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Early response of *Abies balsamea* seedlings to artificially created openings

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Abstract. Small-scale canopy openings are being increasingly recognized for their importance in boreal forest stand development. Yet more work is necessary to understand their effects on seedling growth. This study investigated the effect of different degrees of canopy opening (all trees cut, conifers cut, conifers girdled and control quadrats) in different stand types on *Abies balsamea* seedling recruitment, growth and architecture. The lack of a treatment effect on seedling establishment suggests that gaps primarily affect advance regeneration. In the first year after treatment the seedlings in the cut blocks (both conifer cut and all trees cut) responded with an increase in height growth. Changes in the leader to lateral branch ratio were also significant. Continued architectural change in terms of number of branches produced did not occur until after two years had passed. Although not significantly different from the control, increases can be observed in all measurements for the girdled treatment. It is therefore concluded that the growth response of advance regeneration is more important following canopy opening than new seedling recruitment and that seedling performance is greatest where degree of opening is greatest.

Keywords: Canopy gap; Boreal forest; Experimental opening; Recruitment; Seedling architecture; Seedling growth.

Abbreviations: DBH = Diameter at breast height; LB ratio = Leader to branch ratio; PAR = Photosynthetically active radiation; RHI = Relative height increment.

Nomenclature: Burns & Honkala (1990).

Introduction

Traditionally research on disturbance dynamics in the boreal forest has focused on the impacts of fire. Recently, a growing number of researchers have started to study the impacts of smaller-scale canopy openings (Hytteborn et al. 1987; Leemans 1991; Paré et al. 1993; Bergeron & Charron 1994; Kuuluvainen 1994; Kneeshaw & Bergeron 1998). In terms of stand dynamics, tree response to these openings will be either from existing advance regeneration or due to the recruitment of new individuals.

Following stand-destroying fires, establishment is primarily from seed (or from root suckering for such species as *Populus tremuloides*. On the other hand, despite some mortality (Spencer 1985; Ruel & Huot 1993), advance regeneration is usually abundant following gap formation caused by spruce budworm outbreaks or windthrow (MacLean 1984, 1988; Morin 1990). The creation of gaps may also result in favorable conditions for germination and seedling establishment (Batzer & Popp 1985).

For advance regeneration it has been demonstrated that those individuals growing in an open environment will have a different architecture from those growing in a shaded environment (Sakai 1987; O'Connell & Kelty 1994; Parent & Messier 1995). In shaded environments apical control is reduced. This results in greater lateral branch than leader growth which will lead to seedlings and saplings developing a sympodial or umbrella shaped form (Sakai 1987; O'Connell & Kelty 1994; Parent & Messier 1995). In open environments the opposite is true and seedlings develop a conical form. Increases in height growth have also been reported following canopy openings created both by spruce budworm outbreaks and timber harvesting (Ghent 1958; Hatcher 1964; MacLean 1988; Sundkvist 1994).

Understanding the growth response in trees whose environment has changed from a closed canopy environment with little PAR to a more open environment with more PAR is essential towards explaining and predicting stand development. Such information will also be crucial in supporting all silvicultural decisions that use the release of pre-established individuals. With increasing pressure for sustainable forestry practices that recognize and protect biodiversity and visual aesthetics, alternative silvicultural techniques that use smaller openings and that take advantage of advance regeneration are being increasingly favored by the public. In Québéc's boreal region, harvesting with the protection of advance regeneration is already the dominant silvicultural system.

In Québéc's boreal *Abies* forests, *A. balsamea* is the dominant late successional species. It accounts for more than 80 % of all advance regeneration in the region's forests (Kneeshaw & Bergeron 1996). It therefore constitutes the majority of the softwood component in second growth stands of this region. In naturally regenerated stands it recruits, following fire, beneath a hardwood canopy dominated by *Populus tremuloides* and gradually attains dominance through a series of gap events (Kneeshaw & Bergeron 1998; Bergeron & Charron 1994). This species is also highly vulnerable to the spruce budworm; more than half of all *Abies* adults were killed during the last outbreak (Bergeron et al. 1995). A cyclical successional pattern has been suggested for pure *Abies* forests in Maritime Canada due to high overstory mortality and abundant regeneration in the understory (Baskerville 1975; MacLean 1984). *Abies balsamea* is thus exposed to gaps of different size and degree of canopy opening which may influence its success in recruiting to the overstory (Kneeshaw & Bergeron 1998). The objectives of this study are therefore to investigate the effect of different degrees of gap opening in different stand types on *Abies balsamea* seedling recruitment, growth and change in architecture through a series of experimentally created openings in order to better understand natural stand development and response to cutting.

