Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada

Marie-Josée Simard, Yves Bergeron, and Luc Sirois

Abstract: Most conifer seeds die as seeds or seedlings within 5 years after dispersal. Understanding what factors keep a few of them alive is essential if natural regeneration is to be maintained in managed forests. For example, decaying logs and the conifer seedlings that often grow on them are rare under certain canopies such as deciduous trembling aspen (*Populus tremuloides* Michx.). We conducted a seeding experiment to evaluate the role of certain substrates, and litterfall, on early conifer survivorship. Seeds of balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), and eastern white-cedar (*Thuja occidentalis* L.) were sown during 2 consecutive years on mineral soil, relocated logs, and litter in deciduous aspen and coniferous (*Thuja occidentalis* dominated) stands. Seedling survivorship was monitored at the end of the first growing season and 1 year after each sowing. Conifer seedling survivorship was equivalent or greater under aspen than under cedar-dominated canopies. *Picea* and *Thuja* survivorship was highest on decaying logs of approximately 9 cm high (compared with logs buried at forest floor level) and lowest on forest floor litter during both the first growing season and the following autumn–winter. *Abies* survivorship was little affected by substrate type, except for low autumn–winter survival on litter. *Thuja* autumn–winter survival was significantly reduced by litterfall in both deciduous and coniferous stands.

Résumé : La plupart des graines de conifères meurent en tant que graine ou semis durant les 5 premières années suivant leur dispersion. La compréhension des facteurs qui maintiennent quelques-uns de ces semis en vie est essentielle si l'on veut maintenir la régénération naturelle des peuplements aménagés. Par exemple, les troncs décomposés ainsi que les semis de conifères qui s'y retrouvent fréquemment, sont rares sous certains couverts tels que les couverts décidus de peuplier faux-tremble (*Populus tremuloides* Michx.). Une expérience d'ensemencement a été réalisée afin d'évaluer le rôle de certains substrats et de la chute de litière sur la survie initiale des conifères. Des graines de sapin baumier (*Abies balsamea* (L.) Mill.), d'épinette blanche (*Picea glauca* (Moench) Voss) et de thuya occidental (*Thuja occidentalis* L.) ont été semées durant 2 années consécutives sous des peuplements décidus de trembles et des peuplements résineux (dominés par le *Thuja occidentalis*), sur des substrats de sol minéral, des troncs relocalisés et de la litière. La survie des graines et des semis a été notée une saison et 1 an après chaque ensemencement. La survie sous les peuplements de trembles fut plus élevée ou, généralement, comparable à celle des graines et des semis localisés sous couvert résineux. La survie de *Picea* et de *Thuja* était maximale sur les tronc décomposés d'environ 9 cm de hauteur (comparativement aux troncs enterrés au niveau du parterre forestier) et minimale sur la litière au sol et ce, à la fois durant la première saison de croissance et durant la saison automne–hiver. Le type de substrat a eu un effet moindre sur la survie des graines et des semis d'*Abies*. Toutefois, sur la litière, la survie des semis d'*Abies* était faible durant la période automne–hiver. La survie des semis de *Thuja,* suivant la période automne–hiver, a été significativement réduite par la chute de litière et ce, dans les deux types de peuplements.

Introduction

In southern boreal forests, canopy replacement of deciduous pioneer species by shade-tolerant conifers is a common long-term process initiated by large-scale disturbances such as fire (Heinselman 1981; Bergeron and Dubuc 1989; Bradshaw 1993). After the establishment of the initial postfire deciduous stand, conifer recruitment into the canopy is generally explained by gap formation. In eastern Canada, gaps created by the synchronous death of balsam fir (*Abies balsamea* (L.) Mill.) trees during spruce budworm (*Choristoneura fumiferana*) outbreaks are common (Frelich and Reich 1995; Kneeshaw and Bergeron 1998). Recent studies suggest that these gaps are mostly filled by conifers already established as seedlings before gap formation (Osawa 1994; Parent et al. 2001). However, understory re-

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cruitment from seed to seedling has received less attention despite the fact that for most tree species, important population losses occur during the first 3 years of growth (Place 1955; Harper 1977; Christy and Mack 1984; Fenner 1987; Tan and Bruckert 1992; Jones et al. 1994; DeLong et al. 1997; Farmer 1997). Arguably, initial survival can modify a species' entire demography (Hartgerink and Bazzaz 1984; Gray and Spies 1997; Kuuluvainen and Juntunen 1998).

The distribution of conifer seedlings in the understory is often related to the distribution of specific substrates and microtopography (Day 1964; Knapp and Smith 1982; Christy and Mack 1984; Bartlett et al. 1991; Côté and Bélanger 1991; St. Hilaire and Leopold 1995; Anderson and Winterton 1996; McLaren and Janke 1996; Cornett et al. 1997; Simard et al. 1998). Decaying logs and short mosses are commonly cited as important regeneration seedbeds (see Harmon et al. 1986; Côté and Bélanger 1991; McLaren and Janke 1996; Cornett et al. 1997; Simard et al. 1998). However, few studies attempt to isolate direct canopy type effects such as shade and seed production from more indirect effects such as the abundance of these seedbeds on seedling survivorship (Cornett et al. 1997; Caccia and Ballaré 1998; Simard et al. 1998). If seedbed abundance modulates conifer establishment, then the effect of management practices on the aspect of the forest floor will have to be taken into account to maintain enough seedlings in the understory after the next harvest.

