

Assessment of patterns of response of tree ring growth of black spruce following peatland drainage

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A new procedure was developed for assessing the effects of drainage on tree ring growth. It uses both the pre-drainage growth of the drained site and the post-drainage growth on an adjacent undrained site as controls in estimating tree ring growth response following drainage. The procedure allows the calculation, on a yearly basis, of the net response of tree ring growth to peatland drainage. The new procedure was applied to black spruce on six peatlands in central Alberta; these sites were drained in 1966. The average age of trees on the sites ranged from 33 to 107 years at time of drainage. The response patterns were as follows: for the first 3 to 6 years following drainage, the tree ring growth did not increase in response to drainage. After that, the net increase in tree ring growth increased nearly linearly until reaching a maximum 13 to 19 years after drainage. The maximum net increases ranged from 76 to 766% of the projected growth of the trees if the sites had not been drained. The net increases fluctuated near the maximum value thereafter. The year to year fluctuations in tree ring index on the drained sites corresponded to the yearly fluctuations on the natural sites.

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Un nouveau procédé a été élaboré pour évaluer les effets du drainage sur la croissance radiale des arbres. Ce procédé utilise à la fois la croissance antérieure au drainage dans le périmètre drainé et la croissance postérieure au drainage dans un endroit adjacent au périmètre drainé comme témoins pour évaluer la réponse en croissance radiale des arbres à la suite du drainage. Ce procédé permet de calculer, pour chaque année, la réponse nette en croissance radiale des arbres au drainage d'une tourbière. Ce nouveau procédé a été appliqué à l'Épinette noire dans six tourbières du centre de l'Alberta; ces lieux avaient été drainés en 1966. L'âge moyen des arbres y variait de 33 à 107 ans au moment du drainage. La réponse a donné les résultats suivants : durant les 3 à 6 premières années suivant le drainage, la croissance radiale des arbres n'a pas augmenté par suite du drainage. Par la suite, l'augmentation nette de la croissance radiale s'est faite presque linéairement jusqu'à un maximum qui a été atteint 13 à 19 ans après le drainage. Les augmentations maximales nettes ont varié de 76 à 766% par rapport à la croissance projetée des arbres si le périmètre en cause n'avait pas été drainé. Les augmentations nettes de la croissance ont fluctué autour de la valeur maximale durant les années suivantes. Les fluctuations annuelles de l'indice de croissance radiale dans le périmètre drainé correspondaient aux fluctuations annuelles observées dans les endroits non-drainés.

[Traduit par la revue]

Introduction

The vast areas of peatlands in Alberta and elsewhere in Canada have great potential for forestry (Hillman 1987). However, the productivity of trees in natural peatlands is generally low because high water table, cold substrate, poor aeration, and inadequate available nutrient supply limit tree growth (Payandeh 1973; Mannerkoski 1985; Hillman 1987; Lieffers and Rothwell 1986, 1987b).

The tree growth in peatlands, however, can be improved by drainage. Large increases in tree diameter and height growth after drainage were reported (Heikurainen and Kuusela 1962; Stanek 1968, 1977; Payandeh 1973; Richardson 1981; Trottier 1986). Fine root biomass and the maximum rooting depth of black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch.) increase after drainage (Lieffers and Rothwell 1987b). The nitrogen content of tree foliage also increases after drainage (V.J. Lieffers, unpublished data).

The shape of the curve of net increase in tree growth following drainage is less clear. Lieffers and Rothwell (1987a) suggested that following drainage there might be a period when trees grow more slowly than normal. Studies from Finland (Seppälä 1969) did not report a slowing in growth, but indicated that tree growth did not increase during the first few years after drainage. No quantitative studies

have been conducted on the patterns of annual growth response following drainage.

