This study of peatland black spruce and tamarack addresses questions concerning variability in growth rate among individuals before and after drainage. In this study, the growth rate of peatland black spruce and tamarack before and after drainage was examined. A Response Index (RI) representing the magnitude of release growth for each drained tree was calculated. The objective was to examine variability in drainage-induced growth in peatland black spruce and tamarack and relate it to tree growth rate prior to drainage. This information will allow me to 1) infer causes (genetic or environmental) of variability in growth rate of these species in natural peatlands, and 2) document the effects of drainage on peatland black spruce and tamarack population size variability and distribution. The latter would allow me to determine whether drainage will increase size uniformity of peatland black spruce and tamarack populations as well as increasing growth rate of individual trees.

I hypothesized that drainage-induced growth of peatland black spruce and tamarack is correlated with growth rate prior to drainage. The nature of the correlation will provide insight into the factors influencing variability in growth rate of individuals in even-aged peatland stands of these species (see explanation of hypothesis on page 14). If a negative correlation is found, I can conclude that drainage can be used to increase size uniformity of black spruce and tamarack in a population besides being used to increase growth rate of the trees.

Materials and Methods

Site Description and Sample Collection

The study site was located about 37 km southeast of the town of Slave Lake, Alberta. The site was drained in February of 1984 by the Alberta Forest Service. Fifty hectares were drained with ditch spacing at 25 and 40 m and ditch depth 80 cm, using D6, D7, and D8 bulldozers and Caterpillar 215 and 235 backhoes (Toth & Gillard, 1984).

The sites are forested by an open-canopy, low stem density stand of black spruce and tamarack (80 percent tamarack, 20 percent black spruce). The black spruce and tamarack were approximately 40 years old and were likely established after fire. Above-ground competition was not thought to be important among trees because stem density was very low.

In this area, Betula pumila L, Andromeda polifolia L, and Ledum groenlandicum Oeder were dominant shrubs (Lieffers & Rothwell, 1987a). Sphagnum warnstorfii Russ. and Tomenthypnum nitens (Hedw.) Loeske were common mosses (Lieffers, 1988).

The region is overlain with peat deposits, ranging from 30 to 150 cm (Mäkitalo, 1985), and has cold relatively dry winters and warm, wet summers with total annual precipitation of 470 mm and seasonal evapotranspiration of

390 mm. Mean water pH was 6.7. Mean temperatures are -17^0C for January and 16^0C for July (Lieffers, 1988).

The results from some preliminary studies on the drained area indicate drainage lowered the water table 20-50 cm (Lieffers & Rothwell, 1987a; Lieffers, 1988). Substrate water content on the drained sites was decreased (Rothwell & Silins, 1990). In 1985 the maximum ground temperature (16^0C) at 10 cm depth on the drained area was 4^0C higher than on the undrained site. However, substrate temperatures were lower for the drained site at 40 and 60 cm depths, and there was some delay in thaw compared to the undrained site (Swanson & Rothwell, 1986). Degree-day summations on the drained site were 249 at 10 cm depth and 200 at 30 depth more than those on the undrained site (Lieffers & Rothwell, 1987a). After drainage pH, ash, K, and P values were higher while N and C values were lower at 10 cm level compared with the undrained site (Lieffers, 1988).

Following drainage, leader elongation of both tamarack and black spruce on the drained site was reduced compared with the undrained sites in both 1984 and 1985 (Lieffers & Rothwell, 1987a). Tamarack had 2-3 times greater leader growth and 1-2 times larger standard deviations for annual growth in 1988 and 1989 on the drained site than the undrained site (Rothwell & Silins, 1990). The length and variability of leader growth for black spruce were also larger on the drained site, but to a lesser degree than for tamarack.

My study was conducted in 1991 in a approximate 6 ha area at the north end of the drained area form which trees were selected from the drained area and the undrained area. The ditch spacing in the drained area was 25 m. A control plot was selected in an adjacent undrained area at least 100 m from the drainage ditches. Pre-selection for similar age (38-43) was conducted by coring trees near the base and counting tree rings. Thirty trees of each species from the drained plot and 30 trees of black spruce and 25 trees of tamarack from the control plot were selected. All selected trees were cut down in August 1991.

Discs cut at 25 cm height above the ground were air -dried and sanded in the laboratory. The annual rings were counted and the widths of each annual ring was measured at two radii along the longest and shortest diameters of each disc with a computerized measuring device (Clyde & Titus, 1987). Average (from the two radii) widths of each annual ring were used for further calculation and data analysis.

Discs cut at ground level were used for age determination. Trees with ages above 42 and below 38 were excluded in the experiment. In the end, total 25 of trees of each species from each site were included.

Selected typical trees were used for drawing graphs.

Analysis

Test of Predrainage Site Quality (Drained vs Undrained). It was desirable to test if both the drained and undrained plots had the same site quality before drainage in order for subsequent analyses to be valid. To test this, the amount of cumulative growth for the 10 year period before drainage was used as an indicator of site quality, and a regression model with indicator variables containing interaction effects was used (Neter et al., 1985).

The dependent variable (Y) was radius during the 10 year period before drainage (1974-1983). The first independent variable (time) is quantitative, and is measured by the years since 1974. The second independent variable, type of plot, is qualitative and is composed of two classes -- plots on drained and undrained sites. The first order model with an interaction term in our experiment was:

$$Y_i = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \beta_3 X_{i1} X_{i2} + e_i$$

where:

X_{i1} = time (years)

X_{i2} = 1 if drained plot

0 otherwise

The response function for this model is:

$$E(Y) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2$$

For the undrained plot, $X_2 = 0$ and hence $X_1 X_2 = 0$.

Therefore, the response function for the undrained plot is:

$$E(Y) = \beta_0 + \beta_1X_1 + \beta_2(0) + \beta_3(0) = \beta_0 + \beta_1X_1$$

For the drained plot, $X_2 = 1$ and hence $X_1X_2 = X_1$. The response function for the drained plot, therefore, is:

$$E(Y) = \beta_0 + \beta_1X_1 + \beta_2(1) + \beta_3X_1 = (\beta_0 + \beta_2) + (\beta_1 + \beta_3)X_1$$

Practically, β_1 indicates stem radius each year. β_2 shows whether the intercept is different for the drained plot vs the undrained plot. Similarly β_3 indicates whether there is a difference in slope for the drained plot vs the undrained plot.

To test whether the two regression functions are identical, I hypothesized:

H_0: $\beta_2 = \beta_3 = 0$;

Ha: not both $\beta_2 = 0$ and $\beta_3 = 0$.

Stem cumulative radial increment data for the ten year period prior to drainage (1974-1983) from 22 drained and 22 undrained tamarack trees were used to build a regression function. The same approach was used for 22 drained and 22 undrained black spruce. The relevant regression results for the two species are shown in Table 1.

For $p \leq 0.05$ ($p \leq 0.05$ used throughout this study), $n = 440$, $t = 1.960$. Since t-ratios for β_2 and β_3 are all smaller than 1.960, H_0: $\beta_2=\beta_3=0$ is accepted. The conclusion is that intercepts and slopes for the two equations are not significantly different if we build them using data from drained and undrained plots separately. This indicates that

Table 1. Regression Results from Test of Predrainage Site Quality for Black Spruce and Tamarack

Species	predictor	Coef.	Stdev.	t-ratio
Black spruce	constant	-0.2739	0.2273	-1.20
	β_1	0.49247	0.03664	13.44*
	β_2	-0.2037	0.2876	-0.71
	β_3	0.08882	0.04634	1.92
Tamarack	constant	-0.1688	0.3885	-0.43
	β_1	0.5417	0.06248	8.67*
	β_2	-0.0359	0.2462	-0.15
	β_3	0.06034	0.03969	1.52

Note. * Coefficients are significantly different from zero at $p < 0.05$ level. β_1 = Coefficient of quantitative variable (years from 1974 to 1983), β_2 = Coefficient of qualitative variable (drainage vs undrainage), β_3 = Coefficient of interaction term. Sample Standard Deviation = 1.289, R^2 = 60.4%, R^2(adj) = 60.1% for black spruce. Sample Standard Deviation = 1.141, R^2 = 72.1%, R^2(adj) = 71.9% for tamarack. Twenty-two drained and 22 undrained trees for each species were used. β_2 and β_3 are not significantly different from zero (β_2=β_3=0) for each species.

the drained and undrained plots had the same site quality prior to drainage. The β_1 was significant simply indicating there was a significant change in stem radius over time from 1974-1983.

Test of Piecewise Regression Procedures for Extrapolating 'Postdrainage' Growth. Stem radius over time followed a particular pattern for all undrained trees since 1972 (Fig. 1). In order to use the observed patterns of growth in undrained trees to estimate post-drainage growth of drained trees as if drainage did not occur, four consecutive steps were conducted.

Step 1: For undrained trees, particularly black spruce, a slight change in slope of the radius vs time relationship was evident at about the year of drainage (1984). I, therefore, generated 2 separate regressions for each undrained tree using the piecewise linear regression method (Neter, et al., 1985). Two linear regressions were built by using stem radius as the dependant variable and time (years) as the independent variable for: 1) from 12 years before drainage (1972) to the year before drainage (1983); 2) from the time of drainage (1984) to the time of sampling (1991) (Fig. 1). The regression data for 20 black spruce and 20 tamarack trees are presented in Table 2. As shown in Table 2, the piecewise regression method was reasonable because standard errors of Y estimates were small and R^2 values were large for all the trees.

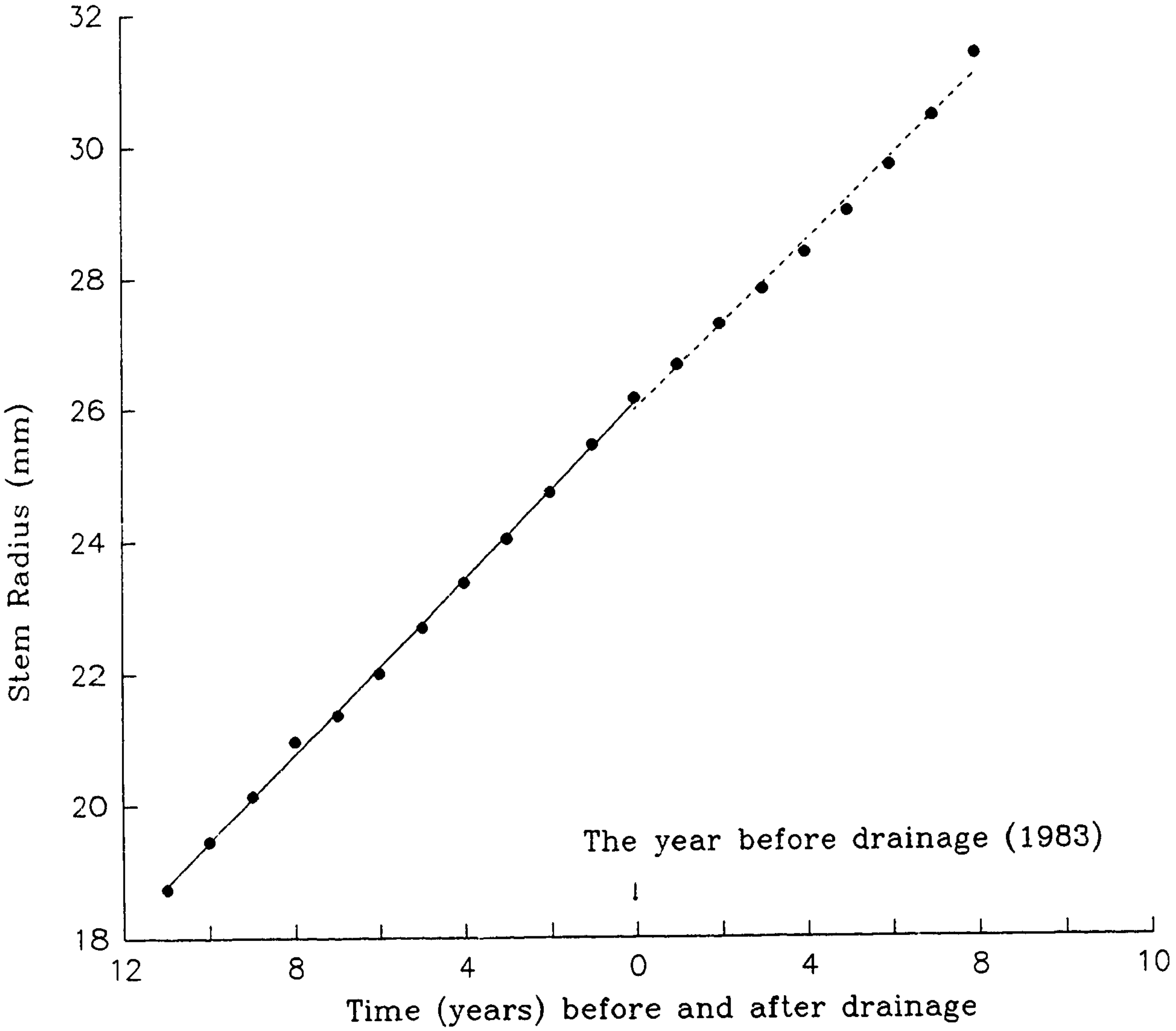

Fig.1. Piecewise regression procedures for undrained tamarack tree # 28. (•) data points. (——) estimated regression line in the period before drainage, the slope = 0.662. (·······) estimated regression line in the period after drainage the slope = 0.636.

