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Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate

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Abstract. In order to explain conifer species recruitment in Canada's southeastern boreal forest, we characterized conifer regeneration microsites and determined how these microsites vary in abundance during succession. Microsite abundance was evaluated in deciduous, mixed and coniferous stands along a 234-yr postfire chronosequence. Conifers were most often found in relatively well-illuminated microsites, devoid of litter, especially broad-leaf litter, and with a reduced cover of lower vegetation (< 50 cm tall). Although associated with moss-rich forest floor substrates, *Abies balsamea* was the most ubiquitously distributed species. *Picea glauca* and especially *Thuja occidentalis* seedlings were frequently found on rotten logs. Light measurements did not show differences among seedling species nor between stand types. The percentage cover of broad-leaf litter decreased significantly during succession. Also, rotten logs covered with moss occupied a significantly larger area in the mid-successionnal stands than in early successional deciduous or late successional coniferous stands. The results suggest that the presence of specific forest floor substrate types is a factor explaining low conifer recruitment under deciduous stands, conifer codominance in the mid-successional stage, and delayed *Thuja* recolonization after fire. Results also suggest that some facilitation mechanism is responsible for the observed directional succession.

Keywords: *Abies balsamea*; Litter; Microsite; Nurse log; *Picea glauca*; Québec; Regeneration; Succession; *Thuja occidentalis*.

Nomenclature: Hosie (1972).

Introduction

In parts of Canada's southeastern boreal forest, the recruitment of *Abies balsamea* (Balsam fir), *Picea glauca* (White spruce) and *Thuja occidentalis* (Eastern white cedar) seems to occur during most of the successional development, from shade-intolerant deciduous species to conifer dominance (Bergeron & Charron 1994; Kneeshaw & Bergeron 1996). The process that modifies species recruitment success during succession is classically viewed as competition for light, the intolerant species being gradually unable to recruit and consequently replaced by more shade-tolerant tree species (Kimmins 1987). Light-regulated processes might explain the lack of recruitment of intolerant deciduous species under their own canopies which results in the replacement of the deciduous species by more shade-tolerant species, in this case conifers. However, field evidence suggests that recruitment success among coniferous species is not primarily explained by shade tolerance. First, *Picea glauca* should be able to recruit as well as, or maybe better than more shade-tolerant conifers in the early successional hardwood stands (Lieffers et al. 1996). However, its seedling density is always very low compared to the more shade-tolerant *Abies balsamea* (Bergeron & Charron 1994; Kneeshaw & Bergeron 1996).

Secondly, *Thuja occidentalis*, the most shade-tolerant (Logan 1969) of the three conifers studied, did not start colonizing a wildfire area until 50 years after fire (Bergeron & Charron 1994) despite nearby seedbearers and the widespread occurrence of shady microsites. Modulators of seedling abundance such as predation, seed viability, and life history traits alone may explain some of this variation. However, when one considers that conifer seedlings are rarely randomly distributed on the forest floor (Maguire & Forman 1983) an alternative hypothesis is that young conifer seedlings are associated with particular microsites, i.e. safe sites (sensu Harper 1977). Such sites may include, for instance, dead logs and stumps (Christy & Mack 1984; Scott & Murphy 1987; Takahashi 1994), areas devoid of leaf litter (Bartlett et al. 1991; Côté & Bélanger 1991) or areas lacking herbaceous vegetation (Maguire & Forman 1983).

Few studies have examined the fine-scale spatial distribution of conifer seedlings (Maguire & Forman 1983; Collins 1990; Hofgaard 1993b; St. Hilaire &

Leopold 1995) and no study has related the abundance of these seedlings to microsite abundance along a successional gradient. Our first goal was to determine if small conifer seedlings (< 30 cm in height) are associated with particular microsites and if so, to determine what constitutes a 'good microsite'. Species-specific microsite differences in the cover of open and lower (< 50 cm tall) vegetation were also evaluated. Secondly, we evaluated the relative abundance of microsites in three stands representing the deciduous, mixed and coniferous stages of succession. Ultimately, we wanted to determine what microsite characteristic(s), if any, could explain coniferous species recruitment patterns in southeastern Canadian boreal forest.