Three methods have been used to evaluate the effects of peatland drainage on tree growth where drainage occurred partway through the life of the trees: (i) some workers (Heikurainen and Kuusela 1962; Stanek 1968; Payandeh 1973, 1975) directly compared the average tree ring growth of pre-drainage and post-drainage; (ii) Stanek (1977) estimated the drainage effects using the difference in site index between the drained site and an adjacent undrained site; (iii) Payandeh (1982) compared the average post-drainage tree growth of drained peatlands with adjacent undrained sites. However, there are drawbacks with these methods:

- (1) Generally, tree ring width varies as the trees age. Ring width increases up to the juvenile stage and then decreases. Method *i*, a simple comparison of ring growth before and after drainage, does not take this intrinsic trend into account.
- (2) In method *ii*, the total height observed after drainage on a drained site is the combination of two parts: the height added before drainage and the height added after drainage. Because drainage changes the site quality, the two parts follow different growth curves even though there might be a transition between them.

TABLE 1. Correlation coefficients for some trees from drained sites

Tree ^a	<i>r</i>	<i>n</i>	Tree ^a	<i>r</i>	<i>n</i>	Tree ^a	<i>r</i>	<i>n</i>
1.1.2	-0.456*	19	1.2.3	-0.647**	18	1.2.2	-0.739**	19
1.2.5	-0.902**	22	1.2.9	-0.942**	21	2.1.5	-0.674**	30
2.1.6	-0.683**	22	2.2.4	-0.692**	20	2.2.7	-0.600**	21
2.2.8	-0.512*	21	3.1.4	-0.818**	15	3.1.7	-0.719**	20
3.1.9	-0.725**	20	3.2.3	-0.905**	23	3.2.7	-0.751**	22
4.1.6	-0.536*	19	4.1.7	-0.512*	20	4.1.8	-0.718**	22
4.2.6	-0.612**	20	4.2.8	-0.615**	19	5.1.1	-0.836**	52
5.1.2	-0.722**	31	5.2.1	-0.627**	60	5.2.7	-0.623**	31
5.2.9	-0.627**	40	6.1.2	-0.437**	26	6.1.5	-0.796**	60
6.2.1	-0.437**	43	6.2.4	-0.653**	65	6.2.5	-0.452*	26

NOTE: *r* is the correlation coefficient and *n* is the number of data points used in developing the regression equation.

^aThe three numbers are site, replicate number within site, and tree number within site, respectively. The trees listed in this table were selected randomly from all the samples, five trees from each site.

**P* < 0.05.

***P* < 0.01.

If drainage improves site quality, then the site index of the drained site, which is determined from the postdrainage tree height, will be lower than the true site index of the current site. Thus, this site index method underestimates the drainage effects.

- (3) In method *iii*, growth rates, stand population structure, and site conditions in natural stands are generally highly variable, and this precludes the direct comparison of post-treatment growth between treatment and control sites without taking into account the pretreatment growth (Salonius et al. 1982; Ballard and Majid 1985).

In fertilization experiments, pretreatment tree growth as well as tree growth on control sites are used in evaluating the fertilizing effects on tree growth (Salonius et al. 1982; Ballard and Majid 1985). The basic assumption for those methods is that the ratio of pretreatment periodic growth to post-treatment periodic growth for the treatment site is equal to that of the control site if the treatment did not occur. This method accurately estimates net increase of periodic growth following treatment, but is not appropriate for evaluating patterns of response.

The objectives of this study were (*i*) to develop a new procedure for evaluating the pattern of response of annual tree ring growth following drainage and (*ii*) to describe the pattern of tree ring growth response of black spruce following peatland drainage.

Materials and methods

Study sites and sample collection

The study area is located east of Slave Lake, Alberta, along provincial highway no. 2. The highway was built across a treed fen in 1966 (Liefers and Rothwell 1987b). The road bed and associated ditches interrupt local shallow groundwater flow, resulting in a lower water table downslope. Upslope of the road and farther away from the ditch, the water table was not influenced by the road building. This situation provided a natural drainage experiment for this study. Stanek (1977), Payandeh (1982), and Liefers and Rothwell (1987b) used similar situations to study the effects of drainage on tree growth. The forests in this area are dominated by black spruce with scattered tamarack. Understorey is dominated by *Ledum groenlandicum* Oeder, *Rubus chamaemorus* L., *Sphagnum magellanicum* Brid., and *S. warnstorffii* Russ. On the drained site, *Pleurozium schreberi* (Brid.) Mitt and *Hylocomium splendens* (Hedw.) B.S.G. are more abundant.