Table 2. Standard error of Y (s.e.), R^2, and regression slopes (slope) for the period 12 years before drainage and the period of 8 years after drainage for undrained black spruce and tamarack

Species	tree	before drainage			after drainage		
	#	s.e.	R^2	slope	s.e.	R^2	slope
Black	5	0.0300	0.9958	0.1763	0.0476	0.9924	0.2066
spruce	6	0.1309	0.9505	0.2171	0.1265	0.9723	0.2839
	8	0.0724	0.9853	0.2246	0.1016	0.9900	0.3831
	2	0.0750	0.9891	0.3014	0.0964	0.9923	0.3465
	3	0.0780	0.9910	0.3801	0.0867	0.9975	0.4917
	62	0.0984	0.9910	0.3916	0.0734	0.9975	0.5578
	30	0.0722	0.9957	0.4170	0.0663	0.9968	0.4433
	61	0.1012	0.9934	0.4722	0.0850	0.9931	0.3875
	65	0.0990	0.9942	0.4925	0.1265	0.9723	0.6449
	67	0.0598	0.998	0.5127	0.2268	0.9845	0.6834
	23	0.0690	0.9977	0.5489	0.1619	0.9895	0.5967
	25	0.0662	0.9983	0.6225	0.0662	0.9983	0.5421
	22	0.0754	0.9982	0.6573	0.1720	0.9985	0.8129
	26	0.0861	0.9980	0.7492	0.3161	0.9875	1.0622
	15	0.1867	0.9972	0.7611	0.2650	0.9928	0.7823
	21	0.2107	0.9984	0.8212	0.2031	0.9895	1.1022
	64	0.2007	0.9917	0.8311	0.1437	0.9938	0.6922

Table 2 continued

Tamarack	68	0.2908	0.9860	0.9244	0.2063	0.9946	1.0647
	10	0.0253	0.9897	0.9276	0.0289	0.9950	1.1094
	66	0.3957	0.9767	0.9699	0.4850	0.9848	1.4795
	62	0.5178	0.9959	0.2765	0.1591	0.9875	0.3752
	22	0.0950	0.9956	0.4912	0.2032	0.9833	0.4126
	60	0.0978	0.9917	0.3667	0.0784	0.9975	0.4201
	67	0.1073	0.9899	0.3647	0.0876	0.9973	0.4516
	61	0.0720	0.9919	0.2738	0.0657	0.9986	0.4668
	23	0.3825	0.9588	0.6377	0.0838	0.9981	0.5213
	66	0.0769	0.9965	0.4486	0.0596	0.9990	0.5647
	50	0.1677	0.9901	0.5741	0.2660	0.9847	0.5658
	1	0.0748	0.9980	0.5943	0.1265	0.9970	0.6201
	19	0.1147	0.9950	0.5531	0.2063	0.9932	0.6614
	28	0.1662	0.9920	0.6358	0.0830	0.9988	0.6619
	20	0.2992	0.9762	0.6556	0.1411	0.9969	0.6764
	18	0.1321	0.9961	0.7233	0.3515	0.9836	0.7219
	63	0.0639	0.9984	0.5617	0.3458	0.9848	0.7385
	29	0.1054	0.9987	0.7074	0.3878	0.9815	0.7479
	49	0.1011	0.9980	0.8914	0.2109	0.9955	0.8382
	17	0.2000	0.9969	1.0124	0.2454	0.9953	0.9448
	15	0.1482	0.9966	0.8755	0.3257	0.9928	1.0119
	65	0.2145	0.9900	0.7322	0.3065	0.9936	1.0130
	11	0.1543	0.9980	1.2498	0.3464	0.9935	1.1283

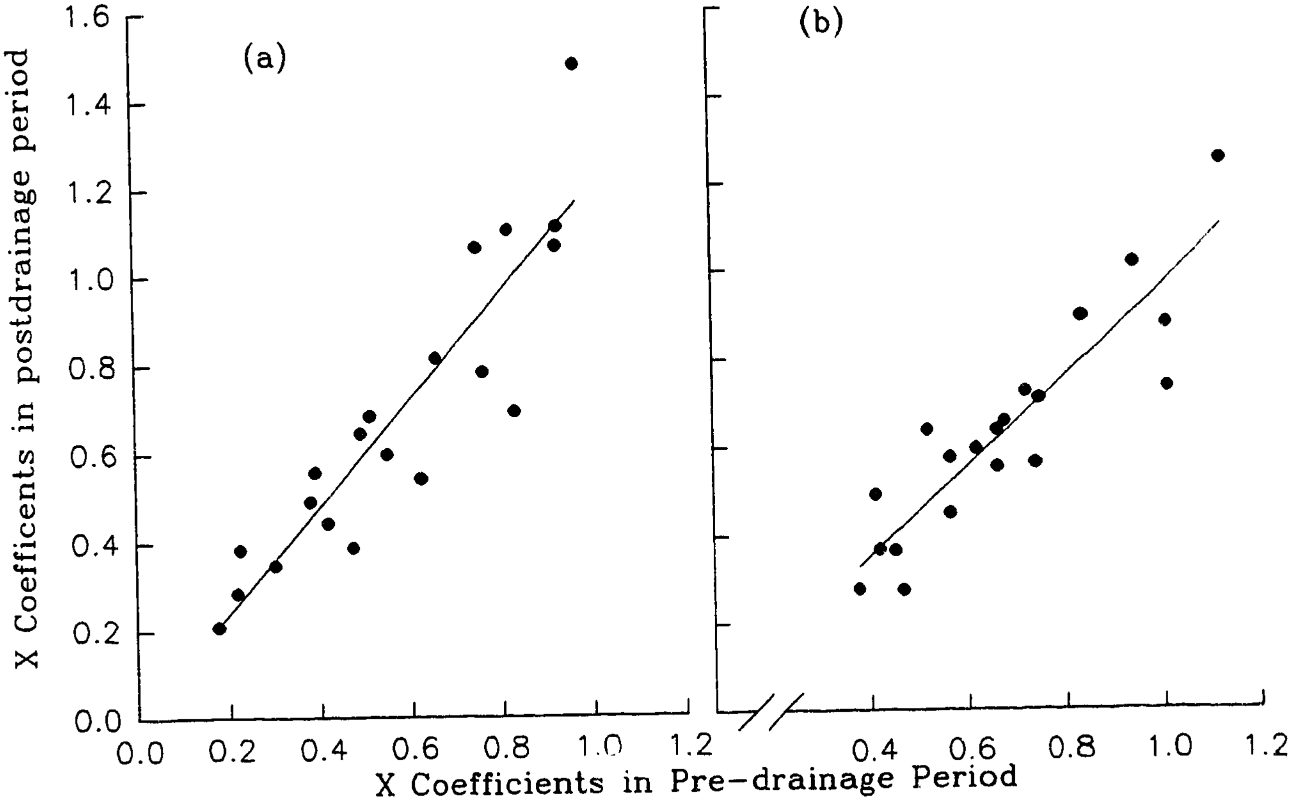

Fig.2. Slopes of radius vs time regression during the pre-drainage period as related to slopes of radius vs time regression during the post-drainage period. (a) for black spruce, Y=-0.005+1.208X, s.e.=0.142, R^2=0.828. (b) for tamarack, Y=-0.052+1.009X, s.e.=0.109, R^2=0.812. n=20 for both species.

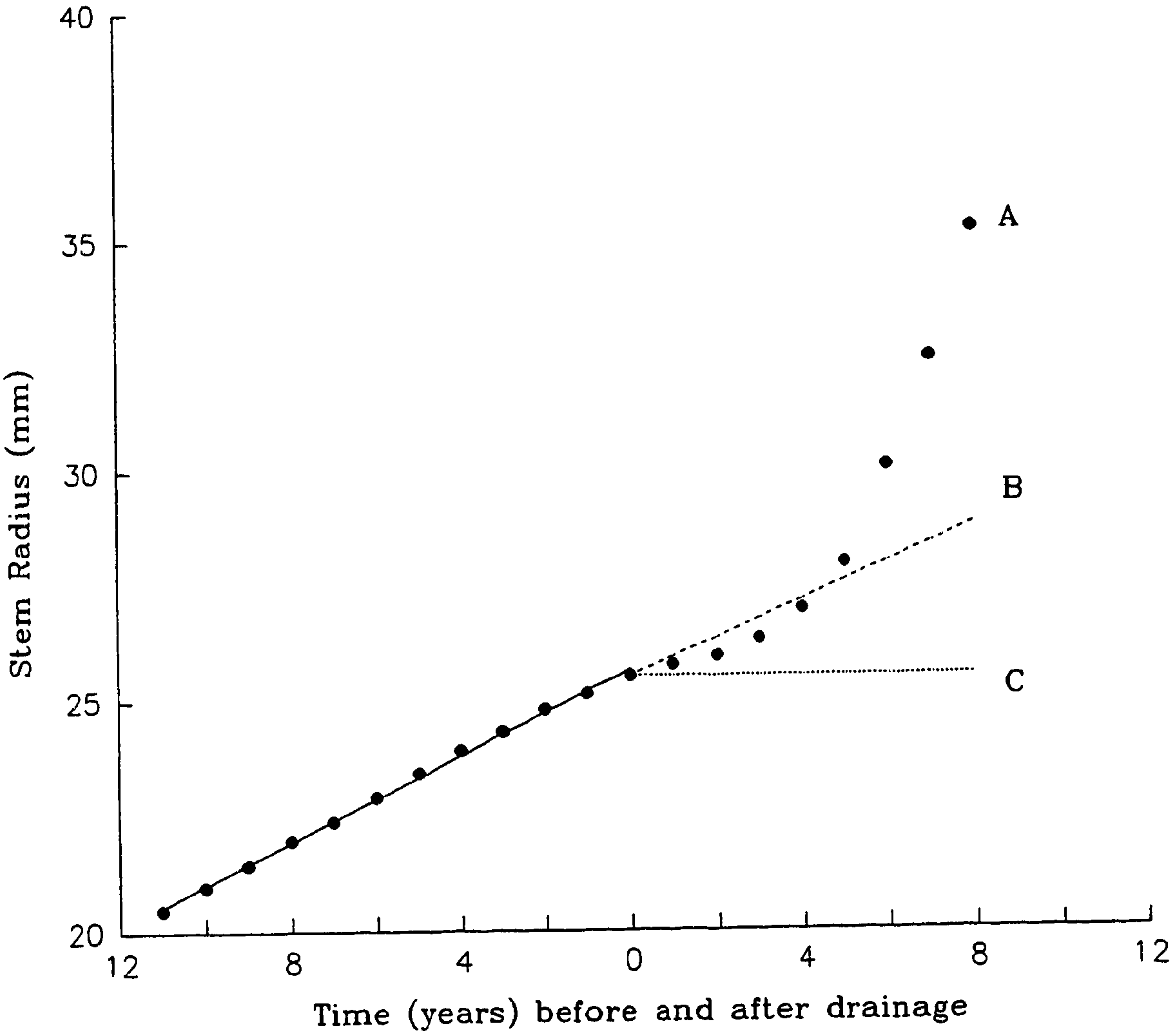

Fig.4. Example of calculation of CRI for drained tamarack tree # 20 in year 8 after drainage. (•)data points; (------) estimated stem radius if drainage did not occur; (.........) stem radius in the year before drainage (1983). CRI= A−C (observed radius in 1991−radius in 1983) / B−C (estimated radius in 1991−radius in 1983). In the year before drainage CRI is close to 1. In the first 4 years of of drainage CRIs are negative.