Study area

The study area is situated around Lake Duparquet in northwestern Québec (79° 15' W, 48° 30' N) at the southwestern limit of the boreal forest in Québec (Rowe 1972) in the *Abies balsamea-Betula papyrifera* ecoregion (Grandtner 1966). The closest meteorological station is 42 km to the north at La Sarre. The climate is continental with a mean annual temperature of 0.8 °C and a mean total annual precipitation of 857 mm (records over the period 1961-1990). Snow represents 25 % of the total annual precipitation. The frost-free period averages 64 days, although occasional frosts may occur throughout the growing season (Anon. 1993a).

Three stand types representing the deciduous, mixed conifer-deciduous and coniferous stages (Table 1) of a 234 year long post-fire successional gradient (Bergeron & Dubuc 1989) were selected. These stand types, located on mesic clay soils, burned in 1916, 1870 and 1760 respectively, as determined by fire scar dating and the systematic dating of post-fire tree cohorts (Bergeron 1991; Dansereau & Bergeron 1993). Each stand type covers at least 100 hectares (Bergeron & Dansereau 1993; Bergeron & Charron 1994).

Methods

Data collection

In July and August 1994, four transects were established in each of the three stand types (deciduous, mixed conifer-deciduous and coniferous forest) around Lake Duparquet. All four transects were situated in different stands of the same stand type as far as possible. Quadrats of 25 m^2 were established at 40-m intervals along the transects. 40 quadrats per stand type were described. The forest floor was characterized by visually estimating the percentage cover of seven substrate classes:

1. Leaves of deciduous broad-leaved trees on forest floor humus (Leaf);
2. Needles of coniferous trees on forest floor humus (Need);
3. Leaves of mixed deciduous broad-leaved and needles of conifers on forest floor humus (Leaf&Needle);
4. Moss on forest floor humus (Moss);
5. Bare decomposed logs (RottenLog);
6. Undecomposed logs covered with moss (FreshLog&Moss);
7. Decomposed logs covered with moss (RottenLog&Moss).

We also evaluated the mean percent cover of substrates by randomly locating three 10 cm × 10 cm sub-quadrats in each quadrat. These sub-quadrats were divided into 100 1-cm^2 cells and the composition of the forest floor was described for each cell. Log and stump cover was also re-evaluated by measuring the area covered by each log and stump and dividing the sum of these areas by the quadrat area (25 m^2). Logs and stumps were divided in two classes. One class (decomposed) included those materials that could be penetrated with moderate pressure to a depth of 10 cm with a pencil; the other (undecomposed) class could not be penetrated. Because various parts of a log can be in different decomposition stages, one log could be separated into two classes when the percent cover of dead wood was evaluated. Our substrate classification was adapted to the seedling microsite scale and therefore does not relate to entire

Table 1. Composition of live trees (> 5 cm DBH) expressed as a proportion of the total basal area in each stand type. Outbreaks of Spruce budworm [*Choristoneura fumiferana* (Clem.)] have considerably reduced the number of live *Abies balsamea* trees in mixed and coniferous stands. The deciduous stands chosen have an exceptionally high proportion of *Thuja occidentalis* – which is probably due to the presence of surrounding seedbearers making it easier to find seedlings of this species – numbers are below 0.11 in other deciduous stands. From Leduc et al. (1995).

	Deciduous	Mixed	Coniferous
Abies balsamea	15.74	12.07	12.29
Betula papyrifera	16.80	22.14	25.10
Populus balsamifera	0.38	0.32	0
Picea glauca	3.99	15.81	7.82
Picea mariana	0.38	2.63	0.33
Populus tremuloides	51.24	46.89	11.59
Salix sp.	4.53	0.04	0
Thuja occidentalis	6.94	0.11	42.88

bole decomposition classifications used in other studies (see Scott & Murphy 1987; Hope 1987; Hofgaard 1993a, b). Rare substrates, such as bare mineral soil, or substrates that do not retain conifer seeds, such as bare undecomposed logs (Harmon 1989a), were included in the general substrate description but percent cover of the frequent substrate classes was later adjusted excluding these rare seedling substrates since they could not be included in the substrate-seedling analyses.

In each 25-m^2 quadrat the percent cover of the lower vegetation, notably the herbaceous plants, prostrate shrubs, and small woody plants (< 50 cm in height) was evaluated in 10 randomly located 10-cm radius plots. These covers were then used to calculate a plot average.