On mesic sites in the southeastern Canadian boreal forest, postfire canopies are composed of shade-intolerant deciduous species (trembling aspen (*Populus tremuloides* Michx.) or white birch (*Betula papyrifera* Marsh.)), while late successional canopies are dominated by balsam fir and eastern white-cedar (*Thuja occidentalis* L.). White spruce (*Picea glauca* (Moench) Voss) trees are less abundant and mostly present in midsuccessional stands (Bergeron and Dubuc 1989). Early successional stands have fewer large decaying logs or stumps on the forest floor (Hély et al. 2000) and this may interfere with conifer establishment. Conifer seedlings have been associated with decaying logs or stumps, especially the smaller seeded, yet shade-tolerant *Thuja occidentalis* (Simard et al. 1998). Moreover, conifers, but particularly *Thuja occidentalis* seedlings, are scarcer under deciduous than under more coniferous canopies (Kneeshaw and Bergeron 1996), even near seed-bearing *Thuja occidentalis* trees (Bergeron and Charron 1994). Therefore, we hypothesize that the presence of specific substrates on the forest floor, such as logs, could modulate the initial survival of conifers more than other canopy-type effects. Also, since broadleaf litterfall can easily smother conifer seedlings (Koroleff 1954), logs could be particularly essential for initial survival in deciduous stands due to their litter-shedding property (Thornburgh 1969; Christy and Mack 1984; DeLong et al. 1997).

In an attempt to dissociate the effects of forest floor characteristics from those of stand composition and age, decaying logs were relocated from the old coniferous stands (230 years old) to pioneer deciduous stands (<80 years old) and mineral soil seedbeds of both stand types were mixed together. We then compared early seedling survivorship on these substrates and litter. We also assessed the effect of litterfall on autumn–winter survival (AW1).

Materials and methods

Study area

The study area is around Lake Duparquet in northwestern Quebec (79°15′W, 48°30′N) at the southwestern limit of Quebec's boreal forest (Rowe 1972) in the *Abies balsamea* – *Betula papyrifera* climax vegetation domain (Grandtner 1966). The closest meteorological station is 42 km north at La Sarre. Climate is continental with a mean annual temperature of 0.8°C and total annual precipitation of 857 mm. Snow represents 25% of total annual precipitation. The frost-free period averages 64 days, although occasional frosts may occur throughout the growing season Environment Canada 1993).

Four circular plots (10 m in diameter, 78.54 m^2 area) were delimited in both *Thuja occidentalis* dominated and *Populus tremuloides* dominated forests (100 m to 4.1 km apart). Fire behavior during wildfires, recurrent spruce budworm outbreaks, topography, and land use have increased compositional variability within forest types (Bergeron and Dubuc 1989; Kneeshaw and Bergeron 1998; Bergeron 2000). The plots are not located in uniform continuous stands but rather in patches representative of the deciduous and coniferous stages of a postfire successional gradient (Bergeron and Dubuc 1989). Plots were established where slope was negligible and canopy closed (Table 1).

In each plot, we measured (*i*) basal area and tree composition (5 cm diameter at breast height (DBH)), (*ii*) litter depth by taking 10 measures per plot (in the L treatments described below), and (*iii*) water content of litter and of all seedbed treatments described below using shallow cores (depth = 5 cm, diameter = 3 cm). Core samples were extracted once in July 1996, 4 days following the most recent rainfall. Water content was expressed as a percentage of the wet mass of the sample.

Experimental design

The experiment began in June 1995 and ended in August 1997. In each circular plot, we randomly located nine 70 × 70 cm quadrats at least within 1 m of the plot circumference. Each quadrat received one of the following treatments.

1. (1) Mineral soil exposed and caged (ms+c): The organic horizons and roots of the forest floor were removed to bare the mineral soil. The mineral soil from both stand types was mixed together to homogenize for nutrient and other soil property differences. Then, a wire cage 60 × 10 × 15 cm (6-mm^2 mesh) was placed on top of the mineral soil to exclude vertebrate predation.
2. (2) Mineral soil exposed (Msoil): Same as treatment 1 without the cage.
3. (3) Forest floor litter (FFLitter): A section of the forest floor covered with litter was left intact.
4. (4) Unburied log (ULog): Well-decomposed logs were carefully collected in the coniferous stand type using wire sheets to keep the bole entire and relocated in sets of three logs per quadrat; the top of the logs averaged 8.78 ± 1.92 cm height above the forest floor (after relocation). Selected logs had soft wood to a depth of at least 10 cm and were covered by moss species. Logs could not be identified to species due to their advanced state of decay. Selected logs were in decay class IV or

Table 1. Characteristics of the deciduous and coniferous plots.

