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Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest

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Abstract

Remnant tree stands left intact following a disturbance constitute the sole seed banks available for regeneration of coniferous species that neither bear serotinous cones nor reproduce vegetatively. The success of regeneration of tree species on these disturbed sites is, therefore, dependent on the distance from potential seed sources. The regeneration of balsam fir (Abies balsamea (L.) Mill.), white spruce (Picea glauca (Moench) Voss) and white cedar (Thuja occidentalis L.) was studied at two sites in Québec's southwestern boreal forest in order to quantify the influence of remnant stands on spatial distribution of regeneration. The first site is located in an area that burned in 1944 while the second site is located in an area that was clear-cut in the mid-1980s. Canonical correspondence analyses were used to determine the respective contributions of environmental data and spatial variables to the pattern of spatial distribution of regeneration. The results reveal that distance from a remnant stand is the most important variable in explaining spatial distribution of regeneration when compared to environmental variables such as soil type, drainage, slope and altitude. The plots of regeneration density against distance from a remnant stand for both the burned site and logged site show that regeneration density decreases abruptly with distance from a remnant stand. Furthermore, spatial autocorrelation analyses (Moran's I) indicate that even small remnant zones can significantly influence the pattern of spatial distribution of regeneration for the three species studied. The results presented here suggest that where preestablished regeneration is not abundant enough, alternative silvicultural systems such as strip clear-cutting or seedtree systems could be used instead of cuts with protection of regeneration and soils (CPRS). © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Boreal forest; Fire; Logging; Regeneration; Remnant stands; CCA; Regression; Spatial autocorrelation; Moran's I; Alternative silvicultural systems

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1. Introduction

Among all the natural disturbances affecting boreal forest dynamics fire is undoubtedly the most important, at least, at the century scale (Heinselman, 1981; Payette, 1992). The boreal forest is characterized by

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intense crown fires, covering large areas and leaving but a few surviving trees behind (Heinselman, 1981). The process of secondary succession initiated by fire results in a landscape mosaic composed of an assemblage of stands of different age, area and composition (Payette, 1992). Many boreal tree species have adapted to the relatively short fire cycle in the boreal forest (between 50 and 200 years depending on the region; Bonan, 1992) in order to survive and persist. For example, jack pine (Pinus banksiana Lamb.) and black spruce (Picea mariana (Mill.) BSP.) bear serotinous and semi-serotinous cones respectively (Rudolph and Laidly, 1990; Viereck and Johnston, 1990). Other types of colonizing species use vegetative reproduction to invade recently burned sites. This is the case of trembling aspen (Populus tremuloides Michx.) and paper birch (*Betula papyrifera* Marsh.) respectively, which produce root suckers and stump sprouts (Perala, 1990; Safford et al., 1990). Other species, however, do not possess any of these adaptations. Among these species, generally known as latesuccessional species, are balsam fir (Abies balsamea (L.) Mill.), white spruce (Picea glauca (Moench) Voss.) and white cedar (Thuja occidentalis L.). Depending on fire intensity and environmental conditions, some forested areas will be left intact (Rowe and Scotter, 1973; Carleton and MacLellan, 1994). Such remnant stands constitute seed banks of a crucial importance for the eventual return on disturbed sites of tree species that depend on seeding from a distance.

Like forest fires, human-induced disturbances, such as tree harvesting also affect boreal ecosystems dynamics. However, the regeneration dynamics of clear-cut logging and fire are somewhat different (Carleton and MacLellan, 1994). The most striking of these differences is that large-scale clear-cuts, unlike forest fires, do not leave any surviving mature trees except for a few ones along road and river margins. In addition, the heavy machinery used during harvesting operations causes soil compaction (Corns, 1988; Brais and Camiré, 1998), which has been linked to seedlings mortality and growth reduction of surviving regeneration (Harvey and Bergeron, 1989). In Québec, provincial standards regarding silviculture require that stands regenerate to levels equal or superior to those present before the cut (Gouvernement du Québec, 1999). Natural regeneration sometimes does not suffice to attain this goal and planting or fill

