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Factors influencing size inequality in peatland black spruce and tamarack: evidence from post-drainage release growth

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Summary

1 We used tree ring analysis to determine stem radius and thus examine size variation over time in two even-aged (approximately 40-year-old) mixed populations of black spruce and tamarack established on peatlands in a boreal forest. We also followed the response of one of these populations to improved edaphic conditions over 8 years following drainage.

2 Populations of trees in undrained areas showed a decline in size variability over time until age 20–25 years, after which size heterogeneity was relatively stable.

3 For trees in undrained areas there was a relationship between age and size for the first 20–25 years, but this relationship then broke down due to a period where relative growth rate and size were inversely related.

4 For the population of trees in the drained area, smaller trees (i.e. those that had been growing more slowly prior to drainage) showed significantly greater drainage-induced release growth, while larger trees (those growing faster prior to drainage) showed an initial reduction in growth following drainage and, overall, less release growth.

5 The response of tamarack to drainage was more dramatic than for black spruce.

6 Despite extensive variation in tree size, drainage dramatically reduced variability in growth rate among trees of each species, such that size variability in the populations declined.

7 We postulate that the heterogeneity of microsites with respect to edaphic conditions, perhaps associated with the hummock to hollow microtopographic gradient, has a major influence on growth variation, and hence size inequality, in peatland populations of black spruce and tamarack.

Keywords: competition, forest heterogeneity, microsite, peatland, relative growth rate, size variability

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Introduction

Size variability among individuals is a ubiquitous phenomenon in populations of plants (Weiner & Thomas 1986) and has been reported for several species of trees (Brand & Magnussen 1988; Knox *et al.* 1989; Stoll *et al.* 1994). Such variation may be due to age differences, genetic or maternal effects, environmental heterogeneity, competition, or other biotic influences (Weiner & Solbrig 1984). Under conditions where growth is exponential even small age differences will lead to increasing size inequality over time, and this trend will be exaggerated further if asymmetric competition is also operating (Weiner & Thomas 1986). Thus, in crowded populations, size variability tends to increase until the onset of self-thinning (Weiner 1990). However, in situations with little competition or where competition is symmetric there should be little divergence in sizes over time. In even-aged plant populations the pattern may change over time, because very early competition is symmetric and occurs primarily below-ground, while asymmetric competition for light increases in importance at later stages (Weiner 1990; Schwinning & Weiner 1998).

In peatlands in the boreal forest in North America

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black spruce [*Picea mariana* (Mill) B.S.P.] and tamarack (*Larix laricina* (Du Roi). K. Koch) commonly establish in open forest stands. Growth of these trees is extremely slow due to the high water table, poor soil aeration, cold substrate, and low nutrient availability of these sites (Payandeh 1973; Lieffers & Rothwell 1986, 1987a; Macdonald & Lieffers 1990). Even-aged black spruce populations on peatlands have a wide variability in growth rate (Jeglum 1972), but Lieffers (1986) found that this did not appear to be related to competition, even in a crowded population.

Drainage of peatlands lowers the water table and can result in increased substrate temperature, improved aeration, and/or increased nutrient availability and uptake (Grootjans *et al.* 1985; Lieffers & Rothwell 1987a; Lieffers 1988; Macdonald & Lieffers 1990), resulting in dramatically improved growth of trees (Richardson 1981; Hillman 1987; Dang & Lieffers 1989). Smaller (Heikurainen & Kuusela 1962) and younger (Stanek 1968; Payandeh 1973) trees show greater release following peatland drainage, which may thus affect the size structure as well as the overall productivity of the stand. Indeed, black spruce trees in an undrained area were characterized by a skewed size distribution, while those in a drained area had a more normal distribution (Hillman *et al.* 1990).

Peatland drainage therefore provided us with an opportunity to examine the underlying causes of size variability in black spruce and tamarack, specifically the effects of competition and microsite variability. The improved rooting environment that follows drainage should be associated with release from, or reduction of, below-ground competition and/or environmental limitations. We used dendrochronology to document changes in size variability of populations of black spruce and tamarack and to quantify drainage-induced release growth as related to tree size or growth rate prior to drainage. We hypothesized that if the smaller trees were those that were limited by poor microsite conditions, and drainage resulted in a greater improvement in edaphic conditions at these sites than at more favourable sites, then small trees would benefit more from drainage. Alternatively, if below-ground competition was operating in these stands then either all trees should, initially, benefit equally from the improved resource availability accompanying drainage (if competition is completely symmetric), or the benefit should be in direct proportion to their size (if competition is size-symmetric), or the benefit should be observed mainly in larger trees (if competition is size-asymmetric).

Materials and methods

SITE DESCRIPTION AND SAMPLE COLLECTION

The study site was a treed fen about 36 km south-east of Slave Lake, Alberta, Canada (55°08′N, 114°15′W) (for a further description see Lieffers & Rothwell 1987a; Toth & Gillard 1988). The site was covered by an open canopy, low stem density mixed stand of black spruce (1875 trees ha^{-1}) and tamarack (2250 trees ha^{-1}), about 40 years old. In this area, *Betula pumila* L., *Andromeda polifolia* L. and *Ledum groenlandicum* Oeder were dominant shrubs and *Sphagnum warnstorfii* Russ. and *Tomenthypnum nitens* (Hedw.) Loeske were common mosses.