	Deciduous	Coniferous
Total number of plots	4	4
% deciduous stems (≥5 cm DBH)	80	2
% coniferous stems (≥5 cm DBH)	20	98
% herbaceous cover	35 (5)	35 (30)
Forest floor thickness (LFH layers) (cm)	6.3 (1.35)	7.9 (1.90)
Soil type	Mesic clay	Mesic clay
Basal area (m^2/ha) (≥5 cm DBH)		
Total	53.6	46.6
Populus tremuloides	50.1	2.1
Betula papyrifera	0.35	0
Abies balsamea	2.4	7.1
Picea glauca	0.68	0.10
Thuja occidentalis	0	37.2
Substrate water content (% based on fresh mass)		
Forest floor litter	45.1 (12.0)a	35.8 (14.4)b
Mineral soil (coarse)	20.5 (3.4)a	21.3 (5.7)a
Decaying log with moss (unburied)	40.3 (19.8)a	36.9 (25.0)a
Decaying log with moss buried at forest floor level	57.2 (14.8)a	46.6 (20.6)b

Note: Data are means with standard deviations in parentheses. Means followed by the same letter do not differ significantly between stand types (α = 0.05).

V (Harmon et al. 1986; Scott and Murphy 1987; Arthur and Fahey 1990).

(5) Buried log (BLog): Same as treatment 4 except logs were "buried" so that the top of the log was at ground level to determine whether log height influences seedling survival. An attempt to test this height effect on mineral soil failed because our clay mounds tended to erode and dry. Moreover, seeds were easily dispersed off the clay mounds by raindrops.

The remaining four quadrats received treatments 2–4 plus the following litterfall exclusion roofs. To test if litterfall affects seedling survival, we prevented coarse litter from falling on the seedlings (litterfall effect) by installing mesh wire (7.95-cm^2 mesh) roofs on top of the second set of quadrats (except treatment 1, since the caging unit also prevented litter from falling on the seedbed). The mesh was small enough to prevent broadleaf litter and coarse litter or debris, which could smother seedlings, from accumulating on the quadrats (M.-J. Simard, personal observation). These wire roofs were installed at 70 cm height with four stakes; the roof was bent from center to prevent litter from accumulating on top. Any remaining litter on the roofs was removed every spring.

To make sure that the caging (treatment 1) results were attributable to predator exclusion and not to modifications of environmental conditions such as reduction of surface evaporation, light, or raindrop impact (Clements 1964; Thomas and Wein 1985), we installed an open cage (four openings of 7 × 10 cm were cut in the center and at both ends of the cage on the sides) next to the closed cage unit and compared the closed cage treatment with the open cage treatment (ms–c). The litter exclusion roofs (lwire) were located high enough to minimize any modifications in the seed and seedling environment.

To avoid any edge effect, a surface of 50 × 50 cm was delimited in the center of each quadrat. We also removed all conifer seeds that we could find on the substrate before seeding. To evaluate undetected natural seed input, half of this surface was nevertheless left unseeded. Natural seed input was important only in autumn 1994, before the setting of the experiment, and negligible after.

One hundred viable seeds of each species were seeded in rows per quadrat in June of 1995, 1996, and 1997. The number of viable seeds sown was determined by previous germination tests. Seeds were provided by the ministère de l'Énergie et des Ressources du Québec. *Abies balsamea* and *Picea glauca* seeds were collected in the township of Hébécourt, Abitibi (48°30′N, 79°25′W), while the *Thuja occidentalis* seeds originated from Rimouski (47°66′N, 55°52′W). Previous germination tests indicated that the seeds did not require stratification (ministère de l'Énergie et des Ressources du Québec, personal communication). The plots were visited during the last week of August and during the first week of June each year. Seedlings were identified using colored sowing pins. Due to time constraints, we only seeded Msoil, ULog, and BLog quadrats, with and without litterfall exclusion roofs, in 1995. However, analyses done on the available treatments (not shown) are in agreement with presented results and allowed us to compare autumn–winter survival of 1995–1996 and 1996–1997.

We use the term "survivorship" when survival includes not only a time interval but also a transition from seed to seedling stage (as a reminder). Seedling survivorship at the end of the first growing season (GS1) was calculated based on the number of viable seeds sown. Seedling autumn–winter survival (AW1) was calculated based on the number of seedlings counted at the end of August.