planting are often necessary, even in cases of cuts with protection of regeneration and soils (CPRS). As the boreal forest generally seems to regenerate adequately after fire (Payette et al., 1989), there has been a recent trend in forest ecology to model new silvicultural practices after natural regeneration dynamics (Attiwill, 1994; Galindo-Leal and Bunnell, 1995; MacDonald, 1995; Lieffers et al., 1996; Bergeron and Harvey, 1997; Fries et al., 1997; Bergeron et al., 1999). The growing number of international agreements regarding sustainable development and biodiversity (Johnston, 1993; Galindo-Leal and Bunnell, 1995) stress the importance of incorporating natural dynamics in ecosystem management. The present study aims at quantifying the spatial distribution of balsam fir, white spruce and white cedar natural regeneration in the boreal forest of Abitibi (Québec), with the goal of furthering ecosystem management.

2. Methods

2.1. Study area

The study area is located in the Lake Duparquet region of Abitibi, Québec (79°20'W, 48°30'N). Lake Duparquet is part of a large drainage basin discharging into James Bay, through Lake Abitibi. The region is within the claybelt of northern Québec and Ontario, a large physiographic region resulting from lacustrine deposits dating back from the maximum extension of pro-glacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). The nearest weather station is located in La Sarre, about 35 km north of the study area. The mean annual temperature is 0.6°C. Precipitation varies between 800-900 mm/year with the majority falling during the growing season (Bergeron et al., 1983). The frost-free period lasts 64 days, but occasional frost episodes may occur anytime during the growing season (Environment Canada, 1993). The fire cycle for the Lake Duparquet area has been estimated at 63 years prior to 1870 and more than 99 years in the period afterwards (Bergeron, 1991).

The first study site (burned site), is located south of lake Duparquet and was burned in 1944. The site was comprised primarily of balsam fir, white cedar and white spruce before the fire (Bergeron, in press). Following the fire, the site has been recolonized by paper birch and trembling aspen, mostly by means of vegetative reproduction. The southerly portion of the site is characterized by rocky outcrops covered with black spruce and jack pine. The proximity of the lake has favored the development of organic soils in the northern part of the site. The remaining is characterized downslope by glacio-lacustrine clay and upslope by glacial till deposits.

The second study site (logged site), is characterized by glacial till deposits and is located about 14 km northwest of the burned site. The site was clear-cut in the mid-1980s and subsequently planted with black spruce. Site preparation was performed before the plantation and competitive species were controlled for 7 years after planting by means of herbicides (Ministère des Ressources Naturelles, pers. comm.). Not all of the site was logged. A small remnant stand, covering 19 ha, was left in the western part.

2.2. Detailed regeneration study (burned site only)

A total of 164 circular plots (400 m² each) were sampled in the burned site, following a systematic sampling grid in which sampling plots were separated by an average of 50 m. The 164 plots covering a total area of about 42 ha were mapped using a global positioning system (GPS, Trimble Basic +) with a precision of ± 15 m. Within each sampling plot, every living balsam fir, white spruce and white cedar having a diameter at breast height (DBH) greater than 10 cm (considered mature) was counted. Some of the trees that established shortly after the fire have DBHs greater than 10 cm and likely influenced the spatial regeneration pattern in a manner similar to remnant trees (Galipeau et al., 1997). This is why they were included in the 'mature trees' category for the purpose of this study. Soil type was noted (clay, till, bare rock or organic soil) for each sampling plot. The slope was estimated and assigned to one of six classes (0-3, 4-8,9-15, 16-30, 31-40 and >41%). Drainage was also noted, varying between 0 (excessive) and 6 (absent) following the classification suggested by Lafond et al. (1992). To study regeneration, five 4 m^2 sub-plots were positioned inside each 400 m^2 sampling plot following a north-south axis. All living balsam firs, white spruces and white cedars of less than 10 cm DBH (considered regeneration) were counted and assigned to one of six height classes (0-25, 25-50, 50–75, 75–100, 100–150 and >150 cm) inside each sub-plot. The term 'regeneration' will, hereafter, refer to the six height classes combined.