All conifer seedlings less than 30 cm in height were tagged, measured and aged by counting terminal bud scars in each 25-m^2 quadrat. Because the apical meristem of *Thuja* seedlings is covered by leaf primordia at various stages of development (see Krasowski & Owens 1991) a subsample of *Thuja* seedlings was aged by annual ring counts. *Thuja* seedlings of vegetative origin (e.g. individuals with roots connected to an adult tree or individuals with a distinctively curved stem at the bottom and no juvenile leaves) were excluded from the census. For all species, most seedlings (> 60 %) were in their second growing season following a mast seed production that occurred in 1992 (Simard 1994) and measured less than 10 cm in height. Seedling microsites were described by identifying the substrate class and the substrate's height above the surface of the forest floor. We also evaluated the percent cover of lower vegetation surrounding the seedlings using the same method as for the 10-cm radius plots. The distance and DBH of the nearest seedbearer of each species tree was also noted.

The proportion of incident photosynthetic photon flux density (% PPFD) striking the apical shoot of a subsample of 108 seedlings situated on all three stand types and at 29 random points was evaluated by taking instantaneous measurements using Li-COR sensors and datalogger (Li-Cor Inc., Lincoln, NE) during completely overcast conditions (Parent & Messier 1996; Messier et al. 1998). These measures were taken on August 12th, 1994.

Data analysis

For the analysis of seedling-substrate associations we used only those 25-m^2 quadrats which were situated found within 10 m from a seed tree. This measure was taken in an effort to ensure that the absence of seedlings was not caused by a lack of seeds. We separated seedlings into two height classes to determine if microsite associations are maintained during size class transitions and therefore represent suitable substrates for further growth and survival. Height was preferred over age class because there were far more differences in height than in age among the seedlings. In the analysis of substrate-seedling relationships quadrats from all stand types were included in order to compare all the preferences of the three species for all seven substrate classes. The analyses were performed using χ^2 goodness of fit tests specifying fixed expected frequencies based on the substrate's mean percentage cover (Anon. 1993b). Analyses of variance and *t*-tests were applied to test microsite differences in surrounding lower vegetation and light. Multiple comparisons were performed using Tukey's HSD test. Percent cover of the lower vegetation was transformed using the equation:

$$x_t = \ln (x + 3/2) \qquad (1)$$

and light measurements were transformed using the equation:

$$x_t = \ln (x) \qquad (2)$$

in order to meet normality and homogeneity of variance assumptions. Kruskal-Wallis One-way Analysis of Variance based on ranks was used to test substrate height differences between the three conifers and microsite abundance differences between stand types.

Results

Seedling microsites

Substrate type and height

All species showed significant associations between substrate type and seedling occurrence ($p < 0.001$). All tree species are found less frequently on Leaf substrate than would be expected according to the proportion of the forest floor covered by that substrate (Fig. 1). This negative association with Leaf litter appears to be stronger for *Thuja* and *Picea* (i.e. the residual values are lower) than for *Abies* seedlings. *Abies* seedlings are more uniformly distributed on the different substrates than seedlings of the other species. Small *Abies* seedlings (0 - 5 cm; < 5 yr) are associated with Moss and Leaf&Needle substrate types. Taller seedlings (> 5 cm; ca. 5 - 12 yr) are mostly associated with Moss. Small (0 - 7 cm; < 7 yr) *Picea* seedlings are highly associated with FreshLog&Moss and, to a lesser extent, RottenLog&Moss while taller seedlings (> 4 cm; ca. 5- 12 yr) are almost entirely confined to RottenLog&Moss although there is a lower favourable association with Moss.