In 1984 a network of ditches was dug in a 50-ha area, resulting in a lowering of the water table by 20–50 cm (Lieffers & Rothwell 1987a), a reduced substrate water content (Rothwell & Silins 1990), an increased rate of decomposition (Lieffers 1988) and increased surface substrate temperatures (Swanson & Rothwell 1989). We established a 6-ha plot at the north end of the drained area, where the ditches were 25 m apart. A similarly sized control plot was established in an adjacent undrained area at least 100 m from any drainage ditches. In order to reduce the effects of initial age differences, we cored 30 trees of each species in each plot and then selected 25 similarly aged specimens (36–41 years for black spruce; 38–44 years for tamarack) for further analysis.

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 width 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 widths (from the two radii) of each annual ring were used for further calculation and data analysis.

PATTERNS OF SIZE VARIABILITY

Using the radius data, the size structure of black spruce and tamarack populations in the two plots was reconstructed for 1960 (when the trees would have been 5–13 years old, depending on the species) 1970, 1983 (the year prior to drainage) and 1991. To examine size variability in the populations, we calculated the Gini coefficient (Weiner & Solbrig 1984) for each species, in the drained and undrained plots, for these 4 years. In addition, relative growth rates [(radius in year x − radius in year y)/radius in year y] for each tree were calculated for the periods 1960–70, 1970–83 and 1983–91.

Simple linear regressions were used to examine the relationships among age, growth and size (Zar 1984). To examine whether size was related to age, we regressed size in 1960, 1970 and 1983 on age (in 1991). To examine whether relative growth rates (RGR) varied by size, we regressed RGR 1960–70 on radius in 1960, RGR 1970–83 on radius in 1970, and RGR 1983–91 on radius in 1983. For each regression the *F*-test ($P < 0.05$) was used to assess whether the slope was significantly different from zero.

EXAMINING DRAINAGE-INDUCED RELEASE GROWTH

Because drainage was applied to the entire plot, individual trees could not be considered true replicates for the purposes of examining treatment effects. We addressed this by: (i) testing for differences in growth between the drained and undrained plots during the time period prior to drainage; and (ii) using each individual tree's pre-drainage growth as a control for quantifying the response to drainage. Thus we did not need to make any statistical comparisons between the drained and undrained plots. We examined tree growth in the two areas during the period 1974–83 using a regression model with indicator variables and interaction effects (Neter *et al.* 1985), as follows:

$$Y_i = {}_0 + ß_1 X_1 + ß_2 X_2 + ß_3 X_1 X_2 + e_i$$

where Y_i = radius of tree i, X_1 = time (1974–83), $X_2 = 1$ (drained) or 0 (undrained), $ß_1$ is the slope of cumulative stem (radial) growth, $ß_2$ is the difference in intercept between the drained and the undrained plot, $ß_3$ is the difference in slope between the drained and the undrained plot, and e_i is the error. Stem radius data for the 10-year period prior to drainage were used to build a regression for each species, and the hypothesis H_0: $ß_2 = ß_3 = 0$ was tested and accepted ($P > 0.05$), indicating that trees in the drained and undrained plots had similar growth prior to drainage.

To examine the amount of drainage-induced release growth in each tree we used a procedure fashioned after Dang & Lieffers (1989). The observed patterns of growth for trees in the undrained plot were used to develop a relationship with which to predict post-drainage growth of the trees in the drained plot if drainage had not occurred. For all trees in the undrained plot stem radius showed a linear increase from 1972 to 1983, but black spruce in particular showed a slight change in slope of the radius vs. time relationship around the year of drainage (1984). We therefore used the piece-wise linear regression method (Neter *et al.* 1985) to generate two separate linear regressions (stem radius vs. time) for each undrained tree for (i) 1972–83 and (ii) 1984–91. Standard errors of Y estimates were small (0.03–0.52) and r^2 values were large (0.95–0.99) for all trees. Slopes of the post-1984 regressions were strongly linearly related to the slopes of the pre-1984 regressions. For black spruce, Y (post-1984 slope) = –0.00503 + 1.2083X (pre-1984 slope), SE = 0.142, $r^2 = 0.828$, $P < 0.001$. For tamarack, $Y = -0.00201 + 1.009114X$, SE = 0.109, $r^2 = 0.812$, $P < 0.001$. Thus we could use the slope of radial growth pre-1984 to estimate post-1984 growth. There was no relationship between the ratio of post-1984 : pre-1984 slope and tree radius in 1983, verifying that the same relationship could be used for trees of all sizes.

For each tree in the drained plot we developed a regression of radius vs. time for the pre-drainage period (1972–83) and used the slope of this relation, and the appropriate coefficient (above), to calculate predicted post-drainage radial growth for each tree if drainage had not occurred. On this basis we calculated the predicted radius from 1984 to 1991 for each tree in the drained plot if drainage had not occurred.

Finally, to quantify drainage-induced release growth, we calculated a release index (RI) as the ratio of actual growth to predicted growth if there had been no drainage (as shown in the example in Fig. 1).

$$\mathrm{RI}_i = \frac{[\text{observed radius in year } i - \text{observed radius in 1983}]}{[\text{predicted radius in year } i \text{ if no drainage occurred} - \text{observed radius in 1983}]}$$

Expressing release growth as a ratio relative to the growth of the tree in the absence of drainage accounts for allometric differences and allows for comparison among trees of different size. Thus a value of 1.0 would indicate no drainage-induced change in growth, a lower value would indicate reduced growth, and a larger value increased (release) growth. RI values were calculated for each year from 1984 to 1991 for each tree in the drained plot.