2.3. Regeneration according to distance from a remnant stand (both sites)

Two transects were sampled in the burned site in order to study the role of remnant stands on the spatial distribution of regeneration. Each started 20 m inside a remnant stand in order to detect differences in regeneration density inside and outside the remnant zone. Transect 1 begins in a large (200 m) remnant zone located alongside lake Duparquet. This transect has a length of 80 m (20 m inside the remnant zone) and is oriented perpendicularly to the fire limit. The remnant zone is mostly composed of balsam fir, white spruce and white cedar (basal areas: 10, 6 and 6 m^2/ha , respectively). Cores taken at breast height revealed that trees from this zone are between-70 and 85-yearsold. Transect 2 is 140 m long and is oriented in the direction of prevailing winds. It starts 20 m inside a remnant stand located in the eastern portion of the burned site. This remnant stand, covering 0.1 ha, is composed of 60-year-old balsam fir and white spruce (basal areas: 4 and 8 m²/ha, respectively). Transect 2 is a particular case since, beside the remnant stand where it starts, two smaller remnant stands are located along it, both being about 250 m^2 in size. Transects 1 and 2 have been subdivided in $2 \text{ m} \times 2 \text{ m}$ quadrats (40 quadrats for Transect 1 and 70 for Transect 2). Inside each quadrat, balsam fir, white spruce and white cedar regeneration was evaluated by counting the number of individuals of less than 10 cm DBH.

The logged site was sampled using the method already described for Transects 1 and 2 of the burned site in order to measure regeneration according to distance from a remnant stand. The remnant stand here is composed of white spruces of 45–85 years of age (basal area: $4 \text{ m}^2/\text{ha}$). Many standing dead balsam firs are present on the site, relics of the last spruce budworm outbreak that occurred between 1970 and 1987 (Morin et al., 1993). The abundant balsam fir regeneration suggests that some of these trees were probably still alive when the site was clear-cut (Hugo Asselin, pers. obs.). White cedar is absent from this site. Five 90 m transects have been sampled, each starting 20 m inside the remnant stand and extending

70 m in the clear-cut zone. The transects, separated by 25 m, are all oriented perpendicularly to the forest border, i.e. in the direction of prevailing winds. Transects 1 and 5 are sufficiently far from the lateral borders (\approx 200 m) so that they do not influence the distribution pattern of regeneration in the sampled zone.

2.4. Analyses

In order to determine the respective contributions of environmental and spatial variables in the explanation of the spatial distribution pattern of balsam fir, white spruce and white cedar, canonical correspondence analyses (CCA) and partial canonical correspondence analyses (partial CCA) were performed using the CANOCO program (ter Braak, 1988; 1990) following the method developed by Borcard et al. (1992). The species matrix contains regeneration density data for each of the three species studied. Because of the large variation in extent of the data, they were transformed $(y'=\ln (y+1))$ as suggested by Borcard et al. (1992). The environmental variables matrix contains, for each sampling plot, the values of soil type, drainage, slope and altitude. The matrix of spatial variables contains, for each sampling plot, geographical co-ordinates, as well as distance to the nearest plot containing at least one mature tree (for each of the three species). The total percentage of variation in spatial distribution of regeneration explained by the variables that were used was partitioned into three components using the method developed by Borcard et al. (1992): the percentage of variation explained by environmental variables only, by space only, and by spatially structured environmental variables (Borcard et al., 1992). The significance of the percentages of variation explained by the different types of variables was verified using a permutation test (Monte Carlo) offered by the CANOCO program. Because survival after the first winter can be very low for young balsam fir seedlings (McLaren and Janke, 1996), the CCAs and partial CCAs were also performed excluding the lowest height class (<25 cm). This precaution allows us to avoid a potential mistake in interpretation that would result from the fact that a site may be suitable for a seed but not for a seedling (Schupp, 1995; Schupp and Fuentes, 1995; Cornett et al., 1997). The lowest height class (0-25 cm) may contain seedlings older than 1 year but finer subdivision was not possible due to method constraints. Results from the CCAs and partial CCAs performed with and without the height class 0–25 cm were compared using a Kolmogorov–Smirnov test (Scherrer, 1984).