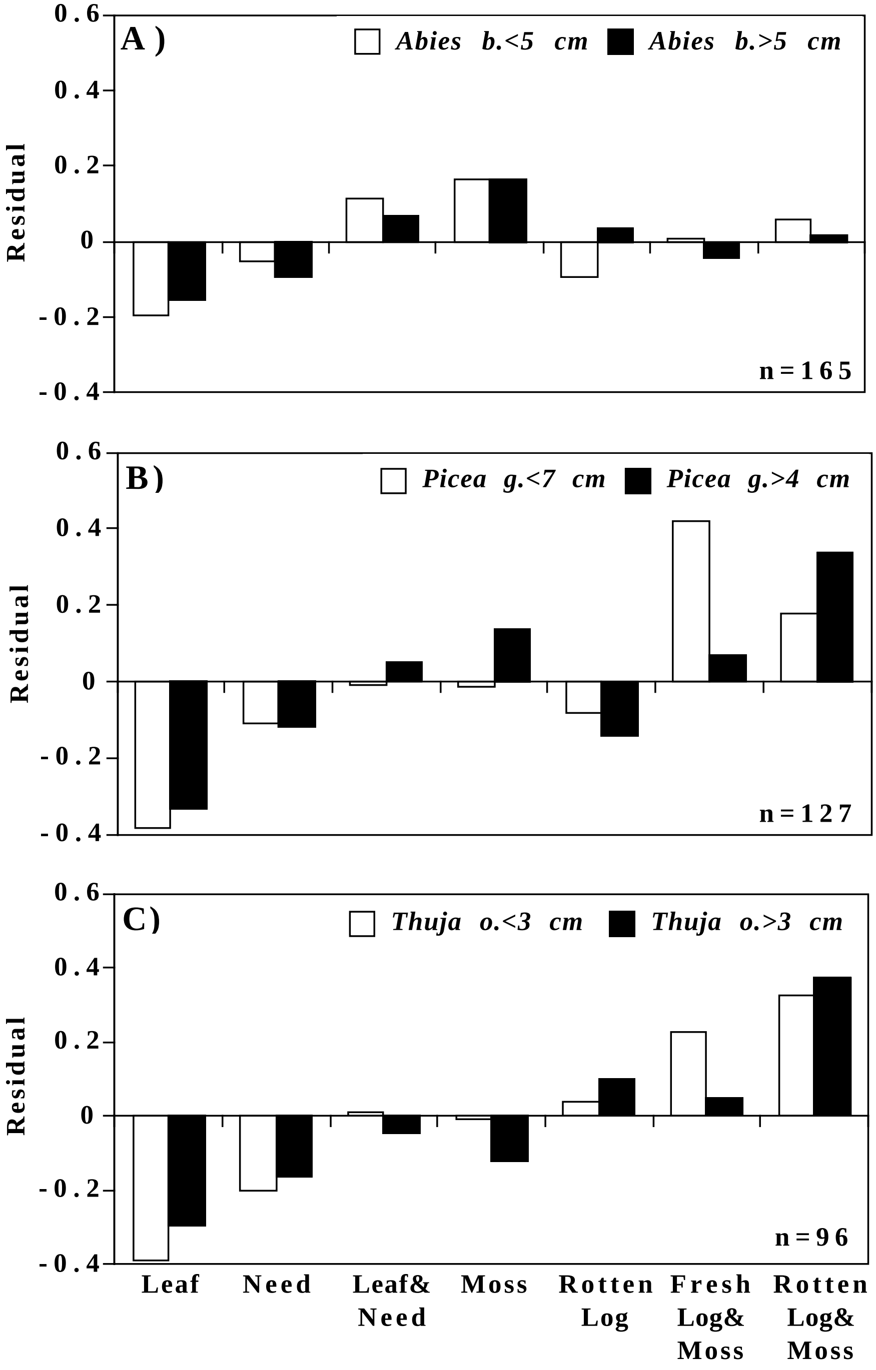

Fig. 1. Residual values from χ^2 analysis of seedlings of *Abies balsamea* (**A**), *Picea glauca* (**B**) and *Thuja occidentalis* (**C**) of different heights. Residual values were obtained by subtracting the expected number of seedlings on a substrate according to the cover that substrate occupies from the observed number of seedlings on that substrate. High positive residual values reflect positive seedling-substrate associations while high negative residual values reflect negative seedling-substrate associations. *Picea* height classes overlap to keep population numbers high enough to meet test postulates. Substrates include: Deciduous broad-leaf on forest floor humus (Leaf), Coniferous needles on forest floor humus (Need), Mixed deciduous-leaf and coniferous needles on forest floor humus (Leaf&Needle), Moss on forest floor humus (Moss), Bare decomposed logs (RottenLog), Undecomposed logs covered with moss (FreshLog&Moss), and Decomposed logs covered with moss (RottenLog&Moss).