Six drained peatland sites were selected. They were located at 55°10'N, 114°16'30"W; 55°10'45"N, 114°20'W; 55°10'15"N, 114°17'W; 55°11'N, 114°20'30"W; 55°09'25"N, 114°13'30"W; and 55°07'25"N, 114°10'10"W. The trees were recruited from seeds after fire, and these stands were relatively even-aged. The stands ranged from 33 to 107 years old at the time of drainage. Downslope of the highway, plots were laid out 5 m from the road right-of-way. Upslope and 90 m from the cleared right-of-way, plots were chosen as control sites. Each site (both drained and undrained) had two replicate plots of 20 × 5 m, which were 20 m apart and parallel to the highway. Each of the pairs of sites (drained and undrained) were distributed in similar landforms. The uniformity among those sites prior to the road construction was confirmed by examination of 1965 aerial photographs. The difference in mean age of the trees between the drained and control sites was less than 2 years in all cases.

In June 1987, a 5 cm diameter perforated plastic pipe was installed in the centre of each of the plots on both drained and undrained sites. The depth to water table in the pipes was measured biweekly from June 11 to August 26, 1987. In mid-September of the same year, 10 dominant-codominant black spruce were selected from each plot on both sites. Cross sections at the tree base and at 130 and 30 cm height positions were cut from each tree for age and tree ring width measurement, respectively. To assure an adequate length of control period (see Discussion for definition and importance of control period), especially for young stands, the tree ring data from 30 cm height were used for analyzing tree-growth response. These trees did not demonstrate significant butt swelling at 30 cm height. The higher sensitivity to climate of tree rings at this height than at the base (Dang and Liefers 1989) also made it more efficient to remove climatic effects when analyzing tree response to drainage. Tree heights were also recorded for calculation of site index. The discs were air-dried and sanded by a belt sander. The width of annual rings at four radii along the longest and shortest diameters of each disc was measured using a computerized measuring device (Clyde and Titus 1987). Cross dating (Fritts 1976) was conducted among radii, trees, and then sites by comparing ring width to age graphs.

Analysis

Estimation of tree ring index for drained sites

As shown by comparing the general shapes of the relationship between ring width and tree age from the undrained site (Fig. 1) and drained site (Fig. 2), the ring growth in the drained site increased following drainage. The first step in estimating the size of this increase was to estimate the ring growth curve for trees in the drained site that the tree growth would follow both before and after drainage, if the drainage did not occur. The procedures were as follows. For each tree from the drained site, regression pro-

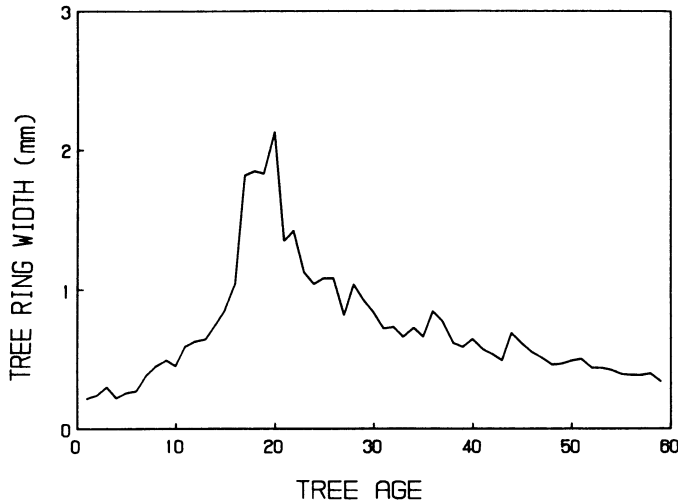


FIG. 1. Tree ring width at 30 cm height of a black spruce from an undrained peatland. Age was determined at 30 cm height.