For the part of the study using transects, spatial structure was estimated by plotting regeneration density against distance from a remnant zone. This allowed us to verify if data of the present study fit the generally accepted model stating that regeneration density decreases with distance form a remnant stand following a negative exponential (Fenner, 1985; Willson, 1993; Chambers and MacMahon, 1994; Greene and Johnson, 1989, 1996). In the present case, regeneration density values were In-transformed, permitting to draw straight lines instead of curves. The steepness of the slope then gives a direct indication of the rapidity of the decline in regeneration density with distance from the remnant stand (Willson, 1993). An analysis of covariance, ANCOVA (Scherrer, 1984) was performed in order to compare the slopes obtained for the three species in both sites.

Transect 2 of the burned site constitutes a particular case in that it would have been inappropriate to simply plot regeneration density against distance because of the presence of three remnant stands located along the transect instead of only one at the beginning. The complex resulting pattern is best seen using Moran's I statistic (Moran, 1950). This allows the degree of spatial autocorrelation of a variable to be measured with values ranging between -1 and +1 for complete negative and positive spatial autocorrelation, respectively. A value of zero means there is no significant spatial autocorrelation pattern. The results are shown on a spatial correlogram, tested for global significance using the Bonferroni correction (Legendre and Fortin, 1989) The number of distance classes used to perform the statistics was determined using Sturge's rule (Legendre and Legendre, 1998).

3. Results

3.1. Detailed regeneration study (burned site only)

CCAs and partial CCAs were used to divide the variation observed in the spatial structure of balsam fir, white spruce and white cedar regeneration density into four distinct portions (Borcard et al., 1992): the

variation explained by the environmental variables (10.8%); by space (24.7%); by spatially structured environmental variables (0.5%); and the variation that remains unexplained by the variables considered (64.0%). From the three types of variables, only spatial variables explain a significant amount of the variation observed in regeneration density data (Monte Carlo, p=0.01). Proportions do not change significantly according to the Kolmogorov–Smirnov test when the height class 0–25 cm is excluded from the calculations (in the same order as previously: 14.3; 20.7; 1.4 and 63.6%).

3.2. Regeneration according to distance from a remnant stand (both sites)

Plots of regeneration density against distance for Transect 1 of the burned site and for the five transects of the logged site tend to show that regeneration density decreases with distance from a remnant zone. This relation was strong for the three species in Transect 1 of the burned site (Fig. 1) but only for balsam fir in the logged site (Fig. 2), the regression for white spruce data being non significant (p=0.189). The analysis of covariance (ANCOVA) indicates that the regression lines for the three species in Transect 1 of the burned site and for balsam fir in the logged site all have different slopes (p>0.05). Fig. 1 shows that balsam fir regenerates more abundantly than white



Fig. 1. Regeneration density against distance from the remnant stand in Transect 1 of the burned site for balsam fir (triangles, solid line; R^2 =0.57), white spruce (squares, dashed line; R^2 =0.24) and white cedar (circles, dotted line; R^2 =0.25). The first 20 m are inside the remnant stand.



Fig. 2. Regeneration density against distance from the remnant stand in the logged site (data from the five transects combined) for balsam fir (triangles, solid line; R^2 =0.57) and white spruce (squares; not significant; p=0.189). The first 20 m are inside the remnant stand.

spruce or white cedar in the burned site. However, the slopes for the latter two species are less steep, meaning that their smaller seeds disperse further. Comparisons should not be made between Fig. 1 (burned site) and 2 (logged site) because the sites are not of the same age.

The correlogram (Moran's *I*) drawn for Transect 2 of the burned site (Fig. 3) shows three distinct peaks of significant positive spatial autocorrelation for balsam fir. These three values represent the three remnant



Fig. 3. Spatial correlograms (Moran's *I*) of balsam fir (triangles) and white spruce (squares) regeneration density against distance in Transect 2 of the burned site. Filled symbols represent significant Moran's *I* values (p<0.05). The spruce correlogram (dashed line) is not globally significant (Bonferroni, p=0.276).

stands located along the transect. White spruce does not show any particular spatial pattern and the spatial correlogram associated with that species is not globally significant (Bonferroni, p=0.276).