In order to examine the relationship between RI and tree size prior to drainage, RI_{1991} was regressed on size (radius) in 1983 and 1960 for each species. A t-test was used to examine differences in the slope of this relation between the two species. Further, trees were divided into three size groups according to stem radius in 1983. For black spruce: group 1 = 13–19.9 mm ($n = 8$), group 2 = 20–26.9 mm ($n = 12$), group 3 = 27–36.9 mm ($n = 5$). For tamarack: group 1 = 15–20.9 cm ($n = 11$), group 2 = 21–26.9 cm ($n = 9$), group 3 = 27–34.5 cm ($n = 5$). We then calculated the mean RI for each group for each year

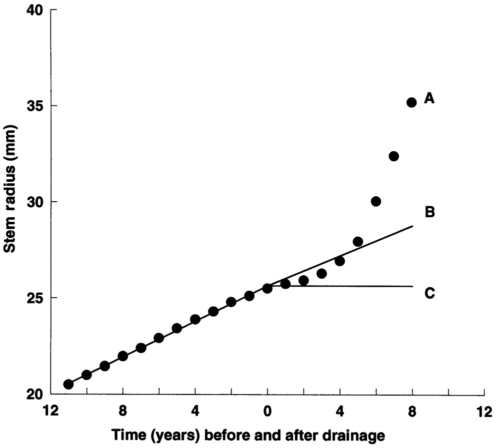

Fig. 1 Sample calculation of release index (RI) for an example tamarack tree from the drained plot in year 8 after drainage. (A) measured radius; (B) estimated radius if drainage did not occur; (C) radius in the year before drainage (1983). RI = (A–C)/(B–C). In the years before drainage RI was close to 1.0. In the first 4 years after drainage RI was < 1.0.

post-drainage and these were plotted over time. For both species we used one-way analysis of variance (Zar 1984) to test for differences in mean absolute growth among the three size groups for the periods 1960–70, 1970–83 and 1983–91. To examine the effects of drainage on size variability, we calculated the Gini coefficient using the predicted sizes of drained trees and compared it to the observed value for the drained population.

Results

PATTERNS OF SIZE VARIABILITY

For trees in undrained areas (undrained plot, drained plot prior to drainage), the radius increased more or less linearly throughout the time period we measured (data not shown). For populations in undrained areas size variability (as measured by the Gini coefficient) declined from 1960 (age 7–13) to 1970 in tamarack and from 1960 (age 5–10) to 1983 in black spruce. Thereafter it remained relatively stable for the populations in the undrained plot, but it declined further for populations in the drained plot to levels substantially lower than predicted if they had not been drained (Table 1a). About 50% of the size variability in 1960 could be accounted for by age (Table 1b). This relationship weakened over time (in 1970 it was only about 20%, with two out of four populations significant) and there was no significant relationship between size in 1983 and age (Table 1b). This was due to an inverse relationship between size and RGR from 1960 to 1970 for both species and from 1970 to 1983 for black spruce (Table 1c). Again, this relationship weakened over time; the RGR(1983–91) of trees in the undrained plot was unrelated to size in 1983 (Table 1c).

DRAINED-INDUCED RELEASE GROWTH

All trees in the drained plot showed dramatic increases in growth following drainage (Figs 2 and 3). As expected, RI values throughout the 10-year pre-drainage period were approximately 1.0 (data not shown). Release growth (RI in 1991) was inversely related to pre-drainage size (radius in 1983) (Table 1d) and the slope of this relationship was significantly steeper for tamarack. There was no relationship between RI_{1991} and size in 1960 for either species (Table 1d). The negative relationship between RI and pre-drainage size was further confirmed by comparison of the mean absolute growth of trees among the three size groups. Prior to drainage there were significant differences in mean growth among the size groups (larger trees had been growing faster) but all had similar growth following drainage (Table 2 and Figs 2 and 3).

The pattern of mean RI over time also differed among the three size groups (Fig. 4). For black spruce, mean RI for smaller trees (group 1) was always the largest, while mean RI for larger trees (group 3) was always the smallest. Larger trees (group 3) showed reduced growth ($RI < 1.0$) for all 8 years following drainage, while medium-sized trees (group 2) had reduced growth in years 3–6 after drainage (Fig. 4a). The smallest trees showed unchanged or accelerated growth ($RI \geqslant 1.0$) for all 8 years after drainage. By 1991 the smallest trees had grown, on average, 58% more than if they were undrained (mean $RI = 1.58$).

Overall, release growth in tamarack was much greater than in black spruce (Fig. 4b). All trees showed some reduced growth in the first 2–3 years following drainage. Thereafter, the smallest trees (group 1) showed the greatest increase in growth, the medium-sized trees (group 2) an intermediate amount, and the largest trees (group 3) the least. By 8 years after drainage, the smallest tamarack trees had grown, on average, 3.8 times more than they would have if drainage had not occurred. The medium-sized (group 2) trees had grown 2.8 times more, and the large (group 3) trees had grown 2.1 times more. Overall, the inverse relationship between pre-drainage size and release growth led to a reduction in size variability in the populations in the drained plot from 1983 to 1991, and substantially less variation in 1991 than predicted if drainage had not occurred (Table 1a).