Study area

The study sites are located in Québec's southwestern boreal forest in the area surrounding Lake Duparquet (48° 15' to 48° 30' N, 79° 15' to 79° 30' W). This region, characterized by clay deposits from large post-glacial lakes, is known as Québec and Ontario's northern clay belt. The study region is dominated by a rolling clay lowland interspersed by small rocky hills up to 550 m in height overlain with reworked till deposits. The climate can be classified as cold and continental with an average annual temperature of 0.8 °C and with an average annual precipitation of 857 mm (Anon. 1993). The average number of frost free days is 64/yr, although frost can occur at any time during the growing season (Anon. 1993).

Lake Duparquet is located at the southern limit of the boreal forest in Rowe's (1972) Missinaibi-Cabonga section where an association of *Abies balsamea*, *Picea mariana* and *Picea glauca* with *Betula papyrifera* and *Populus tremuloides* dominates. *Pinus banksiana* may also be present on some sites, and where fire has not occurred for long periods *Thuja occidentalis* may be abundant (Bergeron & Dubuc 1989).

The fire history of stands in the Lake Duparquet area has been reconstructed using dendroecological techniques (Bergeron 1991; Dansereau & Bergeron 1993). The fire cycle, estimated to be 63 yr for the pre-1870 period, has since decreased and no fires have been recorded since 1944. Spruce budworm epidemics have been reconstructed by Morin et al. (1993) with the 1972 to 1987 outbreak resulting in the death of most of the *Abies* trees (Bergeron et al. 1995). Defoliation due to a 1950s forest tent caterpillar outbreak has also been documented as causing a significant hardwood growth decrease (Bergeron & Charron 1994). Forest harvesting was unimportant until large-scale clear-cuts began in the western part of the region in 1978.

Methods

Field sampling

Four stand types, hardwood, mixed hardwood, mixed conifer, and conifer, were chosen to represent the successional changes found in the region. The youngest of these stands, burned in 1944, is dominated by hardwoods, and the oldest stand, burned in 1760, is dominated by conifers (Table 1). The intermediate aged stands represent different proportions of hardwood to conifer mixes. All sites chosen for cutting within these forests were located on mesic, clay soils.

Three replicates of each of four treatments, in a Randomized Block Design using 10 m × 10 m quadrats, were located within the different stands for a total of 48 quadrats. This chosen gap size is consistent with naturally occurring gaps in these forests (Kneeshaw & Bergeron 1998). These treatments, by removing different proportions of the tree layer, represent different degrees of openings possible within the forest. The first treatment, in which all trees greater than 1 cm DBH were cut and removed from the site, removed the most basal area and therefore resulted in the greatest degree of canopy opening (Table 1). The second and third treatments were attempts to imitate the effect of spruce budworm outbreaks. In the second treatment all *Abies balsamea* and *Picea glauca* (> 1cm DBH) were cut and removed from the site. In the third treatment all *Abies balsamea* and *Picea glauca* trees were girdled by cutting through the cambium to the sapwood in two rings that completely encircled the tree. This treatment leads to the slow death of these trees. The final treatment was the control.

Within each of these treatments, two 1-m wide transects were established perpendicular to each other on north-south and east-west axes. All conifer seedlings within these transects were identified to species and tagged for further analysis. Due to the low numbers of seedlings in the transects of some quadrats, the sampling area within the quadrat was increased until a minimum of 15 *Abies balsamea* seedlings per block were located or until the maximum quadrat size (100 m^2) was attained.

Even so, *Abies balsamea* was limited to less than 15 seedlings in six quadrats. In total 939 seedlings greater than 10 cm in height (to ensure the possibility of branch production) were measured in the 48 quadrats. Poor form, loss of leaders due to browsing or breakage in transport reduced the number of seedlings used in the analysis to 764 in the analyses for branch production, 732 for RHI and 684 for the LB ratio. The latter two ratios required more measurements and were thus limited to a greater degree by breakage.