Step 2: For undrained trees, slopes of the postdrainage regressions were regressed on the slopes of the pre-drainage regressions. For both species pre-drainage regression slopes were linearly related to post-drainage regression slopes (Fig. 2). For black spruce, Y (pre-drainage slope) = -0.00503 + 1.2083X (post-drainage slope). For tamarack, Y (pre-drainage slope) = -0.00201 + 1.009114X (post-drainage slope). This indicates that the regression slopes before 1984 can be reasonably used to estimate the regression slopes after 1984. Even though the slope for tamarack is close to 1, the piecewise regression method was used instead of one simple regression, because I wanted to use the same method for both species.

Step 3: A regression of radius vs time for the pre -drainage period (1972-1983) was developed for each drained tree. From the pre-drainage regression slope and the coefficient determined in step 2 (Fig. 2) I determined the slope of post-drainage radial growth for each drained tree as if drainage had not occurred. The relation between the pre- and post-drainage slopes from the undrained plot could be used to estimate growth rate for the drained plot as if drainage had not occurred because site quality prior to drainage was the same for both plots. In this way the undrained plot is used as an effective control.

Step 4: Using the slope of post-drainage radial growth as if drainage had not occurred, I calculated estimated radius over time (1984-1991) for each drained tree.

Calculation of Response Index. As the trees increased in size, the curve of stem radius changed. The trend of the change was specific to each tree and perhaps was a function of aging, genetic potential for growth, bole geometry, site conditions, and stand history. To compare the effects of drainage on the growth of different sized trees, this individual growth trend must be removed. The best way is to produce an index of tree growth. The index of tree growth is defined as the ratio of the amount of observed growth to the amount of estimated growth.

In this study, in the post-drainage period, the index of tree growth was labelled as Response Index (RI) because it reflected the response of the trees to drainage.

Response Index was defined as the ratio of amount of actual growth after drainage to the amount of estimated growth if drainage had not occurred. This indicates how much faster or slower the tree grew after drainage compared to how it would have grown if it was not drained. Two kinds of RI were calculated: response indices for cumulative increment (CRI) and response indices for annual increment (ARI). CRI illustrates the overall response of trees to drainage after a certain number of years. ARI, however, indicates the response of trees to drainage in each year.

CRI = (observed radius in a given year (X) since drainage - observed radius in 1983) / (estimated radius in

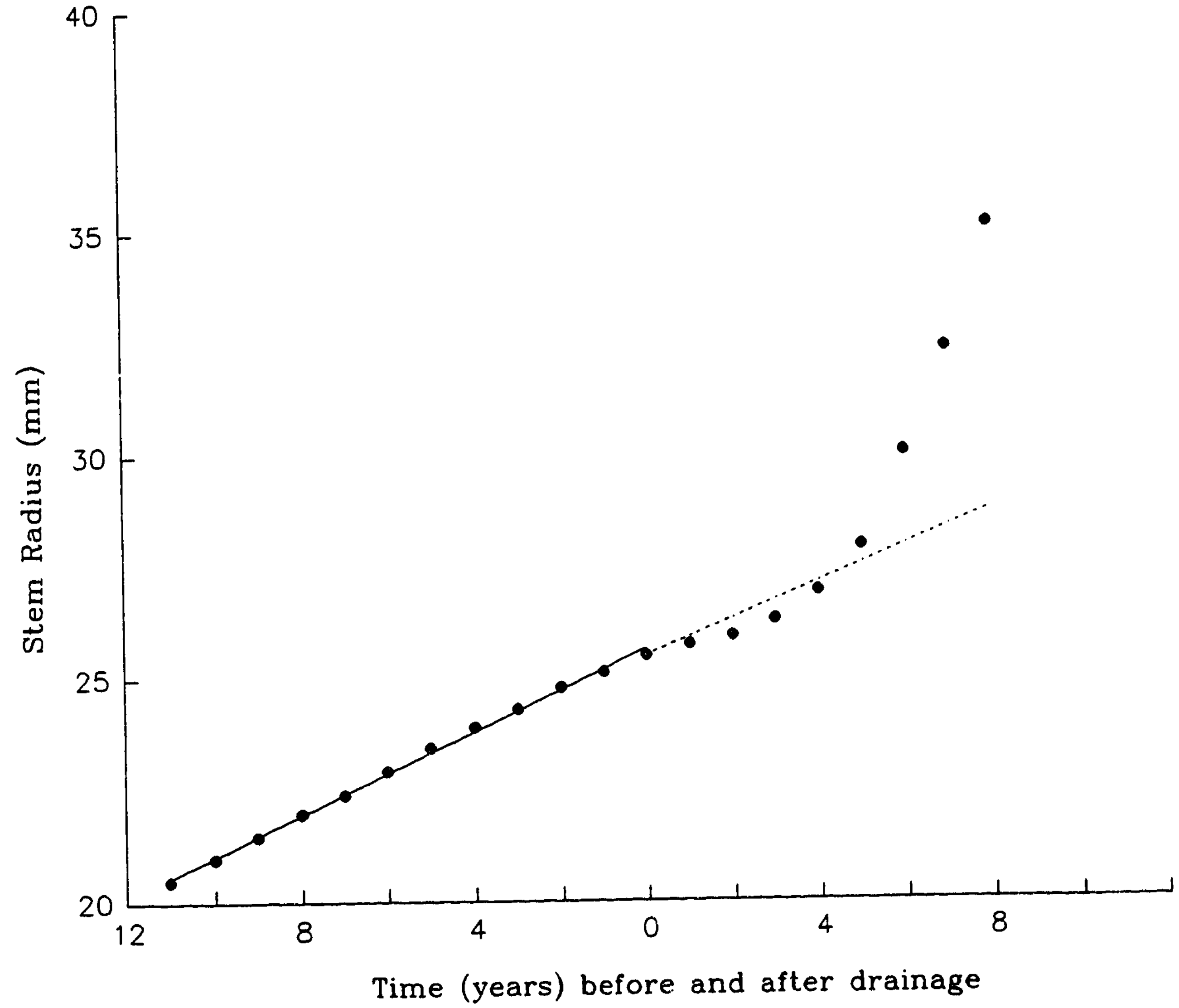

Fig.3. Post-drainage stem radial increment estimation procedures for drained tamarack tree # 20. (●) data points. (——) regression line from the data during the 12 years before drainage (slope=0.458). (·······) estimated post-drainage regression line with a slope 0.409 which was calculated from the pre-drainage regression slope.

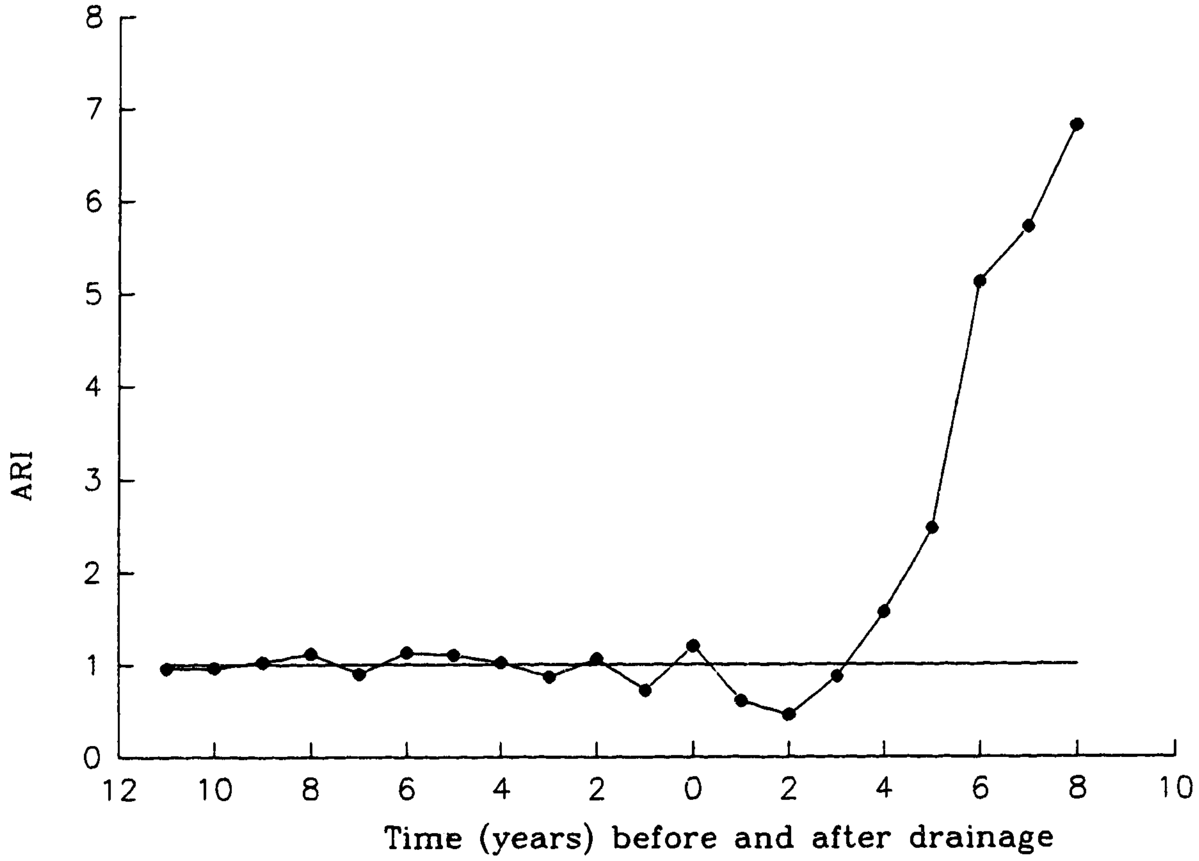

Fig.5. ARI over time before and after drainage for drained tamarack tree # 20. During the period before drainage, the ARI varied around the mean of 1.0.