Discussion

Populations of black spruce and tamarack in undrained areas showed declining size variability over time that was not attributable to self-thinning or a size- or age-related switch from exponential to linear growth (Stoll *et al.* 1994). Both species showed more or less linear radial growth for the entire time period assessed. Lieffers (1986) documented linear height growth of peatland black spruce over a 40-year period and observed that trees recruiting immediately after a fire grew faster than those establishing some years later, although this could not be attributed to above-ground competition. We used a much smaller age range than Lieffers (5 years for each species vs. 20 years) but age still accounted for a significant portion of the variation in size of younger trees. We found, however, that this relationship broke down over the next 10–20 years due to a negative relationship between relative growth rate and size. Thus, size variability declined over time as smaller trees 'caught up' with larger ones. By 15–20 years after establishment trees were following independent growth trajectories, unrelated to age or previous size. Consequently, size variability in the undrained populations remained relatively stable over the next 10–20 years.

The response of these species to improved edaphic conditions following drainage provides insight into the underlying causes of the observed changes in growth, and size variability, over time in the undrained populations. For black spruce and tamarack,

Table 1 Undrained and drained (in 1984) populations of black spruce and tamarack: (a) Gini coefficient (G) for observed distribution of radii in 1960, 1970, 1983 and 1991, and the predicted distribution in drained populations in 1991 if drainage had not occurred; (b) regressions of radii in 1960, 1970 and 1983 vs. age (in 1991); (c) regressions of mean relative growth rate (RGR) (for radius) from 1960 to 1970 vs. radius 1960, RGR 1970–83 vs. radius 1970, RGR 1983–91 vs. radius 1983; (d) release index in 1991 (RI_{1991}) vs. radius in 1960 and 1983 (drained populations only). Slope and intercept are given for significant regressions

Year		Black Spruce		Tamarack	
		Undrained	Drained	Undrained	Drained
(a) Gini coefficient in year *X*					
1960		0.118	0.117	0.077	0.103
1970		0.088	0.082	0.057	0.061
1983		0.072	0.070	0.051	0.061
1991 (observed)		0.070	0.061	0.056	0.047
1991 (predicted)			0.071		0.064
(b) Radius in year *X* vs. age in 1991					
1960	r^2	0.555***†	0.444***	0.491***	0.520***
	Slope	0.871	1.085	0.568	0.814
	Intercept	–28.27	–33.54	–14.73	–24.67
1970	r^2	0.281**	0.157	0.118	0.241*
	Slope	0.971			0.683
	Intercept	–26.11			–11.27
1983	r^2	0.108	0.006	0.065	0.069
(c) RGR years *X*–*Y* vs. radius in year *X*					
1960–70	r^2	0.411**	0.542***	0.442**	0.560***
	Slope	–0.225	–0.152	–0.133	–0.157
	Intercept	2.56	2.32	2.40	2.42
1970–83	r^2	0.281**	0.221*	0.176	0.072
	Slope	–0.034	–0.024		
	Intercept	0.934	0.826		
1983–91	r^2	0.050	0.176* (post-drainage)	0.017	0.251* (post-drainage)
	Slope		–0.012		–0.021
	Intercept		0.589		0.988
(d) RI_{1991} vs. radius in year *X*					
1960	r^2		0.131		0.152
1983	r^2		0.357**		0.599***
	Slope‡		–0.042		–0.147
	Intercept		2.20		6.51

†Slope significantly different from zero (by *F*-test) at $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.
‡Slopes significantly different between the species.

smaller trees, which were those that were growing more slowly immediately prior to drainage, showed greater drainage-induced release growth. Indeed, drainage effectively eliminated the differences in growth rate that existed prior to drainage. This result was quite surprising, given the large variability in sizes of trees.

Previous peatland drainage studies failed to control for effects of tree size or age, but their results are similar to ours. Heikurainen & Kuusela (1962) found an inverse relationship between drainage-induced release growth and tree diameter, while Stanek (1968) found that trees that had been growing more rapidly before drainage showed no marked growth improvement after drainage, in stark contrast to the response of slower growing trees. A population of *Pinus sylvestris* that had naturally established on a previously drained bog showed a decline in size variability (basal area) over a 40-year time period. Stoll *et al.* (1994) attributed this to an earlier switch from exponential to linear growth in older (larger) trees and the fact that competition was symmetric. We have considered three possible explanations for our observations of size variability in peatland black spruce and tamarack (genetic differences, competition and microsite effects), and examined these in light of the observed responses to drainage.

It seems unlikely that genetic differences in growth rate could explain our results. The independent growth trajectories established by 15–20 years after establishment could possibly be an expression of genetic potential. However, to explain the inverse relation between pre-drainage size (growth rate) and post-drainage release growth we would have to invoke a