4. Discussion

Overall, the present study shows that distance from a remnant zone is more important than the environmental variables measured to explain the spatial distribution of post-fire regeneration of balsam fir. white spruce and white cedar in the boreal forest of Abitibi. This pattern has previously been observed by Galipeau et al. (1997), as well as by Kneeshaw and Bergeron (1996). The high percentage of unexplained variation presented here (64.0%) is not an isolated case. Borcard et al. (1992); Jean and Bouchard (1993), and Økland and Eilertsen (1994) obtained similar results (63.3, 51.1 and 63.6, respectively) using the same methods. According to these authors, the great proportion of unexplained variation could be due to non measured factors or to stochastic variation. In the present case, the narrow range of variation of the measured environmental variables limits their discrimination power. This does not mean, however, that environmental variables are not important to explain regeneration structure and dynamics of balsam fir, white spruce and white cedar. In fact, their low variability in the study area highlights the impact that the proximity of a remnant stand has on regeneration pattern. Eventhough we do not discard the possible role of stochasticity, the high percentage of unexplained variation could also be due to some factors that, although not measured, could have significantly changed the results (germination bed, shade, humidity, soil temperature, thickness of the organic matter layer, nutrients availability, competition with shrubs and herbaceous species, etc...). Most of these variables were impossible to measure as the present study was undertaken more than 50 years after the disturbance. In addition, it is important to note that in the present case, trees born from the first post-fire cohort are now able to produce seeds. Indeed, it takes an average 30 years for balsam fir, white spruce and white cedar to attain maturity (Johnston, 1990; Nienstaedt and Zasada, 1990; Zasada et al., 1992). The presence of a second cohort has undoubtedly contributed to dilute the spatial pattern observed.

Another way of assessing the importance of remnant zones to the explanation of spatial distribution of regeneration is to look at plots of regeneration density against distance from a remnant stand. It is generally held that the seed dispersion curve will follow a negative exponential with decreasing regeneration abundance from the border of a remnant zone into a burned or logged area (Fenner, 1985; Greene and Johnson, 1989, 1996; Willson, 1993; Chambers and MacMahon, 1994). Plots of regeneration density against distance from a remnant zone drawn for the burned site as well as for the logged site (Figs. 1 and 2) seem to fit this model. Although it is impossible to compare the burned site and the logged site because of their different ages, a general tendency is observed in both sites. Despite the lack of a good relationship between white spruce regeneration density and distance from the remnant stand in the logged site (Fig. 2), another study by Dobbs (1976) has shown that the negative exponential model was also applicable to this species. The overwhelming abundance of balsam fir seedlings as compared to the other two species studied could explain why the results are more convincing for this species. A dominance of balsam fir regeneration over other shade-tolerant species was also noted in other studies conducted in the boreal forest (Carleton and Maycock, 1978; Harvey and Bergeron, 1989; Zasada et al., 1992; Bergeron and Charron, 1994; Galipeau et al., 1997). A further consideration is that balsam fir is known to have a better capacity of establishment on a wider variety of substrates when compared to white spruce (Bakuzis and Hansen, 1965). Simard et al. (1998) attribute the ubiquity of balsam fir distribution to its large seed size. This is reflected in the present study by the steeper slope obtained for balsam fir, compared to white spruce and white cedar, in the plots of regeneration density against distance from a remnant stand. It is not surprising to note a greater dependence of balsam fir on remnant stands for regeneration as its large seeds disperse close to the parent trees.

5. Implications for forest management

The environmental and spatial variables measured account for 36% of the variation in spatial structure of regeneration with the effect of spatial variables being