Table 2. Percent cover of lower vegetation (< 50 cm tall) in microsites with different conifer seedlings. Standard deviations are given in brackets.

	Vegetation cover	
Abies balsamea	8.0	(11)
Picea glauca	9.5	(14)
Thuja occidentalis	7.4	(12)
Seedlings in deciduous stands	7.4	(12)
Seedlings in mixed stands	8.5	(11)
Seedlings in coniferous stands	8.5	(13)
All seedlings	8.3	(12)

Seedlings of *Thuja* follow a pattern similar to that of the *Picea* seedlings except for the fact that RottenLog&Moss is the best substrate in both size classes and that they are only associated with woody substrates. Seedling height on nurse logs and stumps above the forest floor did not differ between *Picea* (8.0 ± 8.6 cm) and *Thuja* (11.4 ± 10.8 cm) but were significantly higher ($\chi^2 = 39.98$; $n = 176$; $p < 0.001$) than for *Abies* (1.9 ± 4.5 cm).

Surrounding lower vegetation cover and light

Percent cover of lower vegetation around the seedlings does not differ between seedling species ($f = 1.252$, df = 3, $p = 0.292$), averaging 8.3 ± 12%. Percent cover of lower vegetation around the seedlings does not differ between stand types ($f = 1.167$; df = 3; $p = 0.324$) (Table 2). T-tests showed cover around seedlings is significantly lower than around the random points (20 ± 17%) even when we select only those seedlings not found on logs:

All seedlings included: $t = 8.9$; df = 81, $p < 0.001$;

Only seedlings not located on logs: $t = 7.9$; df = 43; $p < 0.001$.

All seedlings were found in areas with more light than expected from random distributions (f = 20.63; $p < 0.001$), i.e. all seedlings were exposed to a light intensity at the forest floor which is higher than average – even if we only select seedlings not located on logs. The percentage PPFD at the level just above the seedlings did not differ between species ($p > 0.05$) (Table 3).

Table 3. Percent of full light over conifer seedlings and random points. Standard deviations are given in brackets. Values followed by the same letter do not differ significantly ($p < 0.05$).

Location	Percentage light	
Abies balsamea seedlings	5.69	(4.6)a
Picea glauca seedlings	6.63	(6.1)a
Thuja occidentalis seedlings	7.13	(3.4)a
Random points	2.22	(0.8)b

The relative abundance of microsites in the successional stands

The surface area covered by Leaf is significantly different between all three stand types ($\chi^2 = 15.8$; $p < 0.001$, Table 4). RottenLog&Moss cover is significantly higher in the mixed stands than in either younger or older stands ($\chi^2 = 14.9$; $p < 0.001$, Table 4). Moss cover, however, did not differ between stand types. Total lower vegetation cover significantly decreases with succession. From 70 % lower vegetation cover in young deciduous stands, values drop to 30 % in mixed stands and 16 % in coniferous stands (p < 0.01). Light intensity measures did not differ between stand types ($\chi^2 = 2.59$; $p = 0.2744$).

Discussion

Preferred seedling microsites

In the study area, most conifers less than 30 cm tall were found on microsites with a light intensity which is higher than average and a cover of the surrounding vegetation (< 50 cm tall) which is lower than average. The conifer species studied, *Abies balsamea* (Balsam fir), *Picea glauca* (White spruce) and *Thuja occidentalis* (Eastern white cedar), were found in comparable microsites in terms of lower vegetation cover and light intensity. Therefore none of the tree conifer species might be able to establish and grow under these average forest floor light conditions. Messier et al. (1998) also found that the light intensity was very low on the forest floor of the same stand types. Still, more light and vegetation cover measurements would be necessary to confirm this result.

All seedlings species are associated with substrates where competition is low and moisture is abundant

Table 4. Percent of decomposed logs covered with moss (RottenLog&Moss) and deciduous broad-leaf (Leaf) in each stand type. Standard deviations are given in brackets. Values followed by the same letter do not differ significantly ($p < 0.05$).