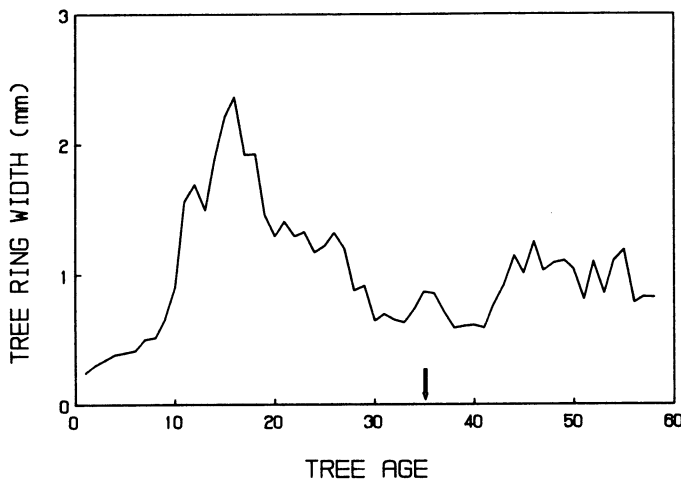


FIG. 2. Tree ring width at 30 cm height of a black spruce from a drained peatland. Arrow indicates the time of drainage. Age was determined at 30 cm height.

cedures were used to fit a negative exponential function (Fritts 1976; Till 1987) to the observed tree ring width data for the period from the growth peak to the time of drainage (Fig. 3). All the regression coefficients were significant ($P < 0.05$): the correlation coefficients ranged from -0.45 to -0.94 , with an average of -0.67 (Table 1). Residuals of these regressions were normally distributed for 91% of the trees (χ^2 test). Each observed ring width, both predrainage and postdrainage, was then divided by the corresponding value from the regression equation to give the tree ring index (Fritts 1976). However, the regression equations were extrapolated for the postdrainage period.

Test for the validity of extrapolation

Negative exponential functions were also applied to the tree ring data from the undrained site for, first, the period from the growth peak to the time of drainage and then the period from the growth peak to the time of sampling. Thus, two equations were generated for the same tree. The correlation coefficients for both sets of regression equations ranged from -0.4 to -0.93 and were statistically significant ($P < 0.05$). By dividing each observed tree ring width by the predicted values from the two different equations, two sets of tree ring indices were obtained for each tree. The first equation and the tree ring indices derived from it, however, estimated the postdrainage tree ring growth by extrapolation of

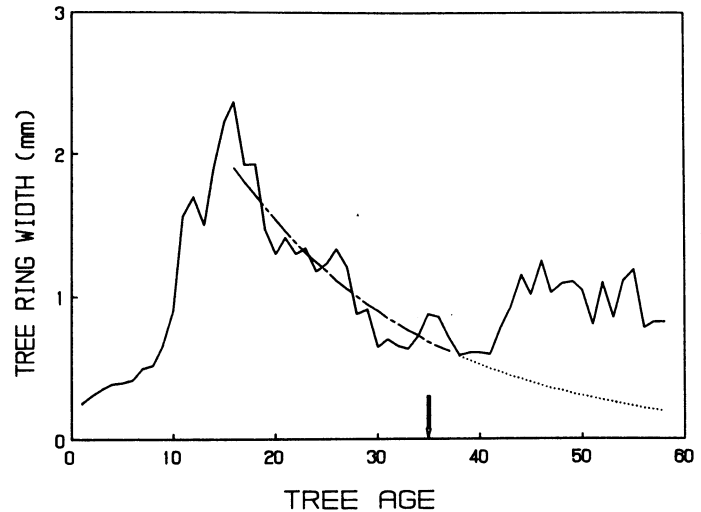


FIG. 3. Tree ring width of the same tree as in Fig. 2 with trend line (---) for the period from peak growth to drainage and its extrapolation (....) into the postdrainage period. The equation of the trend line is as follows: $\ln(I) = 1.5019 - 0.0539 \times \text{age}$, where I is tree ring width and age is tree age; $r^2 = 0.839$, $n = 23$.