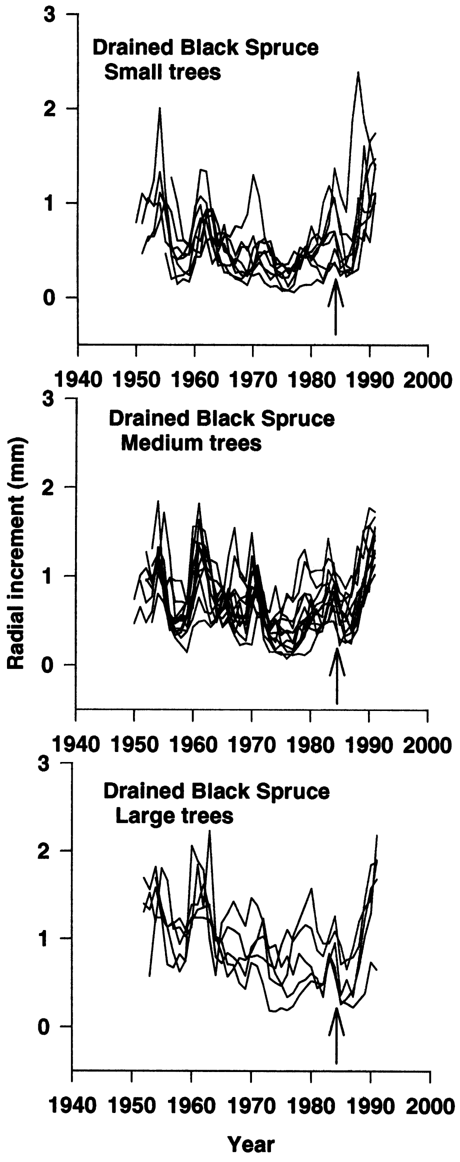

Fig. 2 Ring widths over time pre- and post-drainage for 25 black spruce trees in the drained plot by the three size groups. The arrow indicates the time of drainage (1984).

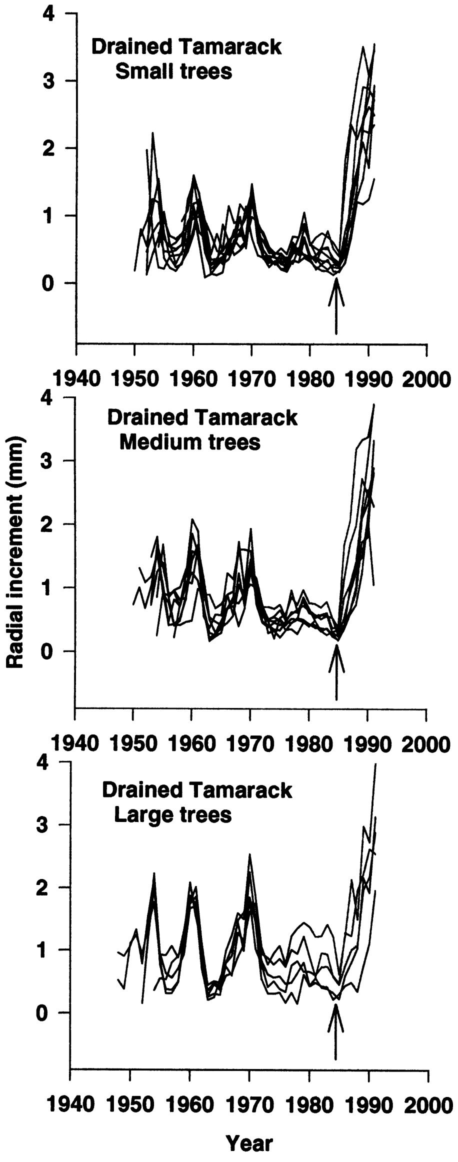

Fig. 3 Ring widths over time pre- and post-drainage for 25 tamarack trees in the drained plot by the three size groups. The arrow indicates the time of drainage (1984).

negative correlation between inherent growth and the ability to respond to improved conditions. Further, although significant genetic variation for growth rate in black spruce (Morgenstern 1978) and tamarack (Park & Fowler 1982) has been observed in nursery studies, such genetic variation would not be likely to be apparent under harsh field conditions. In greenhouse trials of progeny from the black spruce trees used in this study, we found significant family differences in growth rate but they were unrelated to field growth or post-drainage release (Yin 1992).

If below-ground competition was operating in these populations, the improved availability of resources following drainage should have resulted in either similar release growth of all trees (completely symmetric competition) or greater release growth of larger individuals (size-symmetric or -asymmetric competition). Below-ground competition is usually symmetric but it might appear asymmetric if the availability of below-ground resources is sufficiently patchy that individuals with larger root masses are able to locate and monopolise available pools more readily (Weiner 1990; Schwinning & Weiner 1998). Our data could conform with the competition hypothesis if this is the case, but only if smaller individuals are actually larger below-ground. This seems very unlikely, especially given the extremely limited rooting zone in peatlands. Another situation in which competition would lead to smaller trees being expected to show more release growth is if drainage completely eliminated pre-existing size-asymmetric competition. However, competition is rarely strong in low-density populations, or those growing slowly due to poor soils (Schwinning & Weiner 1998), and if size-asymmetric

Table 2 Mean absolute radial growth (mm) (standard error) of (a) black spruce and (b) tamarack trees in the drained plot pre-(1960–70 and 1970–83), and post-(1983–91) drainage for trees from the three size groups. Results (*P*) of one-way analysis of variance testing for differences in mean radial growth among tree size groups

Size group (range for radius in 1983, *n*)	1960–70	1970–83	1983–91
(a) Black spruce			
Small	5.22	4.69	7.13
(13.0–19.9 mm, $n = 8$)	(0.53)	(0.48)	(1.29)
Medium	7.67	6.26	7.01
(20.0–26.9 mm, $n = 12$)	(0.36)	(0.71)	(0.47)
Large	10.13	8.72	7.41
(27.0–36.9 mm, $n = 5$)	(0.67)	(1.30)	(1.13)
P	< 0.001	0.005	0.850
(b) Tamarack			
Small	6.78	5.96	12.06
(15.0–20.9 mm, $n = 11$)	(0.33)	(0.39)	(1.11)
Medium	8.64	7.39	11.39
(21.0–26.9 mm, $n = 9$)	(0.55)	(0.46)	(1.23)
Large	10.12	10.26	11.25
(27.0–34.5 mm, $n = 5$)	(0.60)	(1.71)	(1.77)
P	< 0.001	0.001	0.686