Although the different treatments were established before the beginning of the 1992 growing season their effects on seedling growth were not observable until the following season. This is due to the determinate nature of the growth of *Abies balsamea* and *Picea glauca*, in which the current season's growth is pre-determined in the previous growing season. At the end of the 1994 growing season, tagged seedlings were harvested and taken back to the laboratory for analysis. All seedlings were aged and total height as well as height growth was measured for the previous four years. Similarly, the length of all lateral branches to their first node was measured for each of these years. The number of branches produced in each year was also noted. Seedling recruitment, i.e. the establishment of new individuals, by species was also counted in each quadrat at the end of the 1992, 1993 and 1994 growing seasons.

Since the creation of canopy gaps leads to changes in resource levels available to seedlings (Canham 1988; Canham & Marks 1985; Denslow 1980, 1987), abiotic and biotic factors were therefore measured in order to evaluate their effects on changes in seedling growth and architecture. Percent cover of all herb and shrub species was evaluated in the transects. Species were then stratified into different groups: ground herbs (herbs growing along the ground e.g. *Linnaea borealis*), low growing herbs (> 5 cm and < 50 cm height), tall herbs (> 50 cm), low shrubs (< 50 cm) and tall shrubs (> 50 cm height).

Soil temperature was measured at a depth of 15 cm, at intervals throughout the first two growing seasons. Percent humidity of the organic horizons was also evaluated throughout the first two growing seasons as was the rate of nitrogen mineralization. Nitrogen mineralization was evaluated using plastic tubes inserted into the soil and then withdrawn at different dates (at least 30 days apart) to determine the differences in the quantity of nitrates and ammonium (De Grandpré 1997). Light measurements, in 10 micro-quadrats randomly located in the transects, were made at heights of 5 cm, 1 m above the soil, and above the shrub layer. Light was measured on cloudy days, using the techniques described by Parent & Messier 1996 and Messier & Puttonen 1995. Average light levels per strata (as well as for all other variables) were retained for further analysis, as the object of the study was to evaluate the effect of each treatment on overall seedling performance.

Data analysis

Leader to lateral branch ratio

Several indices were used to evaluate seedling response to the openings. The first, the LB, leader to lateral branch, ratio, reflects changes in architecture and is highly positively correlated to percent light received (Parent & Messier 1995; Klinka et al. 1992). This ratio is calculated as L / (mean [$B_i\ldots B_n$]), where L is the leader length and $B_{i\ldots n}$ are the lengths of the lateral branches produced from the same node as the leader. Individuals growing in high light environments produce longer leaders relative to lateral branches than do individuals growing in low light environments (Chen et al. 1996). Ratios greater than one occur when leaders are longer than the

Table 1. Original tree basal area (m^2/ha) by species for each treatment and stand age as well as basal area removed following the treatment. The conifer type is comprised primarily of *Abies balsamea* with a small proportion of *Picea glauca*. For the girdled treatment, 'removed' is the basal area girdled but remaining in the quadrat. For the other treatments, the trees that are cut are physically removed from the site.