the equation similar to the procedures for the drained site. Paired t -tests showed that for the postdrainage period, the means of the differences between pairs of tree ring indices were not significantly different from zero at 0.05 level for 90% of the trees and at 0.01 level for all of the trees. Where significant ($P < 0.05$), t -values were positive for some trees but negative for others, suggesting that the technique was unbiased. This indicated that the extrapolation technique gave a reasonable prediction of the postdrainage annual ring widths for the drained site if the drainage had not occurred.

Estimation of tree ring response to drainage

Differences in the means of tree ring indices between drained and corresponding undrained sites for the postdrainage period were examined by analysis of variance. The tree ring indices for all of the trees from the pairs of plots at each site were then averaged (separately for drained and undrained sites), year by year, to obtain the average tree ring index series for each site. The average tree ring index series of the undrained site was subtracted, year by year, from that of the corresponding drained site, and the differences for the postdrainage period were used as estimators of net response of annual ring growth to drainage. The net response values were plotted against the time elapsed (in years) after drainage.

Variables for growth response and site quality

The null response period was defined as the time period from the time of drainage to the time when the net response value was approximately equal to the maximum value in the predrainage period. The average slope from this point of minimum net response to that of the maximum net response was defined as the increase rate. The length of the null response period, increase rate, maximum net responses, and the time from the year of drainage to the year of maximum net response were compared with (i) the tree age, (ii) initial site index, i.e., the site index at the time of drainage (Alberta Forest Service 1985), and (iii) the difference in average postdrainage water table between the drained site and corresponding undrained site.

Results

The tree ring indices of the drained and undrained sites generally had similar patterns of year to year fluctuations for both predrainage and postdrainage periods (Fig. 4). This suggests that trees from the drained and undrained sites generally had similar direction of response to environmental

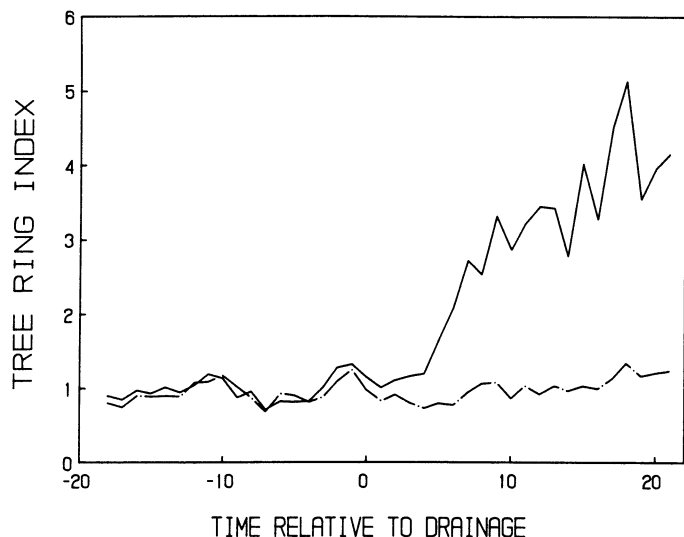


FIG. 4. Tree ring indices of black spruce from site 1 (solid line) and its control site (broken line) for both predrainage and postdrainage periods. The time of drainage is indicated by a time value of 0.