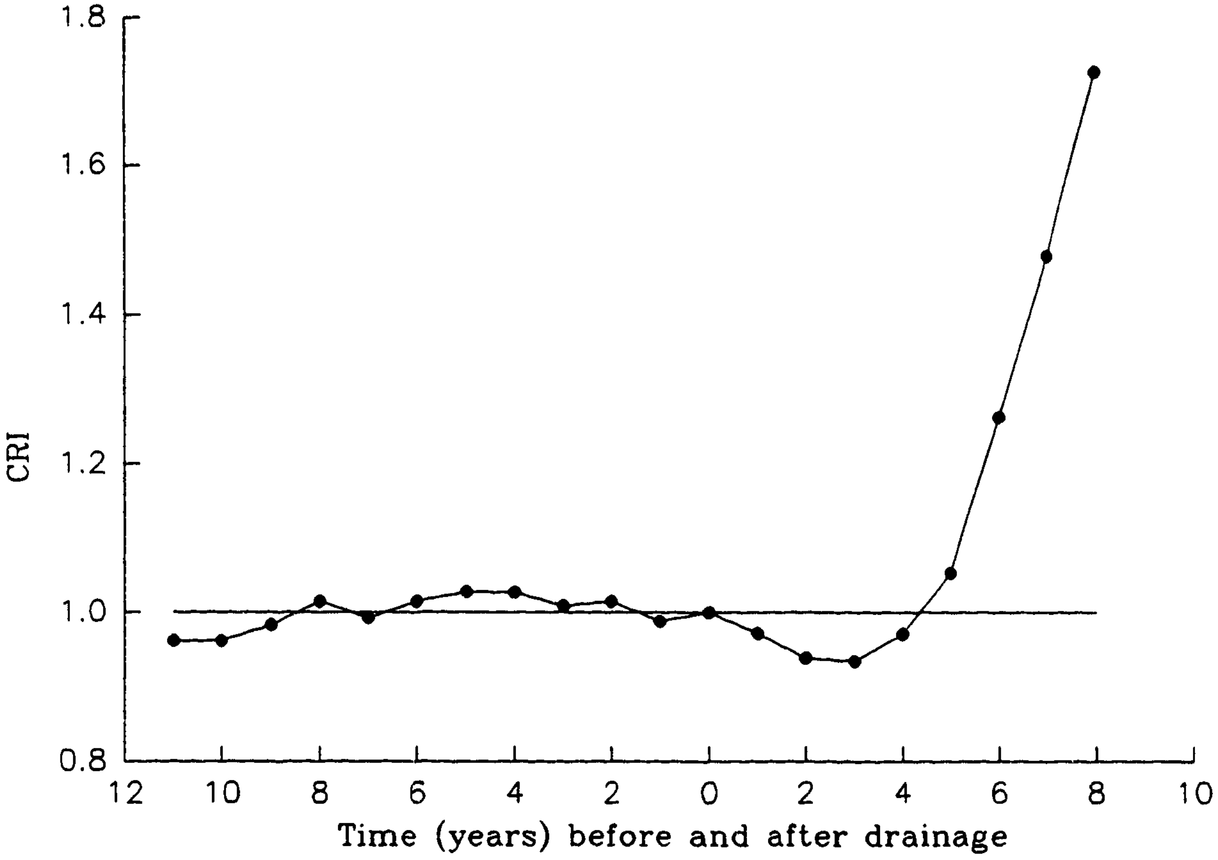

Fig.6. CRI over time before and after drainage for drained tamarack tree # 20. During the period before drainage, the CRI varied about a mean of 1.0.

year X if no drainage occurred - observed radius in 1983).

The numerator refers to the total amount of actual radial increment since drainage. The denominator refers to the estimated amount of radial increment since drainage if drainage had not occurred (for CRI calculation see Fig. 4).

ARI was obtained by using the following formula:

ARI = Radial increment in a given year after drainage / estimated radial increment in that year as if drainage had not occurred.

The estimated annual increment values were calculated by subtracting estimated radius in year N from that in year N+1. CRI and ARI series for each tree were obtained by using year by year calculation.

If there was no major environmental change, the index series should have a mean of about 1.0 (see pre-drainage period in Figs. 5 and 6). significant index deviations from 1.0 are caused by variation in environmental factors (drainage in this study) and any index differences among the trees are due to the different responses of the trees to the environmental change (drainage).

Comparison of RI among Trees with Different Growth Rates before Drainage. All the trees used were of a similar age but there was considerable variability in stem radius at the time of drainage. Stem radius ranged from 13.6 mm to 36.6 mm for black spruce, 15.58 mm to 34.33 mm for tamarack. In order to test the relationship between

Response Index and tree stem radius before drainage, trees were divided into three groups according to stem radius in the year previous to drainage (1983). For black spruce, the ranges of stem radii were 13-19.9 cm (n= 8) for Group 1; 20-26.9 cm (n=12) for Group 2; 27-36.9 cm (n=5) for Group 3. For tamarack the ranges of stem radius were 15-20.9 cm (n=11) for Group 1; 21-26.9 cm (n=9) for Group 2; 27-34.5 cm (n=5) for Group 3. The range of stem radius for Group 3 was wider than that for Group 1 and 2 in order to include enough trees in this group. CRI and ARI series over time for each tree were calculated and then grouped according to the descriptions above. Average CRI and ARI of each group were plotted over time after drainage, and curves were compared.

Estimation of Drainage-induced Changes in Population Size Structure. After drainage, the population size structure could change if trees with different radii (growth rates) before drainage had different responses to drainage. To examine this, I defined two critical lines regarding the relation of CRI to radius in the year of drainage (1983) to compare with regression line of CRI (1991) vs size in 1983 (Fig. 7).

Line 1: If there was no response growth after drainage in any of the trees, the regression line of CRI in 1991 vs radius in 1983 would have zero slope and a 1.0 intercept. In this case the variability and frequency distribution of stem radius would be the same over time as

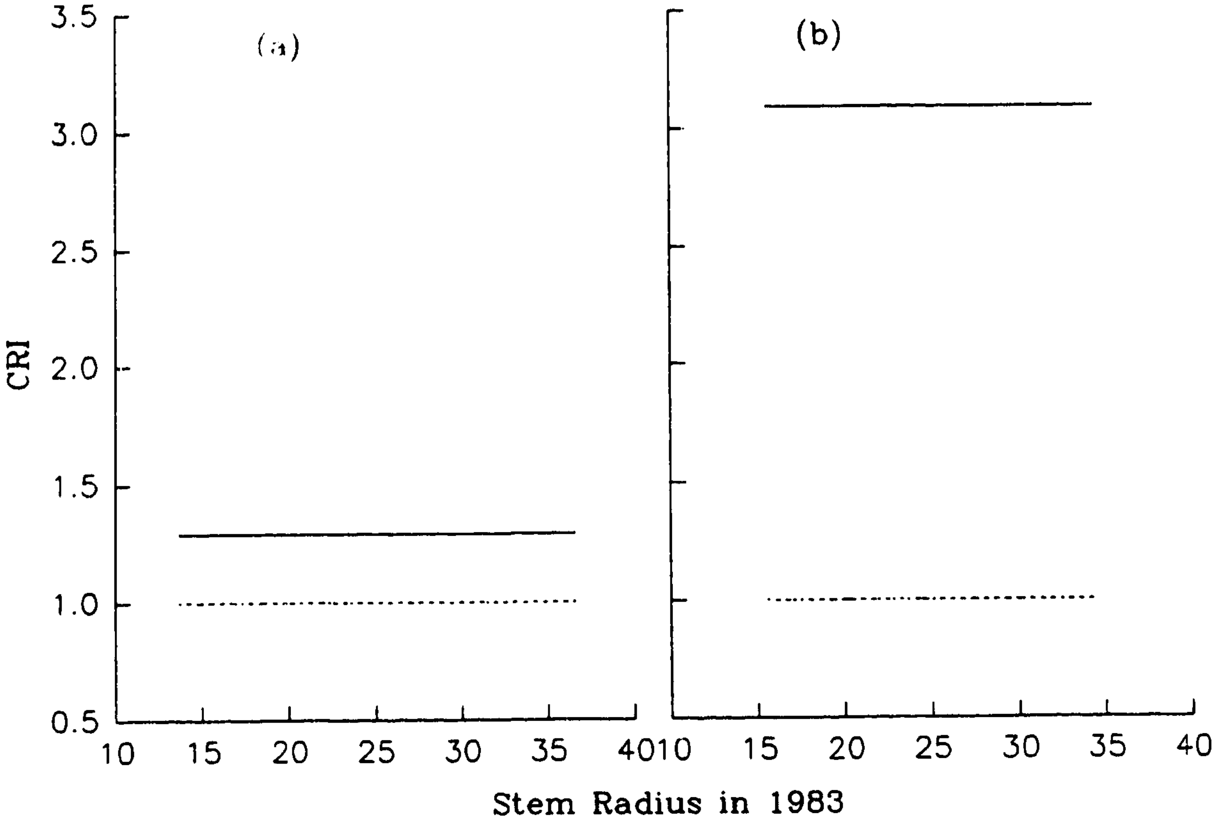

Fig.7. Critical lines of CRI in 1991 vs radius in 1983 for (a) black spruce and (b) tamarack. (·······) Line 1: no response growth after drainage (all CRI=1). (——) Line 2: same response indices for all trees after drainage (all CRI=mean of my calculated CRIs).

if there was no drainage.

Line 2: If CRI was the same for all trees. The line would have zero slope and average CRI in 1991 for an intercept.

The assumption for the line is that CRI in 1991 for every tree equals average CRI in 1991 for all trees. The relative differences in growth rate among the trees would not change after drainage, i.e., fast growing trees would still be growing relatively faster. In this case, variability in stem radius in 1991 would be much greater than it would have been if drainage did not happen. However, variability of the stem radius would be the same as t when the trees grew to the same size without drainage in he future.

Regression line of CRI in 1991 vs radius in 1983 were compared relative to these lines. As long as the regression line of observed CRI vs radius in 1983 has a significant (negative or positive) slope, it means there is an effect of tree growth rate prior to drainage on the observed response growth. As such, size variability and frequency distribution of the drained population would be changed from that expected if drainage had not occurred.

If the slope is negative, it indicates that the slowly growing trees had larger CRI (more response growth) after drainage than the fast growing trees. If the slopes are positive, it means that the fast growing trees before drainage had larger CRI (more relative response growth) after drainage than the slowly growing trees.

Size (radial) frequency distribution of drained trees of the two species for the observed radius in 1983, the estimated radius in 1991, and the observed radius in 1991 were also constructed.

In addition, Coefficients of Variation for radii in the year before drainage, for observed radii in 1991, and for estimated radii in 1991 were calculated.

Results

Different Responses of Trees to Drainage

Black Spruce. Even though differences among the group means were not tested statistically because of small and unequal sample sizes among the groups, some interesting trends emerged in examining the pattern of CRI and ARI for the 3 different size classes (Figs. 8 and 9).

a) The ARI means of Group 1 (smallest trees) were always the largest, while means for Group 3 (largest trees) were the smallest for all 8 years after drainage.

b) In the first year after drainage, Group 3 had a negative ARI mean, while the other two groups had positive responses.

c) The number of years during which ARI was negative was less for smaller trees (Group 1) than for larger trees (Group 3). For Group 1 and Group 2, there were three years where mean ARI was negative (second to fourth year after drainage). For Group 3, ARI was negative for five years (first year to fifth year).

d) The largest negative ARI values for each group happened in different years. For Group 3, the value was -0.4549 and occurred in 1985. For Group 1 and Group 2 they were -0.2148 and -0.2666 and occurred in 1986 and 1987 respectively.