Data analysis

When a known number of seeds is sown, the resulting number of seedlings present is an observation of a variable that follows a binomial law (Bondesson 1988). The logistic model, by taking the logit as an intermediate variable, provides the possibility of doing multiple regressions with binary variables such as survival using maximum likelihood models based on the binomial characteristics of the studied phenomena (see Trexler and Travis 1993). The order in which terms are included in a model is important when processing binomial data because the effect of each term cannot be estimated independently of the others. Therefore, to select a model, we calculated the deviance (–2 ln(likelihood ratio)) for all possible linear logistic models that could be fitted to the data. Model selection was based on the difference in deviance between the simplest model and models with more terms (Collett 1991). Since no statistical package generates multiple comparisons for logistic regressions, these were determined by running the program a second time for each pair of treatments. The analysis was performed using SPSS (Norusis and SPSS Inc. 1997). Stand type differences in substrate water content were compared using rank sum tests (Scherrer 1984).

Results

Substrate water content 4 days following the most recent rainfall was higher (litter and buried log) or comparable (mineral soil and unburied log) in the deciduous plots compared with the coniferous plots (Table 1). The water content of the moss and wood sampled on the buried logs and the unburied logs was also significantly different (Mann–Whitney's $U = 225.5$, $p = 0.0009$).

There was always a highly significant ($p < 0.001$) influence of the seeding year on the number of seedlings present at the end of GS1 (Table 2). For all species, seedling to viable seed ratios were higher in 1997 (approximately 0.46, all species) than in 1996 (approximately 0.15, all species). AW1 (uncaged seedlings) did not depend on seeding year except for *Picea* ($p = 0.0011$) (Table 2) whose survival was best in 1996–1997 (0.29 ± 0.45) compared with 1995–1996 (0.10 ± 0.30)).

For uncaged seeds and seedlings, we found no significant stand effect ($p > 0.1229$) on the number of seedlings present at the end of GS1. There was a significant stand effect ($p < 0.001$) for the caged mineral soil treatments (Table 2). On caged mineral soil, seedling numbers per viable seed sown where significantly higher in the deciduous stand type ($p < 0.001$ for all species) (Fig. 1). We found no significant stand effect ($p > 0.23$) on AW1 of uncaged seedlings (Table 2). We were unable to analyze stand effects on AW1 for caged mineral soil due to low seedling numbers.

Substrate type (uncaged seedlings) had an effect on the number of seedlings present at the end of GS1 per viable seeds of *Picea* and *Thuja* ($p < 0.001$) and *Abies* ($p < 0.05$) (Table 2). Higher GS1 numbers were found on buried logs for *Abies*, unburied logs for *Picea*, and unburied logs and mineral soil for *Thuja*. GS1 numbers were lowest on forest floor litter for *Picea* and *Thuja* (Fig. 2). There was also a substrate type effect on AW1 of *Picea* seedlings ($p = 0.0018$) (Table 3) for which AW1 was best on unburied logs. AW1 on forest floor litter could not be included in the analysis, since no seedlings survived the autumn–winter period on that substrate (Fig. 3).

There was a significant effect of litterfall on AW1 of *Thuja* ($p = 0.003$) (Table 3), which did not significantly vary with stand type or substrate type. *Abies* and *Picea* AW1 was not significantly affected by litterfall ($p > 0.1$) (Table 3; Fig. 4).

Predation on mineral soil for GS1 was significant ($p < 0.001$) for *Abies* and *Picea* (Table 2). There was also a significant stand × predation interaction ($p < 0.001$) for *Abies*. Figure 1 shows that predation was significant only in the deciduous stand type for *Abies*, while *Picea* counts were reduced by predation in both stand types. We found no significant predation effect on AW1 on mineral soil ($p > 0.3039$) (Table 3).

Discussion

In both aspen and *Thuja* stands, *Picea* and *Thuja* seeds falling on nurse logs or mineral soil instead of forest floor litter had a significantly higher chance of being present as live seedlings at the end of the first summer. The survivorship of *Abies* was unaffected by seedbed type during that time. Moreover, paralleling the findings of DeLong et al. (1997) for *Picea glauca*, autumn–winter survivorship was low on forest floor litter for all conifers, and the presence of nurse logs particularly increased *Picea* survivorship during that period.

Abies survivorship was higher on nurse logs buried to ground level compared with unburied logs (of approximately 9 cm height). On the contrary, *Picea* and *Thuja* survivorship from seed until the end of the first summer was best on unburied logs compared with logs buried at the forest floor level, and *Picea* survival was highest on these former logs during autumn and winter. Temperature is higher on raised surfaces such as logs or mounds (Nelson 1950; DeLong et al. 1997), while evaporation and drainage are lower at the forest floor level (also suggested by our scarce water content data) (Place 1955; Anderson and Winterton 1996). The light requirements of the seedlings and the light extinction gradient are probably too small to affect survival in this case (Aubin et al. 2000; Parent 2002). Perhaps early survivorship of the larger seeded *Abies* is more limited by water vapor deficit than temperature in these mixedwood forests, while the opposite would be true for *Picea* and *Thuja*. Simard et al. (1998) have suggested that *Picea* and *Thuja* survival is better on decaying logs than on forest floor moss because logs are colonized by thinner moss carpets (Harmon and Franklin 1989; Nakamura 1992). Results reveal that microtopographic effects are also involved.