TABLE 2. Analysis of variance for the difference in means of postdrainage tree ring indices between drained and undrained sites

Site No.	MS(<i>t</i>)	df(<i>t</i>)	MS(<i>e</i>)	df(<i>e</i>)	<i>F</i> ratio	<i>P</i>
1	132.67	1	14.90	34	8.90	0.00227
2	32.58	1	0.81	35	40.22	0.00000
3	36.44	1	1.92	32	19.02	0.00000
4	9.23	1	2.07	36	4.46	0.02160
5	0.89	1	0.20	33	4.45	0.02190
6	32.58	1	0.94	34	34.76	0.00000

NOTE: MS(*t*) and df(*t*), mean squares and degrees of freedom, respectively, for treatment; MS(*e*) and df(*e*), the mean squares and degrees of freedom, respectively, for the error term; *P*, probability for larger *F* values.

fluctuations. However, the average tree ring indices from all of the drained sites were significantly greater than those of the corresponding undrained sites for the postdrainage period (Table 2).

The length of null response period varied from 3 to 6 years (Fig. 5). After this period, however, the net increase values increased in a pattern that was nearly linear with time (Fig. 5). The annual increase rates varied from 6 to 69%. The net increase reached a maximum value between 13 and 19 years after drainage. The maximum values of net increases ranged from 76 to 766%. The net increases fluctuated at values near the maximum thereafter.

The data also suggest that the amount of water table drop after drainage had a positive impact on the response of tree ring growth to drainage, but the initial tree age and site index had negative effects (Table 3). However, there were not sufficient data in this study for any conclusions to be drawn.

Discussion

The main benefit of this modified dendrochronology technique over the ratio method used in fertilization studies (Salonius et al. 1982; Ballard and Majid 1985) is that the yearly pattern of net response of tree growth to peatland drainage is provided. The use of both the tree growth in a control site and the predrainage growth (control period) of the drained site as controls for postdrainage tree growth of

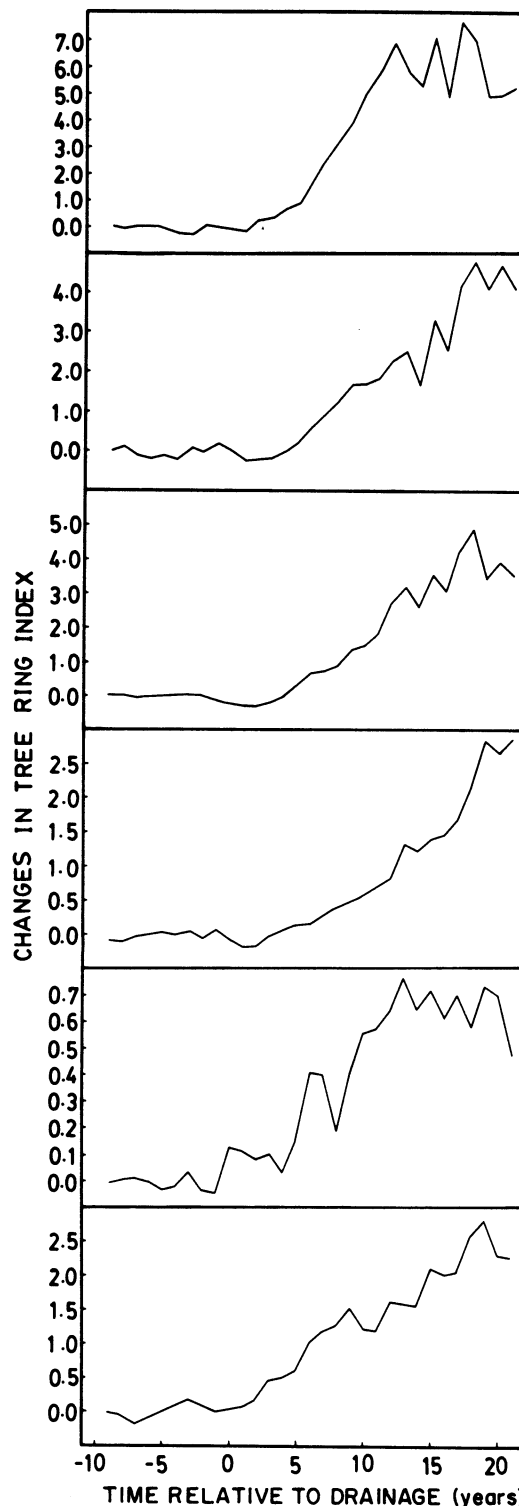


FIG. 5. Differences in tree ring indices of black spruce between drained and undrained sites before and after drainage from six Alberta peatlands. The time of drainage is indicated by a time value of 0. Sites are listed sequentially, site 1 at the top and site 6 at the bottom.