Stand	Control					Girdled				
Type	**Conifers**	***Populus***	***Betula***	***Thuja***	**Removed**	**Conifers**	***Populus***	***Betula***	***Thuja***	**Removed**
Hardwood	1.3 (1.5)	38.7 (17.5)	4.0 (5.7)	0 (0)	0 (0)	1.4 (0.8)	41.4 (11.0)	1.8 (3.2)	0 (0)	1.4 (0.8)
Mixed hardwood	9.4 (3.4)	20.4 (17.7)	11.1 (15.3)	0 (0)	0 (0)	7.9 (5.3)	22.3 (9.1)	10.1 (5.7)	0 (0)	7.9 (0.8)
Mixed hardwood	16.3 (13.6)	30.1 (5.2)	1.4 (1.1)	0 (0)	0 (0)	8.0 (3.0)	23.2 (5.0)	2.6 (2.6)	0 (0)	8.0 (2.9)
Conifer	19.4 (6.2)	3.9 (6.8)	0 (0)	15.9 (7.0)	0 (0)	21.2 (13.4)	0 (0)	0 (0)	22.4 (10.0)	21.2 (13.4)
Stand	Conifers cut					All cut				
Type	**Conifers**	***Populus***	***Betula***	***Thuja***	**Removed**	**Conifers**	***Populus***	***Betula***	***Thuja***	**Removed**
Hardwood	1.7 (1.8)	30.8 (20.5)	6.5 (9.6)	0 (0)	1.8 (1.8)	3.8 (5.2)	18.1 (13.8)	11.4 (9.0)	0 (0)	33.4 (9.3)
Mixed hardwood	11.7 (8.4)	17.0 (16.2)	8.6 (6.3)	0 (0)	11.7 (8.4)	8.7 (4.0)	0.0 (0.0)	10.5 (1.5)	0 (0)	19.2 (3.6)
Mixed hardwood	14.6 (7.8)	21.7 (15.0)	5.9 (0.9)	0 (0)	14.7 (7.8)	20.5 (11.6)	18.1 (2.0)	2.2 (3.8)	0.2 (0.4)	41.0 (11.5)
Conifer	17.6 (6.1)	0 (0)	0 (0)	17.8 (15.2)	17.6 (6.1)	19.5 (9.9)	3.9 (6.8)	0 (0)	15.9 (7.0)	38.5 (9.3)

average of the lateral branch lengths and any increase in the ratio from one year to the next reflects a change in architecture towards a form more adapted to height growth. To evaluate whether treatments had an effect on leader to lateral branch architecture, ratio differences were calculated : (1) from before treatment to one year after, (2) from before treatment to two years after and (3) from the first to the second year after treatment. These year-to-year variations were tested in order to identify the period of time required before a significant response occurred.

Relative height increment

The second index used was the relative height increment (RHI). Since earlier studies have shown that seedling size has an effect on height increment response following openings (Hatcher 1964; Ghent 1958) the traditional technique of using ratios of leader growth to seedling height leads to biased comparisons. We thus used the method proposed by Brand (1986) to permit comparisons in height growth between individuals of different initial size. RHI is the ratio of the height increment in year n to the height increment of year n plus year $n - 1$. This formulation is also more sensitive to changes in relative height than ratios based on leader length to total seedling height. Again statistical analyses were performed on differences from pre-treatment RHIs to one year and two years after treatment as well as the difference between the first and second year RHI.

Number of branches per whorl

The final index used was the total number of branches per node, again compared using year to year differences. The number of branches produced has also been found to increase in environments with higher irradiance for a number of species including *Abies balsamea* (O'Connell & Kelty 1994; Parent & Messier 1995).

Statistical analyses

Treatment effects on changes in these indices were analysed in SYSTAT (version 6.0) using a two-way analysis of variances. Pre-treatment values of these indices are presented in Table 2. A two-way ANOVA was also used to test for differences in seedling recruitment and seedling mortality. To investigate the impact of abiotic variables and competing plant cover on seedling growth response, a step-by-step multiple linear regression was used. Variables that were intercorrelated were identified using SYSTAT's 'tolerance' values and were subsequently eliminated. Transformations were performed on a number of variables in order to respect assumptions of normality and homogeneity of variances. Density of seedling recruitment and mortality as well as light measurements were log transformed, and soil humidity was arc-sine transformed.

Results and Discussion

Seedling recruitment

Natural gap formation in boreal mixed-wood forests may be caused by the spruce budworm, by individual tree senescence and mortality or by windthrow: In our study area, the majority of gaps are caused by the spruce budworm (Kneeshaw & Bergeron In press). Advance regeneration is abundant at many sites in our study area but seedling establishment following canopy openings may be important at sites where advance regeneration is considered inadequate (Kneeshaw & Bergeron 1996). Batzer & Popp (1985), for example, found that 45% of their budworm attacked stands contained only post-outbreak seedlings. Kneeshaw & Bergeron (In press) also show that seedling establishment may continue or increase during and following budworm outbreaks.

In our study, none of the treatments had a significant impact on seedling recruitment or mortality (Table 3). The lack of a treatment effect on seedling recruitment may be due in part to the short period of time that seedling recruitment was followed after the treatment. In eastern Canada, newly established seedlings accounted for less than 2 % of the regeneration immediately following the last spruce budworm outbreak (MacLean 1988). The presence of parent trees, the production of seed crops in the years following disturbance, and the distance to seed trees should also be considered for their effect on *Abies* seedling establishment (Place 1955; Frank 1990; Sims et al. 1990; Galipeau et al. 1997).