at least two times more important than that of the environmental variables. The important role of remnant forest stands in the explanation of the spatial distribution pattern of coniferous regeneration in the boreal forest of Abitibi is directly applicable to forest management. As the presence of such zones seems determinant in insuring the return of late-successional species on disturbed sites, silvicultural practices should be oriented in a manner to leave intact some portions of the exploited area, especially in sites where preestablished regeneration is not present in sufficient amounts. In doing so, it will be important to determine the optimal distance that should separate two portions left intact on a site. Our findings indicate that the maximum dispersal distance lies somewhere between 60 and 115 m, depending on the species and the place. This distance corresponds, although it is a little bit higher, to the mean seed dispersal distance of the species studied, that is between 25 and 60 m for balsam fir (Frank, 1990), between 10 and 60 m for white spruce (Zasada and Lovig, 1983) and between 45 and 60 m for white cedar (Johnston, 1990). Accordingly, the optimal distance between remnant stands should lie between 120 and 230 m. This is consistent with numbers reported by Wedeles et al. (1995). Another important parameter to determine is the size of the stands that will be left uncut. Galipeau et al. (1997) suggest that the impact of small remnant stands (isolated trees or groups of trees) on the regeneration pattern is minimal considering the strong correlation they observed between regeneration density and distance from a large unburned stand. However, according to Greene and Johnson (1996), a stand with a diameter equivalent to five tree heights would be sufficient, if not optimal, to influence positively the distribution pattern of regeneration. Our results agree with this study as, along Transect 2, relatively small remnant stands (250 m^2) had a significant influence on the spatial distribution of regeneration (Fig. 3). Because of the lack of windfirmness of the conifers suddenly exposed by a cut, it is better to reserve dominant trees with wide deep crowns, relatively large live crown ratios, and strong, tapering boles (Smith et al., 1997).

Many alternatives to traditional clear-cutting have already been proposed in the literature (Burton et al., 1992; Wedeles et al., 1995; Lieffers et al., 1996; Arnott and Beese, 1997; Bergeron and Harvey,

1997; Fries et al., 1997). Among these methods, strip clear-cutting and seed-tree systems seem to be the most interesting alternatives for boreal mixedwoods management, both ecologically and economically speaking (Wedeles et al., 1995; Smith et al., 1997). When a coniferous stand with low or absent preestablished regeneration is logged, it would be ideal to leave patches (or strips) of mature trees, evenly distributed on the site (Arnott and Beese, 1997; Fries et al., 1997). Such a practice, while favoring latesuccessional species regeneration on logged sites. would better mimic the complex behavior of fire, resulting from atmospheric conditions, fuel quantity and quality as well as wind and topography (van Wagner, 1983). The trees left standing would create shaded areas that improve the microclimate at soil surface during hot, dry summer days, as in the case of burned areas (Carleton and MacLellan, 1994). Since 'what is left or what replaces what is harvested is more important silviculturally than what is cut' (Smith et al., 1997), and since 'natural regeneration plays a role far more important than plantations in Canada' (Haddon, 1997), the findings brought about by the present study concerning spatial distribution of natural regeneration of three late-successional species will aid in modifying forest management techniques to more closely emulate the effects of natural disturbances like fires.

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References

- Arnott, J.T., Beese, W.J., 1997. Alternatives to clear-cutting in BC coastal montane forests. For. Chron. 73, 670–678.
- Attiwill, P.M., 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manage. 63, 247–300.