Except for their relatively small seed size, *Thuja* spp. have many characteristics associated with high shade tolerance (Johnston 1990; Carter and Klinka 1992; Wang et al. 1994) and compose late successional stands (Bergeron and Dubuc 1989; Frelish and Reich 1995). Our results show that litterfall reduced *Thuja* survival in both stand types, suggesting that small *Thuja* seeds and resulting small seedlings are ill-adapted to understory risks such as falling debris (see Metcalfe and Grubb 1997). Due to their larger surface area and complete autumn shedding, we expected aspen leaves to smother seedlings more easily and therefore reduce survival to a greater extent than coniferous litter (see Moore 1926; Koroleff 1954; Gregory 1966). *Thuja occidentalis* trees do not shed individual scales but entire branchlets and shed most of their litter in autumn (Chandler 1943). Moreover, falling woody branches can significantly reduce the survival

Table 2. Deviance and *p* values for seedlings present at the end of the first growing season per viable seed sown.

(A) Uncaged treatment.

	sy	st	pl	su	sy × st	sy × pl	sy × su	st × pl	st × su	pl × su	Model −2ll
Abies	279.1	1.497	3.976	8.882	0.009	0.68	6.125	1.463	0.749	12.87	354.46
p	<0.0001	0.2211	0.4093	0.0309	0.9244	0.9538	0.1057	0.8331	0.8616	0.3783	
Picea	144.3	0.053	30.85	58.80	2.764	16.18	2.497	5.212	7.517	37.18	849.72
p	<0.0001	0.8179	<0.0001	<0.0001	0.0964	0.0028	0.4758	0.2662	0.0571	0.0002	
Thuja	267.1	2.38	16.67	64.66	0.050	4.020	2.559	1.852	2.552	24.93	387.67
p	<0.0001	0.1229	0.0022	<0.0001	0.8231	0.4033	0.4647	0.7630	0.4660	0.0151	

(B) Open and closed caged on mineral soil treatment.

	sy	st	pl	pr	sy × st	sy × pl	sy × pr	st × pl	st × pr	pl × pr	Model −2ll
Abies	75.24	61.18	22.94	36.64	22.06	27.70	3.260	3.275	19.19	6.946	289.49
p	<0.0001	<0.0001	0.0001	<0.0001	<0.0001	<0.0001	0.0710	0.5129	<0.0001	0.1388	
Picea	12.87	32.93	53.12	51.97	113.6	9.454	3.805	36.77	0.585	19.43	479.89
p	0.0003	<0.0001	<0.0001	<0.0001	<0.0001	0.0507	0.0512	<0.0001	0.4440	0.0516	
Thuja	69.47	13.56	17.36	0.008	14.36	7.680	2.561	15.86	3.685	4.102	468.13
p	<0.0001	0.0002	0.0016	0.9287	0.0002	0.1040	0.1095	0.0032	0.0550	0.3924	

Note: sy, seed year; st, stand type; pl, plot; su, substrate; pr, predation; model −2ll, model −2 log likelihood.

Table 3. Deviance and *p* values for autumn–winter survival.

(A) Uncaged treatment.

	sy	st	pl	lf	su (–L)[a]	sy × st	sy × pl	sy × lf	sy × su	st × pl	st × lf	st × su	pl × lf	pl × su	lf × su	Model −2ll
Abies	2.335	0.346	14.16	2.481	1.980	0.165	5.743	2.592	0.141	5.861	0.434	5.509	7.655	4.635	0.083	379.0
p	0.1265	0.5564	0.0068	0.1152	0.3716	0.6846	0.2192	0.1074	0.9319	0.0788	0.5100	0.0636	0.1051	0.7958	0.9593	
Picea	10.71	0.230	10.12	1.799	12.70	3.598	9.375	0.529	1.041	5.920	2.876	0.268	2.676	10.63	5.874	339.9
p	0.0011	0.6315	0.0385	0.1798	0.0018	0.0578	0.0524	0.4670	0.5942	0.0518	0.0899	0.8746	0.6134	0.2234	0.0530	
Thuja	1.123	0.246	2.680	8.790	2.420	3.187	1.941	0.476	3.242	2.911	0.113	1.674	3.106	12.57	2.033	85.16
p	0.2893	0.6199	0.6254	0.0030	0.2982	0.0742	0.07466	0.4902	0.1977	0.2332	0.7368	0.4330	0.5402	0.1277	0.3619	

(B) Open and closed caged on mineral soil treatment.[b]

	pr	Model −2ll
Abies	1.057	59.08
p	0.3039	
Picea	0.013	63.27
p	0.9092	
Thuja	0.094	41.25
p	0.7592	

Note: sy, seed year; st, stand type; pl, plot; lf, litterfall; su, substrate; pr, predation; model −2ll, model −2 log likelihood.

[a] Numbers too low to include the litter treatment (FFLitter) in the analysis.

[b] Numbers too low to include variables other than predation in the analysis.