Although seedling recruitment was not affected by

Table 2. Pre-treatment LB ratio, RHI and branch production values and standard errors for the treatments and stand types.

Treatment	LB ratio	RHI	Branch production	Stand type	LB ratio	RHI	Branch production
Girdled	0.504 ± 0.022	0.482 ± 0.012	1.356 ± 0.119	Hardwood	0.626 ± 0.039	0.494 ± 0.016	1.778 ± 0.157
Conifers cut	0.511 ± 0.026	0.483 ± 0.010	1.316 ± 0.129	Mixed hardwood	0.525 ± 0.020	0.500 ± 0.010	1.551 ± 0.107
All trees cut	0.538 ± 0.032	0.475 ± 0.019	1.264 ± 0.115	Mixed conifer	0.485 ± 0.023	0.485 ± 0.007	1.104 ± 0.084
Control	0.574 ± 0.029	0.501 ± 0.011	1.457 ± 0.233	Conifer	0.530 ± 0.031	0.462 ± 0.016	0.944 ± 0.129

the creation of openings, it was however, affected by stand type. Much greater seedling recruitment occurred in the hardwood and conifer stands than in the mixed stands (Fig. 1a). The abundance of seedling recruitment in the conifer stand may be explained by the abundant *Abies* seed source. This stand was one of the few conifer dominated stands in our region not devastated by the spruce budworm during the last outbreak. This stand had not only high seedling establishment but also a high density of advance regeneration. In the hardwood stand the recent recruitment of *Abies balsamea* may due to trees that survived the last budworm outbreak (Bergeron et al. 1995) and are only now reaching sexual maturity. This is supported by the young age of this forest, having burned in 1944, the relatively small stature of the trees (Table 1) and the large proportion of the total regeneration accounted for by recent seedling establishment (Table 3, Fig. 2b).

An argument that poorer seedling survival following establishment may explain the higher seedling establishment to total regeneration ratio in hardwood stands does not appear to be valid as seedling mortality was the same among all stand types (Table 3). Longer term observations would distinguish any real patterns in seedling recruitment among stands from short-term temporal variations. However, the lack of any treatment effect or interaction (due to the variation between stand types) and the relatively low ratios of new regeneration to advance regeneration suggest that the initial effect of canopy openings in these forests is on advance regeneration.

Growth response of advance regeneration

In our study, as in similar research on *Pinus sylvestris* (Sundkvist 1994), the greatest response in seedling growth and architecture indices was to the all cut treatment (Fig. 2). Studies of understory regeneration also show that biomass of the understory vegetation increased most where overstory removal was greatest (Stone & Wolfe 1996; De Grandpré 1997). The response, in terms of height increment and branch production – as also demonstrated by Parent & Messier (1995) and O'Connell & Kelty (1994), was primarily related to maximum light