Stand type	Leaf cover	RottenLog&Moss cover
Deciduous	78.3 (20.0) a	2.68 (2.39) a
Mixed	57.0 (25.9) b	8.63 (8.88) b
Coniferous	51.2 (31.3) c	5.55 (4.16) a

(ground moss and decomposed logs covered with moss). However, *Abies* seedlings were more widely distributed than seedlings of *Picea* and *Thuja*. *Abies* and *Picea* (> 4 cm tall) seedlings were positively associated with ground moss which is the second best substrate for *Picea* (> 4 cm tall) after decomposed logs covered with moss. *Thuja* regeneration was almost entirely restricted to these logs.

Studies have shown that, compared to seedlings of *Picea* spp. or *Tsuga* spp. seedlings, seedlings of *Abies* spp. have longer tap roots and longer shoots that enable them to penetrate through, and survive better in, thick forest floor litter (Place 1955; Day 1964; Knapp & Smith 1982; Klein et al. 1991) and communities composed of a thick moss layer as found on the forest floor (Nakamura 1992). *Picea* spp., *Tsuga* spp., or *Thuja* spp. seedlings are often restricted to the shorter moss communities found on logs and stumps (Harmon & Franklin 1989). Hence, *Abies balsamea* seedlings may be more widely distributed because of their deeper initial root penetration and longer shoots compared to *Picea glauca* or *Thuja occidentalis*.

In general, the substrate with which seedlings are most associated with is similar, whatever the size class. However, the best substrate for small *Picea* seedlings is formed by undecomposed logs covered with moss, while taller seedlings are most associated with decomposed logs covered with moss. These undecomposed logs will probably not decompose fast enough to permit sustained growth and most of the seedlings will die (Simard, pers. obs.). Further shifts in habitat suitability could limit the significance of our results if, for instance, later survival on decomposed moss covered logs was very low due to competition among seedlings and bole fragmentation (Harmon 1989b). However, height growth of *Picea glauca* advance regeneration on well decomposed logs was found to be comparable to that of those located on the forest floor (Lieffers et al. 1996).

The relative abundance of microsites during succession

According to our results, high cover values for vegetation (< 50 cm tall) and broad-leaf litter on the forest floor, characteristic of young deciduous stands (see also De Grandpré et al. 1993), reduce overall conifer regeneration in these stands. Moreover, the low abundance of rotten, moss-covered logs results in a strong prevalence of *Abies* regeneration. As the stand ages towards mid-succession (ca. 120 yr), it supports less leaf litter and herbaceous vegetation and more nurse logs. Therefore *Abies* regeneration increases, *Picea* regeneration increases to represent a higher proportion of total conifer recruitment and *Thuja* recruitment is initiated. Sexual regeneration of *Thuja* is so highly associated with woody debris that the recolonization of a site by this species could rely on a facilitation mechanism (Connell & Slatyer 1977, but see also Finegan 1984) generated by the decomposition of windthrown logs originating from the burned stand or from the replacing stand.

As our results show, when the stand reaches 234 years of age, it supports decomposed mossy logs to a lesser extent than in mid-successional stands. At this point, the large dead boles resulting from the high standing biomass present in young stands (Paré & Bergeron 1995) may be too much decomposed and incorporated in the forest floor litter to act as nurse logs. This reduction in nurse log cover should reduce *Picea* and *Thuja* regeneration in old stands. The decrease in *Thuja* regeneration is our only prediction that is not supported by the tree composition, dendro-ecological and regeneration studies done in the area (Bergeron & Dubuc 1989; Bergeron & Charron 1994; Kneeshaw & Bergeron 1996). The nurse log species present in late succession might be more suitable to *Thuja* recruitment than those found earlier during succession. It is also possible that at this stage factors acting on *Thuja* layering promote the dominance of this species.

In conclusion, conifer recruitment success and initiation in the understory during succession appears to be strongly influenced by the types of substrate available. Stand aging until mid-succession enhances conifer recruitment through a reduction in leaf litter cover and an increase in nurse log cover. Moreover, on mesic sites, nurse logs are likely to be a key element permitting the recruitment of *Thuja occidentalis*, resulting in the observed directional succession. By keeping stands young and removing all future nurse logs, sylvicultural practices prevent *Thuja* recolonization and limit overall conifer recruitment in the area and possibly in other mixed wood forests.

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