Fig. 1. Mean number of *Abies balsamea*, *Picea glauca*, and *Thuja occidentalis* seedlings present at the end of the first growing season on caged mineral soil (ms+c) and uncaged (i.e., open cage) mineral soil (ms–c) in deciduous (aspen) and coniferous (*Thuja*) stand types. ***, Differences between predation treatments significant at α = 0.001.

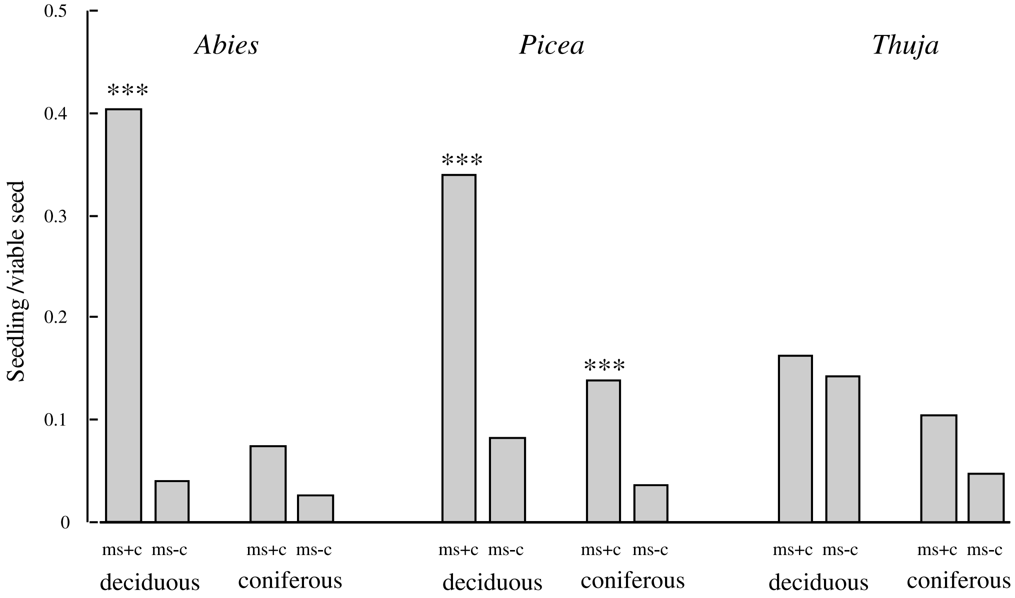
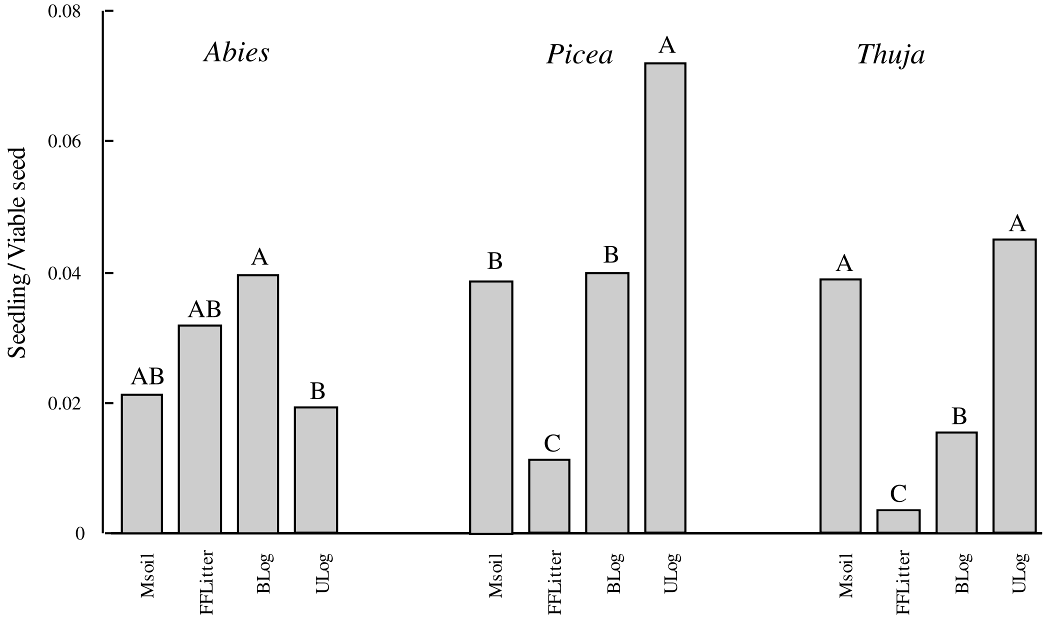


Fig. 2. Mean number of *Abies balsamea*, *Picea glauca*, and *Thuja occidentalis* seedlings present at the end of the first growing season per viable seed sown on different substrate treatments (uncaged). Msoil, mineral soil; FFLitter, forest floor litter; BLog, moss-covered decaying log "buried" to forest floor level; ULog, unburied moss-covered decaying log (top at approximately 9 cm height above forest floor level). For each species, means topped by the same letter do not differ significantly at α = 0.05.