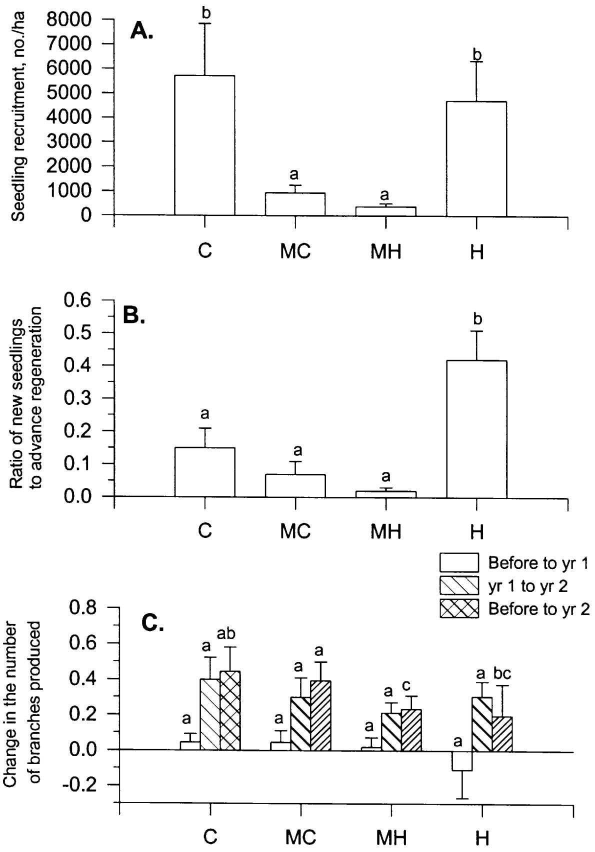

Fig. 1. Seedling response to the different stand types in terms of **A.** Seedling recruitment; **B.** Ratio of seedling recruitment to total regeneration; **C.** Changes in branch production. Significant differences ($p < 0.05$) between stand types are noted by different letters.

Table 3. Two-way ANOVAs for the growth and architecture indices as well as for seedling recruitment, showing their *F*-values for Stand, Treatment and Interaction effects. Significance levels: * = < 0.05, ** = < 0.01 and *** = < 0.001.

	Leader to lateral branch ratio			Relative height increment		
	2 yr difference	1 yr difference	2nd - 1st yr diff.	2 yr difference	1 yr difference	2nd - 1st yr diff.
Treatment	13.049 ***	9.969 ***	3.314 *	5.462 ***	12.006 ***	1.164
Stand	0.870	0.713	0.895	0.979	0.555	0.786
Treatment × stand	0.630	3.320 **	1.017	1.551	1.453	1.156

	Branch number			Seedling recruitment	Seedling recruitment to advance	Seedling mortality regeneration ratio
	2-yr difference	1-yr difference	2nd - 1st yr diff.			
Treatment	4.251 **	1.554	4.601 **	1.193	0.610	0.172
Stand	7.154 ***	1.068	3.705 *	3.519 *	0.000 ***	0.793
Treatment × stand	2.358 *	1.399	2.917 **	0.908	0.881	0.521

Table 4. Regression equations for the different growth and architecture indices based on abiotic and competition variables. These equations were calculated only for those periods that were significantly affected by the treatments.

		R^2
Leader to branch growth ratio difference:		
Before treatment to two years after treatment	= – 2.108 + 1.849 <July soil moisture> + 0.072 <June soil temperature> + 0.3 (2 yr change in total shrub and herb cover)	0.50
Before treatment to one year after treatment	= – 0.913 + 1.10 <July soil moisture> + 0.012 <1-yr change in total herb cover>	0.23
Relative height increment difference:		
Before treatment to two years after treatment	= – 0.146 + 0.082 <Above-shrub light>	0.29
Before treatment to one year after treatment	= – 0.193 + 0.104 <Above-shrub light> + 0.058 <Nitrogen leaching>	0.41
Branch production difference:		
Before treatment to two years after treatment	= – 1.073 + 1.573 <July soil moisture>	0.134
Year one to year two	= – 0.191 + 0.194 <Above-shrub light>	0.104

levels in the different quadrats (Table 4). Changes in the LB ratio were, on the other hand, positively correlated to summer soil temperatures and moisture content as well as to changes in the percent cover of understory plants. Soil temperature and moisture content were also characteristics found to be important by Carter & Klinka (1992), Lorimer (1983) and Sundkvist (1994). The relationship of the LB ratio to moisture, temperature and understory vegetation cover suggests that this index is sensitive to many variations in the environment and thus reflects well the effect of changes in canopy opening on seedling growth.