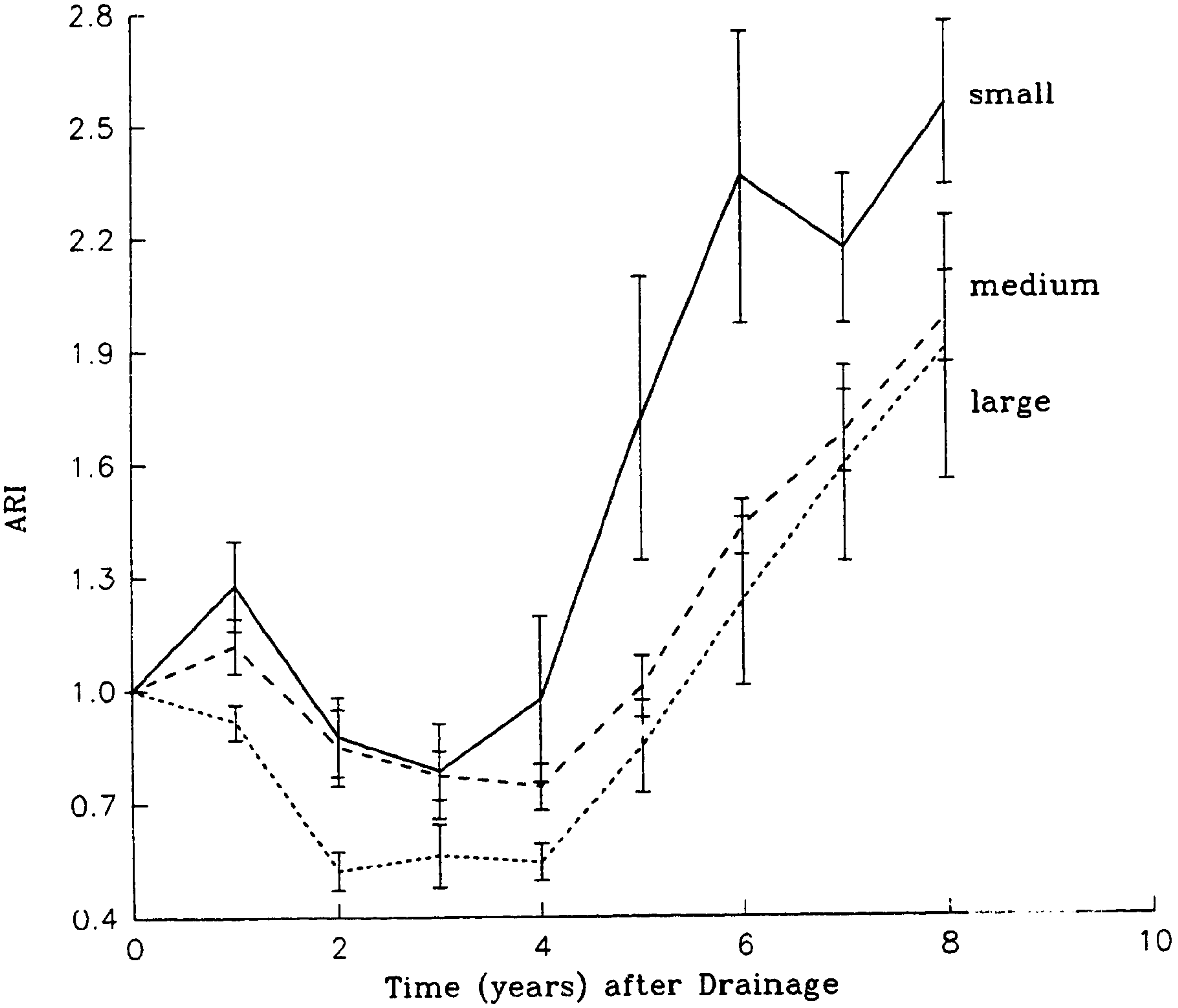

Fig.8. ARI of black spruce over time for the 3 groups of trees with different stem radius in the year before drainage (1983). Group 1 (——): the range of stem radius was 13–19.9 mm, n=8; Group 2 (- - - -): 20–26.9 mm, n=12; Group 3 (·······): 27–36.9 mm, n=5. Error bars = standard error of the mean.

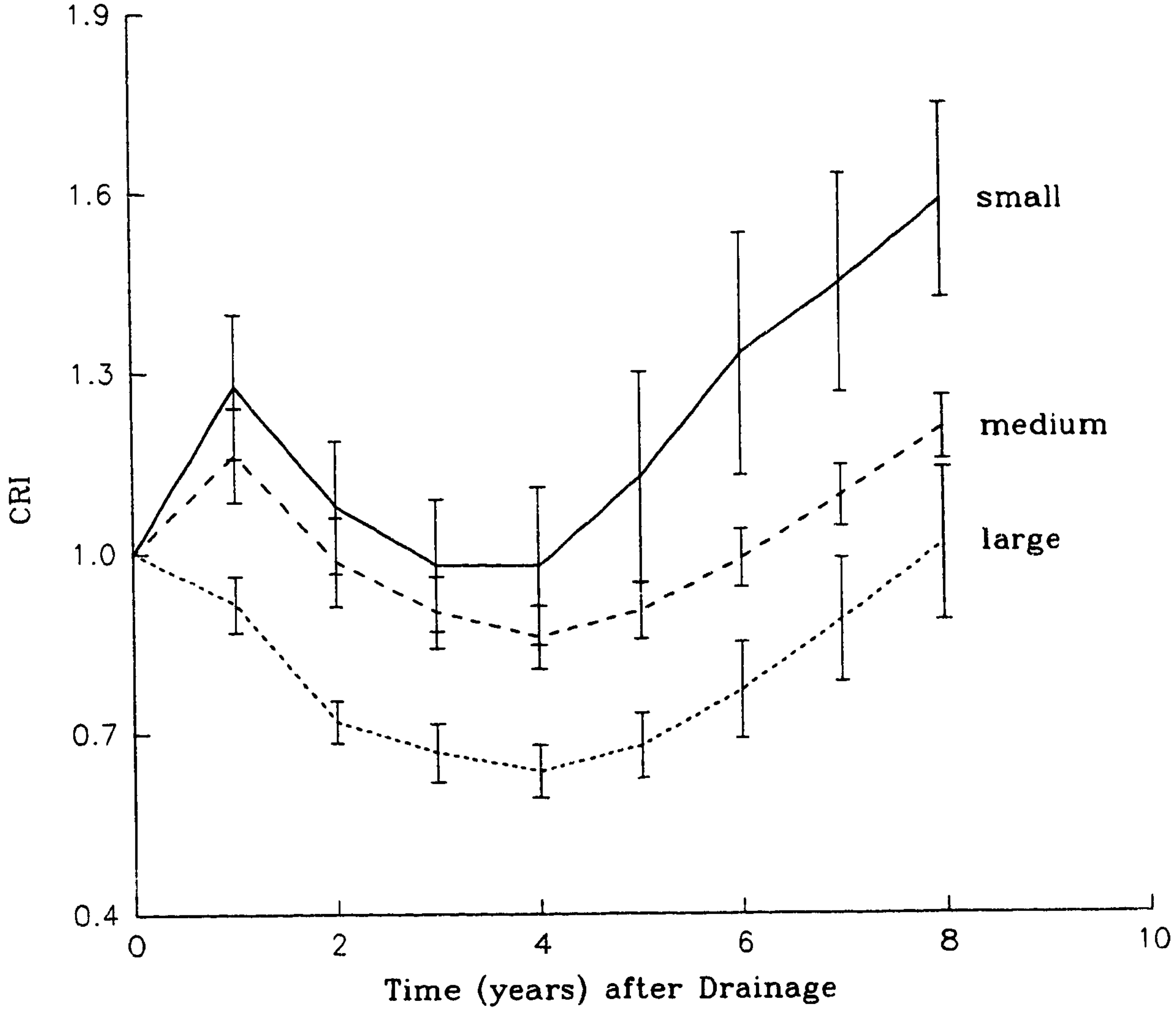

Fig.9. CRI of black spruce over time for the 3 groups of trees with different stem radius in the year before drainage (1983). Group 1 (——): the range of stem radius was 13–19.9 mm, n=8; Group 2 (----): 20–26.9 mm, n=12; Group 3 (·······): 27–36.9 mm, n=5. Error bars = standard error of the mean.

e) Group 1 had the fastest increase in ARI during the first three years after it became positive (year 4 to 6 after drainage) resulting in a great difference of mean ARI of Group 1 from those of the other two groups in the sixth year. After that, the ARI of Group 1 seemed to level off. During the seventh and eighth years after drainage, the differences in ARI among groups became smaller.

The relations of CRI among the three groups were similar to relations of ARI (Fig. 9). However, it took a longer time to get positive CRI values. It took roughly five years for Group 1, seven years for Group 2, and eight years for Group 3 to get a positive CRI. After eight years of drainage, trees in Group 1 grew 58% more than if they were undrained; trees in Group 2 grew 20% more; and trees in Group 3 had almost no response growth.

Tamarack. In the first two years after drainage, all trees had similar negative ARI (Fig. 10). From the third year, all groups had positive ARI. After that, ARIs for all groups increased almost linearly and the differences in mean ARI among groups became larger. ARI increase in the 3 groups was different. The small trees increased faster (Group 1 > Group 2 > Group 3). From the seventh year after drainage, ARI for Group 1 showed a slight levelling off like in black spruce.

Group 1 had negative CRIs for the first two years, while Group 2 and Group 3 had negative CRIs for the first

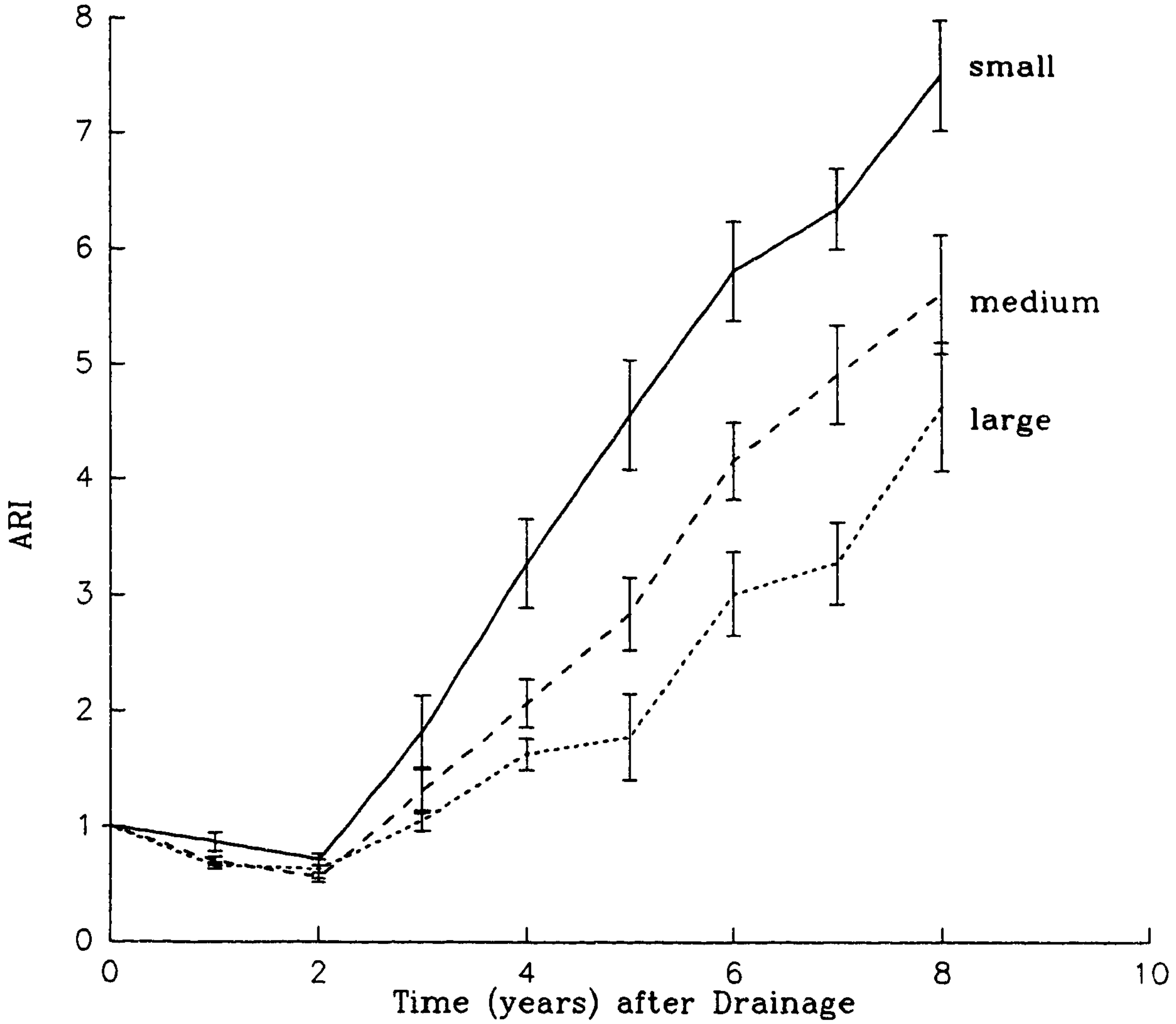

Fig.10. ARI of tamarack over time for the 3 groups of trees with different stem radius in the year before drainage (1983). Group 1 (——): the stem radius range was 15–20.9 mm, n=11; Group 2 (- - - -): 21–26.9 mm, n=9; Group 3 (·······): 27–34.5 mm, n=5. Error bars = standard error of the mean.