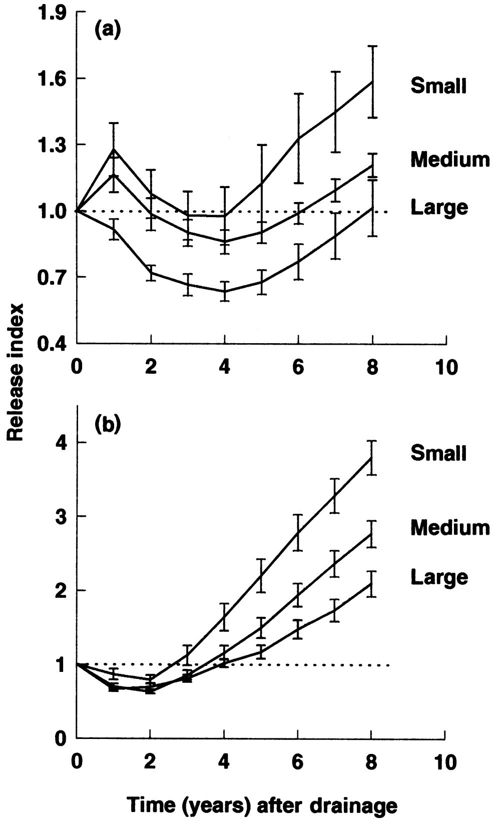

Fig. 4 Mean (SE) release index (RI) over time since drainage for the three size groups for (a) black spruce and (b) tamarack. RI of 1.0 indicates no change in growth accompanying drainage, RI < 1.0 indicates reduced growth post-drainage, RI of > 1.0 indicates drainage-induced release growth.

competition was operating it should have been indicated by increasing size variability with time in the population prior to drainage.

If smaller, slower-growing, trees were thus because they were established on poorer microsites, they would stand to benefit more from drainage if these microsites showed greater improvement in edaphic conditions. This final alternative appears to be the most probable explanation. Peatlands exhibit heterogeneity in pH, substrate chemistry, bulk density, moisture and moss species along a microtopographic gradient from hollow to hummock (Vitt *et al.* 1975; Karlin & Bliss 1984; Crum 1991) and this variation has been shown to influence germination, survival (Ohlson & Zackrisson 1992) and gas exchange (Astridge 1996) of seedlings and saplings. Hollows typically are situated just at or below the water table. Thus they, and trees established there, are likely to be more positively affected by the drop in water table accompanying drainage. As hummocks are generally more favourable sites, and rooting is already largely confined to them (Mannerkoski 1985; Lieffers & Rothwell 1986; Oswald & Neuenschwander 1993), these microsites, and trees established there, may benefit less from drainage.

Along with a general improvement in edaphic conditions, drainage may also affect changes in the microsite conditions along the hollow–hummock gradient. Variability along the gradient could decline or hummocks could even become temporarily less favourable as a result of drying and warming (Pessi 1958; Lieffers & Rothwell 1986; Swanson & Rothwell 1989; Macdonald & Lieffers 1990; Rothwell & Silins 1990). Indeed, we found that larger trees showed an initial growth reduction following drainage. A probable cause is water stress, associated with the immediate, dramatic, lowering of the water table (50–60 cm in 2 years; Lieffers & Rothwell 1987a), perhaps exacerbated by surface warming (Mannerkoski 1985; Lieffers & Rothwell 1986; Dang & Lieffers 1989; Swanson & Rothwell 1989).

Another possibility is that larger trees were experiencing a time-lag in their response to improved conditions, owing to differences (vs. smaller trees) in the ratio of stem to crown, photosynthetic surface to non-photosynthetic surface, root to shoot, and/or distance from root to leaf (Kramer & Kozlowski 1979). Larger trees might be expected to show a greater initial allocation to root growth at the expense of above-ground growth if they had lower root:shoot ratios than smaller trees. White spruce shows such an initial preferential allocation to root growth following release from above-ground competition (Urban *et al.* 1994). However, if such a time lag was operating we would expect to see an eventual increase in release growth of larger trees. Over the 8 years following drainage we saw no evidence of convergence of RI values for trees of different size.

Overall, drainage dramatically reduced the extensive heterogeneity in growth rate observed pre-drainage, suggesting that the microtopographic gradient became less marked. Peatland subsidence, which typically follows peatland drainage (Rothwell *et al.* 1996; Minkkinen & Laine 1998), would be likely to contribute to increased micro-scale homogeneity in drained peatlands.

Extensive microsite heterogeneity has been documented in other forest types (Boerner & Koslowsky 1989; Bell *et al.* 1991; Lechowicz & Bell 1991) and shown to affect establishment (Collins & Good 1987; Ruel *et al.* 1988; Oswald & Neuenschwander 1993) and height growth of seedlings (Hartgerink & Bazzaz 1984; Messier & Kimmins 1992; Kuuluvainen *et al.* 1993). We postulate that mature trees may also be affected by microsite heterogeneity and that this contributes to the high degree of size heterogeneity in peatland black spruce and tamarack. Our data suggest that such effects may be important for 40 or more years after establishment. The patterns of size variability we observed in undrained populations can be explained as follows. The initial size hierarchy was related to slight variation in the time of establishment. This was followed by a period of declining size variability as trees became limited by below-ground resources. Earlier limitation of larger trees explains declining size variability and the temporarily inverse relationship between size and growth rate. Eventually individual trees establish independent growth trajectories based on microsite conditions.