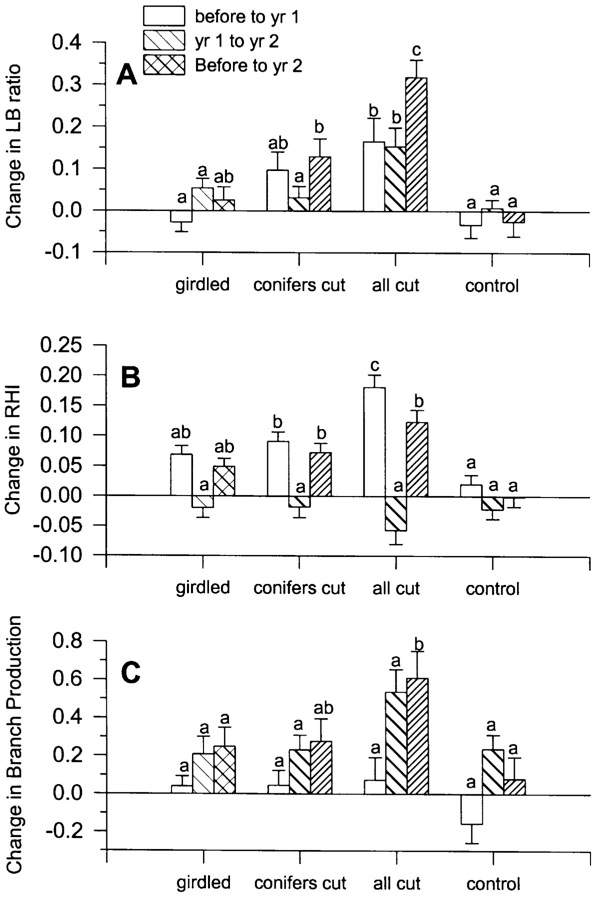

Fig. 2. Seedling response to the different treatments in terms of **A.** Changes in the LB ratio; **B.** Changes in the RHI; **C.** changes in branch production. Significant differences ($p < 0.05$) between treatments are noted by different letters.

In large openings or on drier sites a period of acclimation may be required for plants to adapt to new growing conditions. In fact, Sundkvist (1994) and Gordon (1973) did not find, as we did, a first year response in height growth to canopy openings but rather they observed a delay or a relative decrease in seedling height growth in the first year. In our study, the greatest change in growth, as observed for the RHI, occurred in the first year with a smaller response in between the first and second year following treatment (Fig. 2).

The number of branches produced did not, however, respond immediately (Fig. 2). The first year following treatment the number of branches produced was the same among treatments but after two years the number of branches produced in the all cut treatment was greater than in either the control or girdled treatments. Seedling response to these openings therefore seems to be first in terms of height growth and secondly in terms of increased architecture.

Silviculturally, it has been suggested that the minimum sized opening to be used should result in irradiance great enough to permit height growth to equal or to be greater than lateral growth (Klinka et al. 1992). In *Abies* forests in the same area, height growth equalled lateral growth at 25% full light (Parent & Messier 1995). The results from our study show that LB ratios greater than one can be achieved with 100-m^2 openings in which all trees are cut.

Suddenly created small-sized openings, occur naturally in the clay belt region of the boreal forest primarily due to the snapping of aspen stems. However this type of gap opening is minor compared with those created by the spruce budworm (>80% of tree mortality in all but the youngest hardwood dominated stands is due to the budworm, Kneeshaw & Bergeron 1998). During spruce budworm outbreaks trees die slowly over a number of years with maximum mortality usually occurring a number of years after the onset of an outbreak (Baskerville & MacLean 1979).

The girdled quadrats were the ones designed to most closely mimic this disturbance. Although not significant, the girdling treatment resulted, for all indices, in increased values when compared to the control (Fig. 2). Furthermore, after two years its effects were also similar to the conifer cut treatment. Since the girdling treatment does not result in an immediate increase in light, but rather in a gradual increase in light as needles fall off and the tree dies, it is not surprising that significant results are not apparent after two years. The implications are, thus, that in gaps created by spruce budworm outbreaks, advance regeneration is released gradually. In natural systems, height growth following epidemics has been found, with time, to increase up to five times pre-outbreak levels (Ghent 1958; see also Batzer & Popp 1985).

Conclusion

In *Abies*-dominated boreal forests, small openings in which all trees are removed do not affect seedling establishment of *Abies balsamea* (at least in the short term) but rather influence tree growth and architecture. Silvicultural decisions should therefore focus on concentrating operations where there is sufficient advance regeneration. Stand development in even small cuts of 100 m^2 will be faster than in naturally created spruce budworm gaps due to greater seedling height growth and greater investments in the structure needed to maximize growth. The results of the girdling treatment suggest that responses of seedlings to budworm outbreaks will be delayed or reduced due to the slow mortality of the overstory trees. Our three year study does not, obviously, provide conclusive results on long-term changes following gap creation but it does suggest that a long-term response to a prolonged increase in light would include not only increased height growth and an increase in the leader to lateral branches ratio but also an overall increase in the number of branches produced that is proportional to the degree and rapidity of canopy opening.

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