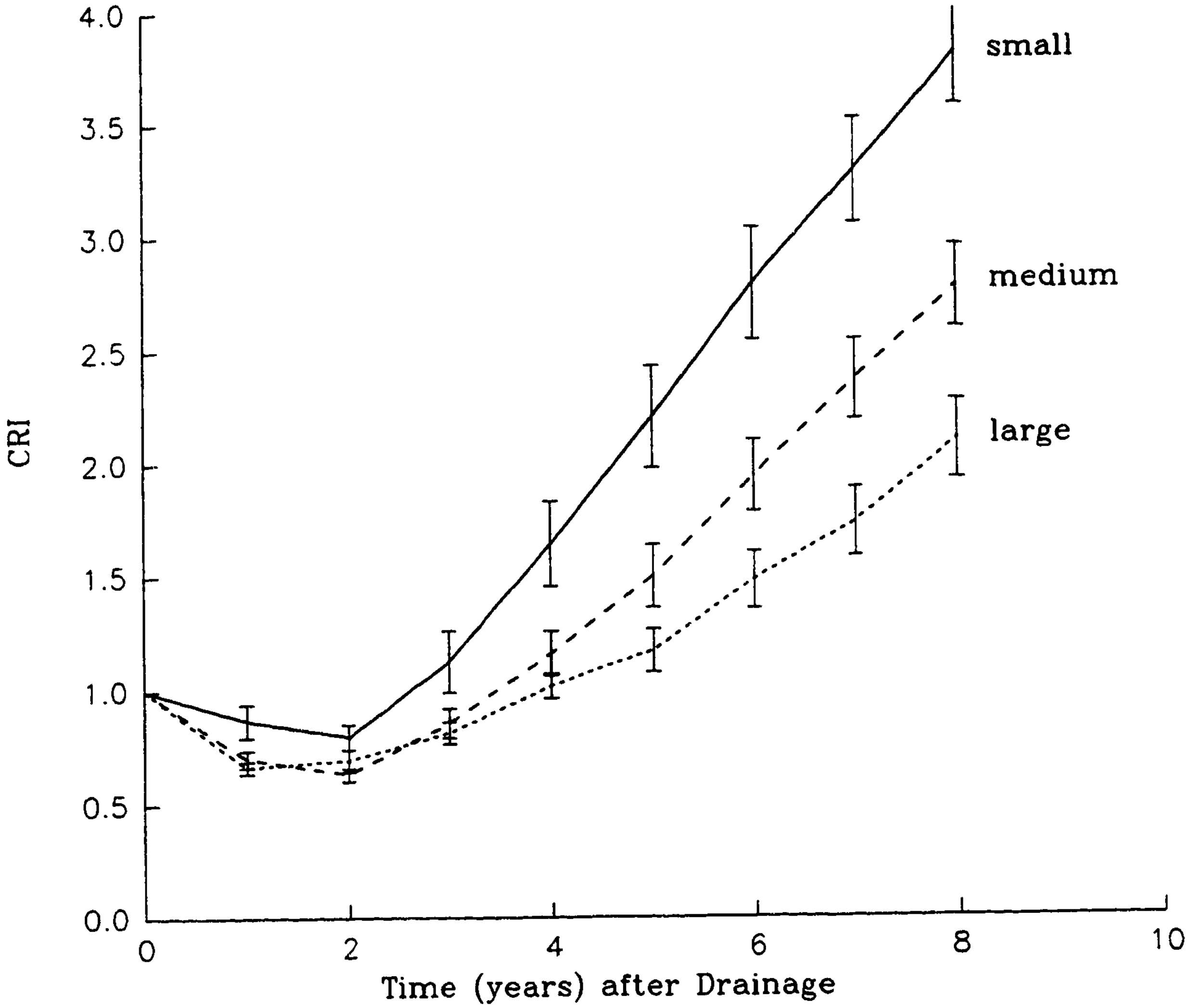

Fig.11. CRI of tamarack over time for the 3 groups of trees with different stem radius in the year before drainage (1983). Group 1 (——): the stem radius range was 15–20.9 mm, n=11; Group 2 (----): 21–26.9 mm, n=9; Group 3 (·······): 27–34.5 mm, n=5. Error bars = standard error of the mean.

three years (Fig. 11). From the third to eighth year, CRI of the smaller trees (Group 1) was larger than that of the larger trees (Group 3) with Group 1 > Group 2 > Group 3.

After eight years of drainage, CRI and ARI were 3.806 and 7.517 for Group 1, 2.774 and 5.622 for Group 2, and 2.10 and 4.643 for Group 3 respectively. Trees in Group 1, Group 2 and Group 3 grew 286%, 177% and 110% , respectively, more 8 years after drainage than if they were undrained.

Drainage-induced Population Size Structure Changes

CRI values of 1991 were regressed on radius of 1983 for both species (Fig. 12). The two regression functions had significant negative slopes (t-test, $p < 0.05$). This means that smaller (slowly growing) trees before drainage had larger CRI than larger (fast growing) trees. This response indicates that population (radius) variability and distribution in 1991 is different than it would have been if drainage did not occur. It is also different than it would be in the future if undrained trees grew to the same size as the drained trees were in 1991. For both species the regression slopes tell us that variability of tree size in the populations after drainage would be less than if drainage did not occur.

Coefficients of Variation of drained black spruce trees were 5.04 for the radius in 1983, 5.08 for the estimated radius in 1991, and 4.25 for the observed radius in 1991. For tamarack tney were 4.27, 4.52, and 3.37 respectively.

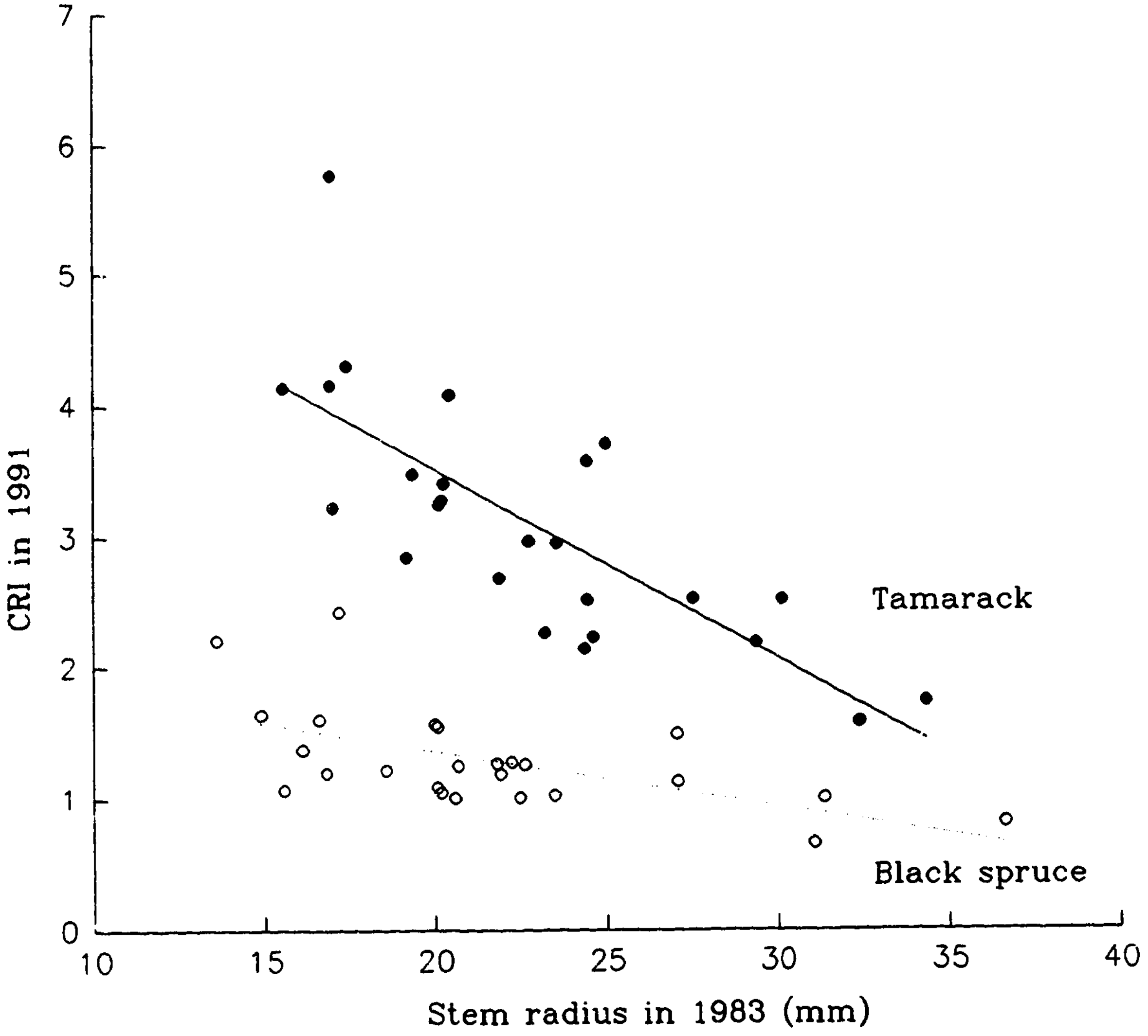

Fig.12. Regression of CRI in 1991 vs stem radius in 1983 for black spruce (○) and tamarack (●). The regression function is $Y=1.196-0.042X$, $R^2=0.357$ for black spruce, $Y=5.4048-0.1447X$, $R^2=0.586$ for tamarack. The slopes and intercepts between the two founctions are significantly different ($p<0.05$). The slopes of the two regressions are significantly different from 0 ($p<0.05$).

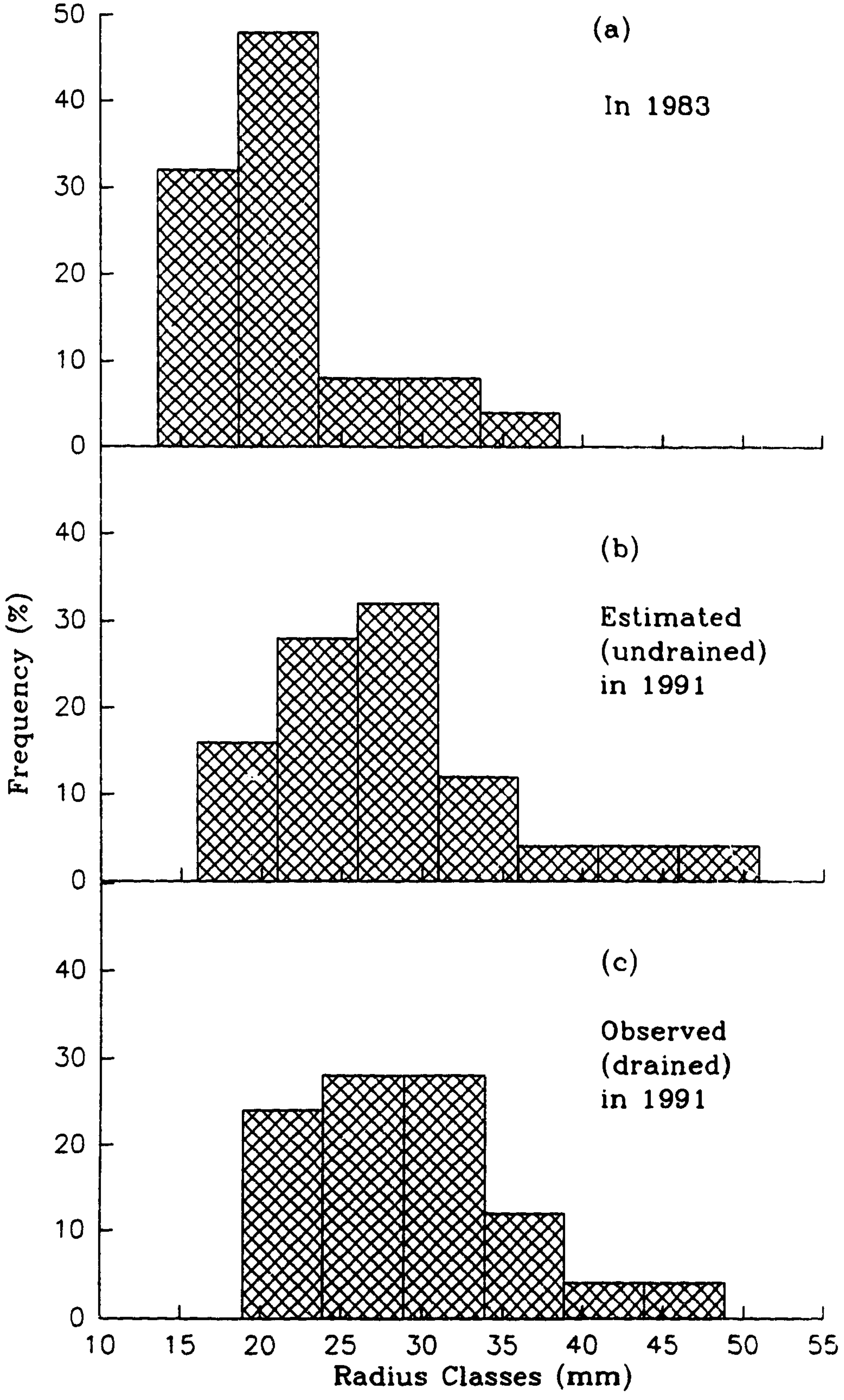

Fig. 13. Size (radius) frequency distribution of drained black spruce trees for (a) radius in the year before drainage (1983); (b) estimated radius in 1991; (c) observed radius in 1991. n=25 for each graph.