Tamarack showed greater release growth than black spruce, and this is consistent with previous studies (Lieffers & Rothwell 1987a; Macdonald & Lieffers 1990; Rothwell & Silins 1990). Tamarack has an inherently faster growth rate (Strong & La Roi 1983), a greater ability to take up and utilize nitrogen (Macdonald & Lieffers 1990), a deeper root system, greater fine-root biomass (Lieffers & Rothwell 1987b) and a larger root:shoot ratio (Strong & La Roi 1983) than black spruce. Therefore, it may be better suited to take rapid advantage of improved conditions following drainage. In addition, as a deciduous species with indeterminate growth of long shoots, while black spruce is an evergreen species with determinate growth, tamarack may be able to adjust more quickly to changing growing conditions. This greater potential for plasticity may help explain the persistence of this deciduous conifer on peatland sites throughout the boreal forest, as well as its dramatic response to peatland drainage.

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References

Astridge, K. (1996) *Effect of microhabitat variation in peatlands on* Picea mariana *and* Larix laricina *seedlings*. MSc Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada.

Bell, G., Lechowicz, M.J. & Schoen, D.J. (1991) The ecology and genetics of fitness in forest plants. III. Environmental variance in natural populations of *Impatiens pallida*. *Journal of Ecology*, **79**, 697–713.

Boerner, R.E.J. & Koslowsky, S.D. (1989) Microsite variation in soil chemistry and nitrogen mineralization in a beech–maple forest. *Soil Biology and Biochemistry*, **21**, 795–801.

Brand, D.G. & Magnussen, S. (1988) Asymmetric, two-sided competition in even-aged monocultures of red pine. *Canadian Journal of Forest Research*, **18**, 901–910.

Clyde, M.A. & Titus, S.T. (1987) A new computerized system for tree ring measurement and analysis. *Forestry Chronicle*, **63**, 23–27.

Collins, S.L. & Good, R.E. (1987) The seedling regeneration niche: habitat structure of tree seedlings in an oak–pine forest. *Oikos*, **48**, 89–98.

Crum, H. (1991) *A Focus on Peatlands and Peat Mosses*. The University of Michigan Press, Ann Arbor, MI.

Dang, Q.L. & Lieffers, V.J. (1989) Assessment of patterns of tree ring growth of black spruce following peatland drainage. *Canadian Journal of Forest Research*, **19**, 924–929.

Grootjans, A.P., Schipper, P.C. & van der Windt, M.J. (1985) Influence of drainage on N-mineralization and vegetation response in wet meadows. *Acta Oecologia Planta*, **6**, 403–417.

Hartgerink, A.P. & Bazzaz, F.A. (1984) Seedling-scale environmental heterogeneity influences individual fitness and population structure. *Ecology*, **65**, 198–204.

Heikurainen, L. & Kuusela, K. (1962) Revival of the tree growth after drainage and its dependence on tree size and age. *Metsantutki Muslaitoksen Julk*, **55**, 1–15.

Hillman, G.R. (1987) *Improving Wetlands for Forestry in Canada*. Information Report NOR-X-288. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada.

Hillman, G.R., Johnson, J.D. & Takyi, S.K. (1990) *The Canada–Alberta Wetlands Drainage and Improvement for Forestry Program*. Project £ 1413-1417-86. Canada–

Alberta Forest Resource Development Agreement Report. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada.

Jeglum, J.K. (1972) Boreal forest wetlands near Candle Lake, central Saskatchewan. *Musk-Ox*, **11**, 41–58.

Karlin, E.F. & Bliss, L.C. (1984) Variation in substrate chemistry along microtopographical and water-chemistry gradients in peatlands. *Canadian Journal of Botany*, **62**, 142–153.

Knox, R.G., Peet, R.K. & Christensen, N.L. (1989) Population dynamics in loblolly pine stands: changes in skewness and size inequality. *Ecology*, **70**, 1153–1166.

Kramer, P.J. & Kozlowski, T.T. (1979) *Physiology of Woody Plants*. Academic Press Inc, Orlando, FL.

Kuuluvainen, T., Hokkanen, T.J., Jarvinen, E. & Pukkala, T. (1993) Factors related to seedling growth in a boreal Scots pine stand: a spatial analysis of a vegetation–soil system. *Canadian Journal of Forest Research*, **23**, 2101–2109.

Lechowicz, M.J. & Bell, G. (1991) The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. *Journal of Ecology*, **79**, 687–696.

Lieffers, V.J. (1986) Stand structure, variability in growth and intraspecific competition in a peatland stand of black spruce (*Picea mariana*). *Holarctic Ecology*, **9**, 58–64.

Lieffers, V.J. (1988) *Sphagnum* and cellulose decomposition in drained and natural areas of an Alberta peatland. *Canadian Journal of Soil Science*, **68**, 755–761.

Lieffers, V.J. & Rothwell, R.L. (1986) Effects of depth of water table and substrate temperature on root and top growth of *Picea mariana* and *Larix laricina* seedlings. *Canadian Journal of Forest Research*, **16**, 1201–1206.

Lieffers, V.J. & Rothwell, R.L. (1987a) Effects of drainage on substrate temperature and phenology of some trees and shrubs in Alberta peatland. *Canadian Journal of Forest Research*, **17**, 97–104.