the drained site adds another benefit. There is a less strict requirement for matching site quality or tree age of control and treatment sites (Fritts 1976). The output from these methods is a net relative increase and thus is comparable between different regions and sites with different initial site quality and (or) different tree ages.

TABLE 3. Postdrainage changes in tree ring index in relation to the tree age and site index at the time of drainage, and depth to water table after drainage

No.	Age	Depth 1 (cm)	Depth 2 (cm)	Difference (cm)	SI	NP	IA	IR	Max	YM
1	33	87.9	30.9	57.0	8.0	4	4.70	0.69	7.66	17
2	41	61.5	42.8	18.7	7.0	6	2.02	0.27	4.80	18
3	43	87.0	53.4	33.6	8.5	6	2.01	0.31	4.93	18
4	45	45.0	27.6	17.4	8.2	6	1.01	0.16	2.86	19
5	49	59.1	38.2	20.9	9.1	6	0.46	0.06	0.76	13
6	107	69.0	45.1	23.9	2.8	3	0.97	0.13	2.82	19

NOTE: Depth 1 and depth 2 are depth to water table for drained and undrained sites, respectively, and are averages of seven measures (June to August 1987); difference = depth 1 - depth 2; age = tree age at the time of drainage; SI = initial site index (tree height in metres at the age of 50 years); NP = length of null response period; IA = average of change in tree ring index after drainage; IR = increase of tree ring index per year in the postdrainage period; max = maximum increase of tree ring index after drainage; YM = years from the time of drainage to the time of maximum increase.

The precision of this technique, however, depends on the number of years of tree ring data prior to treatment. If this period is too short, the regression line, which is used to derive tree ring index, could deviate considerably from the true growth trend and result in unreliable predictions for postdrainage tree growth. This method could also be used in other situations where the yearly pattern of net response of tree growth to treatments is desired (e.g., estimating effects of air pollution on tree growth).

Whereas there is some information on climate and tree ring growth of black spruce on natural peatlands (Dang and Lieffers 1989), the relationship between climate and tree growth on drained peatlands is less understood. In natural peatlands, tree ring growth of black spruce is positively related to summer precipitation and mean minimum temperature, but negatively related to summer mean maximum temperature (Dang and Lieffers 1989). From the reasonably good matching of the patterns of tree ring index between drained and undrained peatlands (Fig. 4), it appears that the relationships between tree growth and climate may also hold for black spruce in drained peatlands.

Even though the drainage improves substrate aeration and speeds decomposition of organic matter (Lahde 1966; Lieffers 1988), the change in growth rates in response to these improved conditions is not immediate. The root system (Lieffers and Rothwell 1987b) and leaf area of black spruce in natural peatlands is small. Thus, in early stages after drainage the amount of photosynthetic product is probably still low. Also, it is hypothesized that stemwood has a lower priority for resources than leaves or root systems (Waring and Pitman 1985). Therefore, immediately following drainage, little increase in tree ring growth is possible as the trees are probably allocating resources to develop root systems and leaf area. This period of null increase lasts from 3 to 6 years (Fig. 5). This agrees with results from Finnish sites (Seppälä 1969). The 13 to 19 years for the trees to reach a stable condition after drainage probably relates to the same factors of gradual development of roots and leaf area. It may also relate to the gradual increase in available nutrients and the improvement in substrate conditions. It is difficult to isolate the sources of the increased tree ring growth. The improvement in tree root systems, leaf area, and substrate conditions are themselves interrelated.

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