- Bakuzis, E.V., Hansen, H.L., 1965. Balsam fir, *Abies balsamea* (Linnaeus) Miller: A Monographic Review. The University of Minnesota Press, Minneapolis.
- Bergeron, Y., 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology 72, 1980– 1992.
- Bergeron, Y., in press. Species and stand dynamics in the mixedwoods of Quebec southern boreal forest. Ecology, in press.
- Bergeron, Y., Charron, D., 1994. Postfire stand dynamics in a southern boreal forest (Québec): a dendroecological approach. Écoscience 1, 173–184.
- Bergeron, Y., Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. 92, 235–242.
- Bergeron, Y., Bouchard, A., Gangloff, P., Camiré, C., 1983. La classification écologique des milieux forestiers de la partie ouest des cantons d'Hébécourt et de Roquemaure, Abitibi Québec. Études écologiques 9. Université Laval, Québec.
- Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. For. Chron. 75, 49–54.
- Bonan, G. B., 1992. Processes in boreal forests. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, pp. 9–12.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045– 1055.
- Brais, S., Camiré, C., 1998. Soil compaction induced by careful logging in the claybelt region of northwestern Quebec (Canada). Can. J. Soil Sci. 78, 197–206.
- Burton, P.J., Balisky, A.C., Coward, L.P., Cumming, S.G., Kneeshaw, D.D., 1992. The value of managing for biodiversity. For. Chron. 68, 225–237.
- Carleton, T.J., MacLellan, P., 1994. Woody vegetation responses to fire versus clear-cutting logging: a comparative survey in the central Canadian boreal forest. Écoscience 1, 141–152.
- Carleton, T.J., Maycock, P.F., 1978. Dynamics of the boreal forest south of James Bay. Can. J. Bot. 56, 1157–1173.
- Chambers, J.C., MacMahon, J.A., 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. Annu. Rev. Ecol. Syst. 25, 263–292.
- Cornett, M.W., Reich, P.B., Puettmann, K.J., 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. Écoscience 4, 353–364.
- Corns, I.G.W., 1988. Compaction by forestry equipment and effects on coniferous seedling growth on four soils in the Alberta foothills. Can. J. For. Res. 18, 75–84.
- Dobbs, R.C., 1976. White spruce seed dispersal in central British Columbia. For. Chron. 52, 225–228.
- Environment Canada, 1993. Normales climatiques au Canada. Environement Canada, Service de l'environment atmosphérique, Ottawa.
- Fenner, M., 1985. Seed Ecology. Chapman and Hall, London.

- Frank, R., 1990. Abies balsamea (L.) Mill. Balsam fir. In: Burns, R.H., Honkala, B.H. (Eds.), Silvics of North America, Vol. 1. Conifers. U.S. Dep. Agric. Agric. Handb., 654, pp. 26–35.
- Fries, C., Johansson, O., Pettersson, B., Simonsson, P., 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. For. Ecol. Manage. 94, 89–103.
- Galindo-Leal, C., Bunnell, F.L., 1995. Ecosystem management: implications and opportunities of a new paradigm. For. Chron. 71, 601–606.
- Galipeau, C., Kneeshaw, D., Bergeron, Y., 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. 27, 139– 147.
- Gouvernement du Québec, 1999. Loi sur les forêts. L.R.Q., c. F-4.1.
- Greene, D.F., Johnson, E.A., 1989. A model of wind dispersal of winged or plumed seeds. Ecology 70, 339–347.
- Greene, D.F., Johnson, E.A., 1996. Wind dispersal of seeds from a forest into a clearing. Ecology 77, 595–609.
- Haddon, B., 1997. The status of forest regeneration in Canada. For. Chron. 73, 586–589.
- Harvey, B.D., Bergeron, Y., 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. Can. J. For. Res. 19, 1458–1469.
- Heinselman, M.L., 1981. Fire and succession in the conifer forests of northern North America. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Application. Springer, New York, pp. 374–405.
- Jean, M., Bouchard, A., 1993. Riverine wetland vegetation: importance of small-scale and large-scale environmental variation. J. Veg. Sci. 4, 609–620.
- Johnston, B.E., 1993. Forests and UNCED '92: a foundation for the future. For. Chron. 69, 539–544.
- Johnston, W.F., 1990. *Thuja occidentalis* L. northern white-cedar. In: Burns, R.H., Honkala, B.H. (Eds.), Silvics of North America, Vol. 1. Conifers. U.S. Dep. Agric. Agric. Handb., 654, pp. 580–589.
- Kneeshaw, D.D., Bergeron, Y., 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. 26, 888–898.
- Lafond, R., Cauchon, C., Ducruc, J.-P., 1992. Pédologie forestière. Modulo éditeur, Mont-Royal, Québec.
- Legendre, P., Fortin, M.-J., 1989. Spatial pattern and ecological analysis. Vegetatio 80, 107–138.
- Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd English Edition. Elsevier Science, Amsterdam.
- Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K., Stewart, J.D., 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72, 286– 292.
- MacDonald, B., 1995. The case for boreal mixedwood management: an Ontario perspective. For. Chron. 71, 725–734.
- McLaren, B.E., Janke, R.A., 1996. Seedbed and canopy cover effects on balsam fir seedling establishment in Isle Royale National Park. Can. J. For. Res. 26, 782–793.
- Moran, P.A.P., 1950. Notes on continuous stochastic phenomena. Biometrika 37, 17–23.