of tree regeneration (Clark and Clark 1989). Our results suggest that *Thuja* tree litter would be as adverse as aspen tree litter to *Thuja* seedlings. Because *Picea glauca* has smaller seeds than *Abies* and is negatively associated with litter to the same extent as *Thuja* seedlings (Simard et al. 1988), we expected *Picea* to be significantly affected by litter smothering. *Picea* seedlings have higher growth rates and a more vertically extended morphology than *Thuja* seedlings. These factors could have lessened *Picea* mortality by litter smothering. Our results indicate that litterfall was not less damaging on unburied logs. Although we handled our decaying logs with care, they somewhat flattened during relocation and this could have reduced their litter shedding property. Measuring litterfall mass and distribution in space and time on different microtopographies along with *Thuja* survival would be of interest.

On mineral soil, conifer survivorship was best in the aspen stand type, and seedling survival during autumn and winter was equivalent in both stand types. Differences in light conditions hardly explain this former discrepancy, since

Fig. 3. Mean autumn–winter survival (live seedling present at the beginning of the second growing season per seedling present at the end of the first growing season) of *Abies balsamea*, *Picea glauca*, and *Thuja occidentalis* on different substrate treatments (uncaged). £, no seedlings were alive at the beginning of the second growing season on forest floor litter; Msoil, mineral soil; FFLitter, forest floor litter; BLog, moss-covered decaying log "buried" to forest floor level; ULog, unburied moss-covered decaying log (top at approximately 9 cm height above forest floor level). For each species, means topped by the same letter do not differ significantly at α = 0.05.

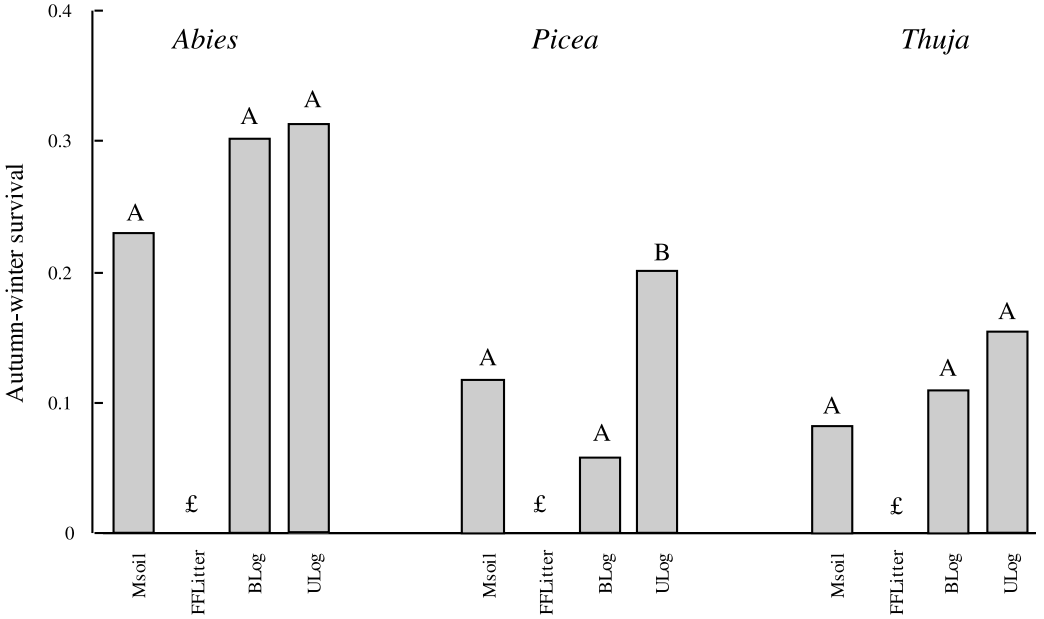
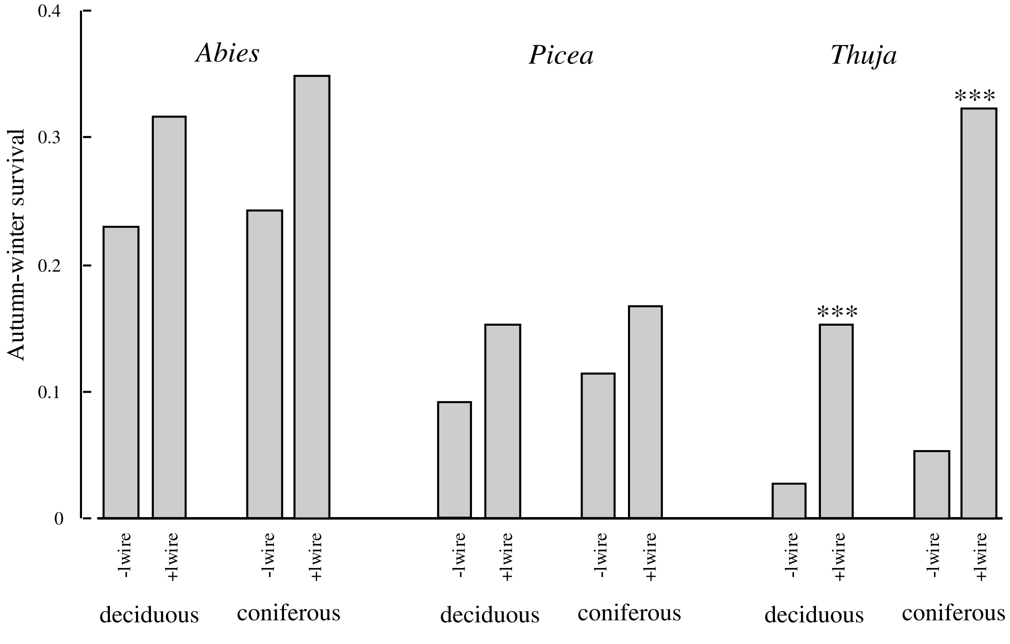