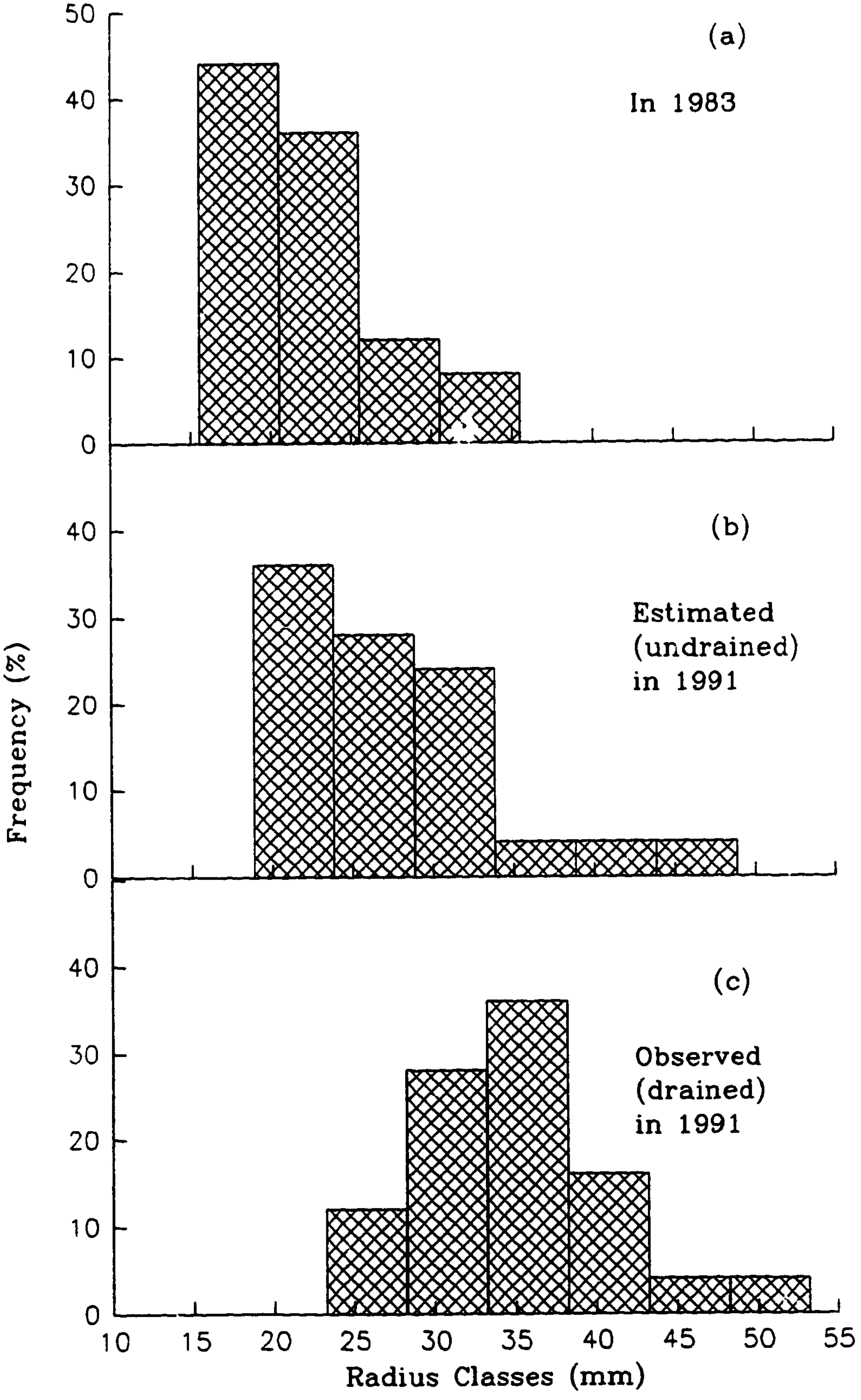

Fig. 14. Size (radius) frequency distribution of drained tamarack trees for (a) radius in the year before drainage (1983); (b) estimated radius in 1991; (c) observed radius in 1991. n=25 for each graph.

Figs. 13 and 14 show that diameter frequency distributions of drained trees are more normal than those if drainage did not occur.

The regression slope and intercept for CRI in 1991 vs radii in 1983 were more significantly different for tamarack than for black spruce (Fig. 12). For tamarack, the regression had a larger mean value, a significantly greater slope and a larger intercept. This indicates that a) tamarack had larger drainage-induced growth than black spruce, b) the effect of pre-drainage growth rate on release growth was stronger for tamarack than for black spruce, and c) the tamarack population would become more homogenous within a given time period after drainage than the black spruce population.

Discussion

Responses of trees with different growth rates prior to drainage

Trees with different growth rates prior to drainage had different responses to drainage. For both black spruce and tamarack trees growing more slowly before drainage showed greater release growth (ARI and CRI). Also, slow growing trees prior to drainage (Group 1) had the shortest time period with negative indices, the smallest negative ARI and CRI values, and the greatest increase in ARI and CRI once they became positive. The results conform to those expected if microenvironmental variability was influencing variability in growth rate of trees in natural peatlands (see explanation of hypothesis on page 14). Slower growing trees was primarily limited by poor microsite conditions prior to drainage and so benefitted more than faster growing trees from improved edaphic conditions accompanying drainage.

These results are consistent with those found in previous studies conducted by Heikurainen and Kuusela (1962) and Stanek (1968). In Heikurainen and Kuusela's (1962) study on the tree growth after drainage, they found that the greater the diameter the smaller was the release growth. The growth rate of trees which had been about 15 cm in diameter at the time of drainage was not improved. The growth rate of trees which were more than 15 cm in diameter, in fact, declined. The result from Stanek's (1968) study showed that trees growing well before drainage did not show marked growth improvement after drainage when compared to the trees which were not growing well. These previous studies, however, did not relate release growth to growth rate prior to drainage because trees were of different age and size.

The results from the present study may be attributed to many factors. Kramer and Kozlowski (1979) suggested that an abrupt change in environment does not alter growth similarly in all trees of the same species in a stand. They thought this may be the result of differences among trees in inherent growth characteristics, physical preconditioning of trees, and microenvironmental heterogeneity.

In my study, above and below-ground competition were not considered to be important because the trees were small and density was low. Also, the larger growth response of smaller size trees to drainage does not support my hypothesis concerning the existence of below-ground competition. I feel that inherent (genetic) differences in growth characteristics might not account for the different responses to drainage because the population was severely suppressed by environmental conditions and so genetic differences may have been masked. The most likely factors affecting the responses of trees to drainage are microenvironmental variability and tree size prior to drainage.

Microenvironmental factors. Variability in the microenvironment along the hummock-hollow complex may be very great. Some studies (Karlin & Bliss, 1983; Vitt et al., 1974; Crum, 1991) show differences along the hollow to hummock gradient in depth to water table (Karlin & Bliss, 1983), pH values (Karlin & Bliss, 1983; Vitt et al., 1974; Crum, 1991), substrate chemistry (Karlin & Bliss, 1983), bulk density (Karlin & Bliss, 1983), moisture (Karlin & Bliss, 1983; Vitt et al., 1974; Crum, 1991), and order of moss species (Karlin & Bliss, 1983; Vitt et al., 1974; Crum, 1991).

Microenvironmental effects on tree growth don't depend only on hummock-hollow differences. However, different positions in the hollow-hummock complexes are associated with different microenvironmental conditions which can affect tree growth such as water availability, soil aeration, temperature, and nutrient availability. These differences may then cause variability in tree growth if trees are growing at different positions on the hollow-hummock complex. According to Johnston and Carpenter (1985), hummocks of slow-growing Sphagnum moss generally favour seedling establishment. In their study on rooting of peatland black spruce and tamarack in relation to depth of water table, Lieffers and Rothwell (1987b) found that tree roots were largely restricted to hummock positions radiating from the base of the trees and maximum root depth was closely related to depth to water table. It is likely that the trees growing in or near hollows are under more stress and, therefore, grow more slowly.

After drainage, the microenvironment along the hollow -hummock complex must change although there are few direct studies showing how it changes compared with undrained peatlands. Trees growing in the changed micro-environment might have different growth responses because the drainage-induced changes in microenvironment might vary along hummock-hollow complex. Slowly growing trees responded better to drainage than fast growing trees. It is possible that slowly growing trees were situated in less favourable microenvironment prior to drainage so that they benefitted more from the improved and more uniform edaphic conditions following drainage. In addition, it is possible that drainage, in fact, resulted in a period of temporary stress which was more severe for faster growing trees.

Drainage can increase the uniformity of the substrate microenvironment in peatlands. Lowered water table after drainage lowers water content (Rothwell & Silins, 1990), increases soil aeration (Pessi, 1958), soil temperature (Lieffers & Rothwell, 1986; Swanson & Rothwell, 1989) and nutrient availability (Macdonald & Lieffers, 1990). All these improved soil conditions will favour peat decomposition, leading to soil mineralization and a more uniform soil microevironment. From casual observation, the physical differences between hollow and hummock were much smaller on the drained site than those on the undrained site. From this improved and more homogenous microenvironment, trees growing in poorer microsites might show more release following drainage.

After drainage, microenvironmental factors along the hummock-hollow complex may, from the plant point of view, even be reversed compared with those before drainage. For example, the hummock which may favour tree growth before drainage might become too dry and too high in temperature after drainage. After drainage trees growing on hummocks might be under more severe drought stress than those in hollows.

Tree size prior to drainage. Growth rate of the trees (tree size) prior to drainage may also influence the different responses to drainage. As trees increase in size, the ratio of stem to crown, the ratio of photosynthetic surface to nonphotosythetic surface, and the root-shoot ratio decrease gradually. The sheath of new xylem becomes progressively thinner. The distance from root to leaf increases (Kramer & Kozlowski, 1979). All these physical changes inevitably result in increasing difficulty in the translocation of carbohydrates, water, minerals, and hormones. Given this, it is not surprising that smaller trees should benefit more from drainage and grow faster than larger trees.

Initial Period of Growth Recession

There was evidence of an initial period of decreased growth after drainage for both tamarack and black spruce. CRI values became positive 5-8 years after drainage for black spruce, 3 years for tamarack. This was consistent with previous studies (Dang & Lieffers, 1989; Lieffers & Rothwell, 1987a). Dang and Lieffers (1989) showed that it took 3 to 6 years for any significant increase in annual radial increment. Lieffers and Rothwell (1987a) indicated that there was a reduction in leader elongation in 1984 and 1985. The latter study was conducted on the same site as this study.