- Morin, H., Laprise, D., Bergeron, Y., 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. 23, 1497–1506.
- Nienstaedt, H., Zasada, J.C., 1990. *Picea glauca* (Moench) Voss. White spruce. In: Burns, R.H., Honkala, B.H. (Eds.), Silvics of North America, Vol. 1. Conifers. U.S. Dep. Agric. Agric. Handb., 654, pp. 204–226.
- Økland, R.H., Eilertsen, O., 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. J. Veg. Sci. 5, 117–126.
- Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, pp. 144–169.
- Payette, S., Morneau, C., Sirois, L., Desponts, M., 1989. Recent fire history of the northern Québec biomes. Ecology 70, 656– 673.
- Perala, D.A., 1990. *Populus tremuloides* Michx. Quaking aspen. In: Burns, R.H., Honkala, B.H. (Eds.), Silvics of North America, Vol. 2. Hardwoods. U.S. Dep. Agric. Agric. Handb. 654, pp, 555–569.
- Rowe, J.S., Scotter, G.W., 1973. Fire in the boreal forest. Quat. Res. 3, 444–464.
- Rudolph, T.D., Laidly, P.R., 1990. *Pinus banksiana* Lamb. Jack pine. In: Burns, R.H., Honkala, B.H. (Eds.), Silvics of North America, Vol. 1. Conifers. U.S. Dep. Agric. Agric. Handb. 654, pp. 280–293.
- Safford, L.O., Bjorkbom, J.C., Zasada, J.C., 1990. *Betula papyrifera* Marsh. Paper birch. In: Burns, R.H., Honkala, B.H. (Eds.), Vol. 2. Hardwoods. U.S. Dep. Agric. Agric. Handb. 654, pp. 158–171.
- Scherrer, B., 1984. Biostatistique. Gaëtan Morin éditeur ltée, Montréal.
- Schupp, E.W., 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am. J. Bot. 82, 399–409.
- Schupp, E.W., Fuentes, M., 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Écoscience 2, 267–275.

- Simard, M.-J., Bergeron, Y., Sirois, L., 1998. Conifer recruitment in the southeastern Canadian boreal forest: the importance of substrates. J. Veg. Sci. 9, 575–582.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The practice of silviculture. Applied Forest Ecology, 9th Edition. Wiley, New York.
- ter Braak, C.J.F., 1988. CANOCO a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis. Version 2.1. Agricultural Mathematics Group, Ministry of Agriculture and Fisheries, Wageningen.
- ter Braak, C.J.F., 1990. Update notes: CANOCO Version 3.10. Agricultural Mathematics Group, Wageningen, The Netherlands.
- van Wagner, C.E., 1983. Fire behaviour in northern conifer forests and shrublands. In: Wein, R.W., MacLean, D.A. (Eds.), The Role of Fire in Northern Circumpolar Ecosystems. Wiley, New York, pp. 65–80.
- Viereck, L.A., Johnston, W.F., 1990. *Picea mariana* (Mill.) B.S.P. Black spruce. In: Burns, R.H., Honkala, B.H. (Eds.), Silvics of North America, Vol. 1. Conifers. U.S. Dep. Agric. Agric. Handb. 654, pp. 227–237.
- Vincent, J.S., Hardy, L., 1977. L'évolution et l'extinction des grands lacs glaciaires Barlow et Ojibway en territoire québécois. Géog. phys. Quat. 31, 357–372.
- Willson, M.F., 1993. Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107/108, 261–280.
- Zasada, J., Lovig, D., 1983. Observations on primary dispersal of white spruce, *Picea glauca*, seed. Can. Field-Nat. 97, 104–106.
- Zasada, J., Sharik, T.L., Nygren, M., 1992. The reproductive process in boreal forest trees. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, pp. 85–125.
- Wedeles, C.H.R., Van Damme, L., Daniel, C.J., Sully, L., 1995. Alternative silvicultural systems for Ontario's boreal mixedwoods: A review of potential options. NODA/NFP Technical Report TR-18.