Lieffers, V.J. & Rothwell, R.L. (1987b) Rooting of peatland black spruce and tamarack in relation to depth of water table. *Canadian Journal of Botany*, **65**, 817–821.

Macdonald, S.E. & Lieffers, V.J. (1990) Photosynthesis, water relations, and foliar nitrogen of *Picea mariana* and *Larix laricina* from drained and undrained peatlands. *Canadian Journal of Forest Research*, **20**, 995–1000.

Mannerkoski, H. (1985) Effect of water table fluctuation on the ecology of peat soil. Publ. of Dept. of Peatland Forestry, Univ. of Helsinki, Vol. 7, pp. 1–190.

Messier, C. & Kimmins, J.P. (1992) Growth of western red cedar seedlings in relation to microtopography, forest floor nutrient status, and fireweed and salal on clear-cut sites in coastal British Columbia. *Canadian Journal of Forest Research*, **22**, 273–278.

Minkkinen, K. & Laine, J. (1998) Effect of forest drainage on the peat bulk density of pine mires. *Canadian Journal of Forest Research*, **28**, 178–186.

Morgenstern, E.K. (1978) Range-wide genetic variation of black spruce. *Canadian Journal of Forest Research*, **8**, 463–473.

Neter, J., William, W. & Kutner, M.H. (1985) *Applied Linear Statistical Models*: *Regression*, *Analysis of Variance*, *and Experimental Designs*. Richard D. Irwin Inc., Homewood, IL.

Ohlson, M. & Zackrisson, O. (1992) Tree establishment and microhabitat relationships in north Swedish peatlands. *Canadian Journal of Forest Research*, **22**, 1869–1877.

Oswald, B.P. & Neuenschwander, L.F. (1993) Microsite variability and safe site description for western larch germination and establishment. *Bulletin of the Torrey Botanical Club*, **120**, 148–156.

Park, Y.S. & Fowler, D. (1982) Effects of inbreeding and genetic variance in a natural population of tamarack in eastern Canada. *Silvae Genetica*, **31**, 21–26.

Payandeh, B. (1973) Analysis of a forest drainage experiment in northern Ontario. I. Growth analysis. *Canadian Journal of Forest Research*, **3**, 387–398.

Pessi, Y. (1958) On the influence of bog draining upon thermal conditions in the soil and in the air near the ground. *Acta Agriculturae Scandinavica*, **24**, 359–374.

Richardson, J. (1981) Growth of natural tree seedlings on a fen following drainage and fertilization. *Canadian Forest Service Research Notes*, **1**, 22–24.

Rothwell, R.L. & Silins, U. (1990) *Variability of Soil Temperature*, *Substrate Moisture Content*, *and Tree Growth on two Drained and Undrained Alberta Peatlands*. Technical Report to Alberta Forest Service Research Branch. Alberta Environmental Protection. Edmonton, AB.

Rothwell, R.L., Silins, U. & Hillman, G.R. (1996) The effects of drainage on substrate water content at several forested Alberta peatlands. *Canadian Journal of Forest Research*, **26**, 53–62.

Ruel, J.C., Loustau, D. & Pineau, M. (1988) Relations entre la microtopographie, les caracteristiques de la couverture morte et la repartition des essences dans une erabliere a Bouleau jaune. *Canadian Journal of Forest Research*, **18**, 1196–1202.

Schwinning, A. & Weiner, J. (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, **113**, 447–455.

Stanek, W. (1968) A forest drainage experiment in northern Ontario. *Pulp and Paper Magazine of Canada*, **69** (18), 58–62.

Stoll, P., Weiner, J. & Schmid, B. (1994) Growth variation in a naturally established population of *Pinus sylvestris*. *Ecology*, **75**, 660–670.

Strong, W.L. & La Roi, G.H. (1983) Root-system morphology of common boreal forest trees in Alberta, Canada. *Canadian Journal of Forest Research*, **13**, 1164–1173.

Swanson, E.L. & Rothwell, R.L. (1989) Substrate freeze–thaw in a drained Alberta fen. *Canadian Journal of Forest Research*, **19**, 1024–1029.

Toth, J. & Gillard, D. (1988) Experimental design and evaluation of a peatland drainage system for forestry by optimization of synthetic hydrographs. *Canadian Journal of Forest Research*, **18**, 353–373.

Urban, S.T., Lieffers, V.J. & Macdonald, S.E. (1994) Release in radial growth in the trunk and structural roots of white spruce as measured by dendrochronology. *Canadian Journal of Forest Research*, **24**, 1550–1556.

Vitt, D.H., Crum, H. & Snider, J.A. (1975) The vertical zonation of sphagnum species in hummock–hollow complexes in northern Michigan. *Michigan Botanist*, **13**, 190–200.

Weiner, J. (1990) Asymmetric competition in plant populations. *Trends in Ecology and Evolution*, **5**, 260–264.

Weiner, J. & &. Thomas, S.C. (1986) Size variability and competition in plant monocultures. *Oikos*, **47**, 211–222.

Weiner, J. & Solbrig, O.T. (1984) The meaning and measurement of size hierarchies in plant populations. *Oecologia*, **61**, 334–336.

Yin, F. (1992) *Variability in drainage-induced response growth and its relation to pre-drainage growth rate of peatland black spruce and tamarack*. MSc Thesis, Department of Forest Science, University of Alberta, Edmonton, Alberta, Canada.

Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall Inc., Englewood Cliffs, NJ.

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