Water Deficit. Many factors might have contributed to the initial period of growth recession. However, water stress was thought to be the cause (Lieffers & Rothwell, 1987a). Immediately after drainage, the soil-plant water relations are disturbed. The root systems of the drained trees were forced to grow in a new condition, probably under some level of drought stress. The drained trees needed sufficient time for full adjustment to the new growing conditions.

The direct reason for the drought stress would be lowered water table. Peatland trees usually have a very shallow root system (Lieffers & Rothwell, 1987b; Strong & La

Roi, 1983) because of the high water table. On wet and very wet sites, roots of black spruce and tamarack were generally restricted to the upper surface from 10 cm (Mannerkoski, 1985) to 20 cm on hummock position (Lieffers & Rothwell, 1986). Sometimes, they were 7-10 cm below ground level, just above the water table (Strong & La Roi, 1983). If the water table was reduced drastically, the root system might lose contact with the moist substrate. On the same site as I used, Lieffers and Rothwell (1987a) found drainage decreased the depth of the water table by as much as 50 cm one year after drainage and by more than 60 cm two years after drainage. This suddenly lowered water table might have resulted in a temporary disconnection of root systems from moist substrate, causing drought stress in the trees.

High water table has a greater inhibitory effect on growth of roots than on shoots, thus causing reduced root-shoot ratio and predisposing trees to drought injury following drainage (Kozlowski, 1982).

The water stress may have been exacerbated by increased substrate temperature. Generally, the drained sites had higher maximum temperature in the peat surface layers (Lieffers & Rothwell, 1986; Pessi, 1958; Swanson & Rothwell, 1989). This high temperature could lower relative moisture and accelerate soil evaporation, further exacerbating the drought stress. Higher diurnal temperature fluctuations on the drained site (Swanson & Rothwell, 1989) may also have resulted in drought stress.

Carbohydrate Distribution. Another factor influencing the reduction in diameter growth might be a change in carbohydrate distribution between the stem and the root system. After drainage, tree root growth might increase resulting competition for carbohydrates with the stem. Thus, the proportion of carbohydrate allocated to stems might be less than that before drainage. For a given species, the root-shoot ratio is rather constant (Kramer, 1979). Unfortunately, the most efficient root-shoot ratio is often altered by unfavourable environmental factors such as an excess of soil water (Kozlowski, 1982; Lees, 1973). When unfavourable environmental conditions are improved, physiological changes will occur, which would lead to additional root growth in order to bring the root-shoot ratio back into its characteristic balance (Kramer, 1979). It is possible that a higher proportion of carbohydrates are allocated into the roots of peatland trees after drainage. Therefore, the reduction in radial growth immediately after drainage might be due to preferential resource allocation to the root systems.

Other Factors. Delay of spring thaw in the drained site might also be involved in the reduction in initial growth after drainage. Lieffers and Rothwell's (1987a) study conducted on the same site used for my study showed that the substrate was warmed to above 0^0C later in spring

(5-6 days and 18-19 days later at both 10 and 30 cm depth) than in the undrained area. Because of low heat capacity and high heat conductivity in the fall, the drained substrate might cool sooner. This is supported by results from Swanson and Rothwell (1989) which suggest late warm-up and early cool-off in drained peatlands may reduce the time period for physiological activity of roots.

Nutrient availability and uptake are influenced by soil water conditions. Following drainage, the dried surface peat layer may not favour nutrient movement towards the roots. Initially, then, nutrient availability and uptake could be reduced.

Drought stress, a shortened warm temperature period and changed nutrient conditions may all be associated with the initial growth reduction after drainage. However, because water, temperature and nutrient conditions are always related with one another it will be difficult to separate the specific effects of each factor. Nevertheless, it was assumed that drought stress had a leading role (Lieffers & Rothwell, 1987a).

Growth Slow-down Seven Years after Drainage.

Seven years after drainage, ARI and CRI for group 1 of black spruce and tamarack began to decline. This trend was more clear for black spruce.

According to the principle of growth limiting factors, although several factors may be affecting tree growth rate, the factor present in the smallest amount may limit and control tree growth rate at a given time. Before drainage, high water level was likely the critical factor restricting the tree growth (Lieffers & Rothwell, 1986). In the initial years of drainage, drought stress may have played a leading role in reduction of the tree growth (Lieffers & Rothwell, 1987a). After that, the trees took advantage of the improved edaphic conditions and grew faster (Rothwell & Silins, 1990). However, this fast-growing period is unlikely to last forever because different growth limiting factors might be develop over time.

Swanson and Rothwell (1989) found that soil temperatures in the drained area were warmer at the surface and cooler at depth than the undrained areas. The warming of the surface layers as a result of drainage should have a positive effect on root growth in the upper substrate layer for a certain period of time. However, the cooler deep layers may have a negative effect on root penetration into deep strata. Lieffers and Rothwell (1987a) found that no coarse or very coarse roots and only few medium roots reached 30 cm depth, and most roots were distributed in the upper 20 cm layer 20 years after drainage. This suggests that after a certain time following drainage, the cooler temperatures in deeper layers may become more important in affecting the tree growth. The roots of small trees which presumably have smaller root systems may grow faster than those of the large trees in the initial years after drainage. They may then reach the cold layer earlier. Therefore, they show earlier slow-down of release growth.

Over time as the trees grow and the soil microenvironment becomes more uniform, release growth among groups may become more similar. At that point, the population will have reached a new balance of population size structure. Further studies are needed to confirm this hypothesis.

Changes in Population Size Structure

Size variability and distribution of the drained populations changed significantly 8 years after drainage. Compared with those estimated for populations if no drainage occurred or of no drainage-induced response growth occurred or if all trees showed similar response growth, the drained population had less size variability and a more normal size frequency distribution (Figs. 12. 13. 14). The drained populations also had the smallest Coefficient of Variation.

The pre-drainage radius frequency distribution showed most of the trees were in the smaller size classes (figs. 13. 14). This observation was similar to results from Lieffers'(1986) study. He found the frequency distribution of girth for natural peatland black spruce was positively skewed, which is probably typical in suppressed populations. The observed radius frequency distribution of this study in 1991 was more normal than the estimated frequency distribution in 1991. The direct reason was that smaller trees before drainage had greater response to drainage. A study by Hillman et. al. (1990) supports my results by showing a skewed frequency distribution in tree height before drainage and an almost normal distribution after drainage. In my study, the population size structure changed after drainage because trees that were growing more slowly prior to drainage showed greater response growth.

Different Responses of Black Spruce and Tamarack to Drainage

Figs. 12 shows that black spruce and tamarack responded differently to drainage. Average response growth and change in variability in population size structure were smaller for black spruce than for tamarack (Fig. 13 vs Fig. 14). These results were consistent with some other studies (Lieffers & Rothwell, 1987a; Rothwell & silins, 1990; Macdonald & Lieffers, 1990) which report larger responses of tamarack than of black spruce to drainage.

Because the two species grew in the same environmental conditions, the different responses may be caused by genetic factors. The following genetically controlled characteristics might contribute to the different responses of black spruce and tamarack to drainage.

Inherent Growth Rate. Tamarack is a fast growing tree species (William & Carpenter, 1985), while black spruce is a slow-growing species (Elias, 1985). Strong and La Roi (1983) found that tamarack had a higher rate of net biomass accumulation than did black spruce growing on the same site and of similar age. This inherent difference in growth rate may explain why the two species responded differently to drainage. The slow-growth trait of black spruce might result in lower levels of average response growth and changed population size structure for black spruce than those for tamarack.

Nutrient Uptake Ability. Macdonald and Lieffers (1990) thought that the different responses of black spruce and tamarack to drainage were due to differences in their abilities to take up and utilize nitrogen. They found the foliar nitrogen content and photosynthetic nitrogen use efficiency for black spruce were lower than those for tamarack. Therefore, tamarack may be better suited to take advantage of improved conditions following drainage.

Root System. Lieffers and Rothwell (1987b) showed that tamarack has a deeper root system than black spruce, especially on wet sites. The fine-root biomass for tamarack was generally larger than that for black spruce. Strong and La Roi (1983) also found that tamarack had a larger root : shoot ratio (0.53) than black spruce (0.45) and a larger root-spread : tree-height ratio (0.87) than black spruce (0.75). These root characteristics may be the key cause for the different response of the two species. Larger and deeper root systems have a greater ability to absorb water and nutrients, especially on a dry substrate after drainage.

Leaf characteristics. Tamarack is a deciduous species with indeterminate growth, while black spruce is an evergreen species with determinate growth. It might be easier for tamarack to adjust its leaf structure, leaf area and leaf photosynthetic ability to the changed environment (drainage) than black spruce. For black spruce, leaves formed in unfavourable conditions prior to drainage might be smaller, have lower surface area per weight, and display limited photosynthetic ability. These properties will not be easily changed in response to improved conditions accompanying drainage and the needles may be retained for up to 10 years. This may explain why black spruce took longer to show response growth to drainage than tamarack.

Summary and Recommendations

Summary

The results of my study showed that black spruce and tamarack trees with different growth rates prior to drainage had different response growth after drainage. Generally, slow growing trees had greater growth response than fast growing trees. Several factors may have contributed to the result. First, slow growing trees might get more benefit from the more uniform microenvironmental conditions along the hollow-hummock gradient after drainage. This suggests that variability in growth rate of trees in natural peatlands is influenced by microsite environmental variation. Second, the hummock top which might be a favourable microsite for tree growth before drainage might become too dry and too high in temperature for optimal tree growth after drainage. Therefore, fast growing trees which might grow on hummocks before drainage may be under greater drought stress after drainage than slowly growing trees located in different microsites. Finally, tree size may influence the ability of an individual to take advantage of improved conditions.

Eight years after drainage, variability in stem radius for the population of drained trees was smaller than that for the undrained trees. Tree size in a drained population can become more uniform after drainage. This is assumed to be the direct result of the different responses of trees with different size (growth rate) to drainage. The result shows that peatland drainage can not only increase tree productivity, but also may lead to decreased variability in tree size in populations.

Immediately after drainage, there was an initial period of reduced stem radial growth. This may be due to a sudden decrease in water table following drainage which could result in significant drought stress. Competition for carbohydrates by the root system, later warm-up and earlier cool-off of the drained substrate, and lowered nutrient movement may also be associated with this reduction in stem growth.

Seven years after drainage, release growth began to decline. This might be related to some newly produced growth limiting factor, such as cooling of the deep peat layer.

Black spruce and tamarack showed different responses to drainage. Tamarack had a greater average response growth and a larger change in population size structure. Factors such as inherent growth rate, nutrient up-take ability, root morphology and leaf characteristics might contribute to the different responses between the two species.

Recommendations

Results from this study suggest that tree size should be considered as one important factor in selecting sites to be drained along with site quality, species and tree age. Small trees may have larger relative release growth after drainage. However, this does not always mean it would make more economic sense to drain sites with smaller trees. Even with greater response growth, smaller trees may still have smaller absolute growth than larger trees which show less responses to drainage. There must exist a tree size at which the best results can be obtained both biologically and economically.

My results also showed that there was a reduction in stem radial growth in the initial years after drainage possible due to the sudden drop to 50-60 cm in water table in the initial years after drainage. Therefore, a system of drainage which allows for a gradual step-wise reduction in water table may produce a better result. Theoretically, there should exist a ditch depth for each stage of the drainage operation at which trees will not show a negative response to drainage. Practically, the depth of water table reduction at each step should depend on site conditions. The time intervals between each operation should be long enough to let drained trees have full adjustment to the new conditions.

The two tree species differed in their responses to drainage. Eight years after drainage, tamarack had much greater release growth than black spruce. It is strongly recommended that priority should be given to tamarack if black spruce stands and tamarack stands are both being considered for drainage and stand conditions are similar to those in this study.

Further intensive studies are necessary to confirm my results because this study was based on only one site and a small sample size. Specifically, further studies should give special consideration to larger sample size, more populations and age classes, a wider range of diameter classes and site quality, and a longer period of time after drainage (chose a site which has been drained for many years). The response of height and volume to drainage should also be examined.

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