Fig. 4. Mean autumn–winter survival (live seedling present at the beginning of the second growing season per seedling present at the end of the first growing season) of *Abies balsamea*, *Picea glauca*, and *Thuja occidentalis* with litterfall exclusion roofs (+lwire) and without litterfall exclusion roofs (–lwire) in deciduous (aspen) and coniferous (*Thuja*) stand types. ***, Differences between litterfall treatments significant at α = 0.001.



light levels measured in summer on the ground of these stand types are equivalent (Messier et al. 1998). Moreover, we seeded in June, and during the first summer, low regeneration is rarely attributable to low light levels (Place 1955; Tan and Bruckert 1992; Oswald and Neuenschwander 1995; McLaren and Janke 1996). However, better survival under aspen could be attributable to spring conditions under deciduous canopies. Higher light penetration (Constabel and Lieffers 1996) is probably accompanied by higher forest floor temperature, which hastens germination. Early-emerging seedlings typically have increased survival (Farmer 1997). The water content of our soil cores was equivalent among stand types. Although increased sampling would have been necessary, there is no good method to measure moisture at the soil–seed interface (Winsa 1995). Methods need to be developed to characterize the microenvironment of seeds that are not buried in soil. The stand effect on survival disappears when all uncaged substrates are analyzed. This could be the result of stand × substrate × predation interactions or of higher microclimatic stand effects on mineral soil, which is more homogenous compared with moss and litter. More caged quadrats would have been needed to test interactions. Excluding rodents without modifying microenvironmental conditions, including litterfall, is a challenge. Many other variables associated with a particular canopy type could also alter seedling survival at that stage. These factors range from nutrients and allelopathic chemicals to insect herbivory and fungal pathogens (see Fox 1977). Nevertheless, for analogous substrates, we get equal or better conifer survivorship under aspen than under *Thuja*-dominated canopies. This result is noteworthy given the scarcity of *Picea* and *Thuja* seedlings in these stands, even near seed bearers.

Our caging experiments on mineral soil show that *Picea* survivorship was reduced by predation in both aspen and *Thuja* stand types. *Picea* predation is not surprising at that stage, since *Picea* seeds are a preferred food for small mammals (Abbott 1962; Smith 1970; Janzen 1971; Nienstaedt and Zasada 1990), especially when spring seeded (Radvanyi 1970). Results also show that *Abies* survivorship from seed until the end of the first summer can be decreased by predation in aspen stands. Seed predation of *Abies balsamea* was observed in both *Thuja occidentalis* and *Betula papyrifera* stands in Minnesota (Cornett et al. 1998). Further investigations are needed to explain the low *Abies* predation observed in our *Thuja* stands compared with aspen stands. Our results are in agreement with studies indicating that *Thuja* spp. seeds and seedlings are scarcely predated by vertebrate ground foragers (Moore 1940; Gashwiler 1967, 1971; Bartlett et al. 1991). Therefore, the low abundance of *Thuja occidentalis* regeneration from seed in mixedwood stands compared with *Picea glauca* or *Abies balsamea* cannot be attributed to predation from ground foragers.

Implications for species and stand dynamics

Our results show that substrate type had similar effects on early seedling survivorship in both aspen and *Thuja* stands. This substrate effect could somewhat be indirect by acting on predation pressure (Shaw 1968; Vander Wall 1994; Nystrand and Granström 1997*a*, 1997*b*). Nevertheless, substrate preferences agree with studies done in the area and in other forests (Nelson 1950; Scott and Murphy 1987; Nienstaedt and Zasada 1990; McLaren and Janke 1996; DeLong et al. 1997; Simard et al. 1998). In numerous boreal and subalpine forests, *Abies* spp. regeneration is more abundant than codominant species such as *Picea* spp. and *Thuja occidentalis* (Knapp and Smith 1982; Perkins et al. 1992; Kubota et al. 1994; Kneeshaw and Bergeron 1996). In all of these cases, *Abies* spp. are found on a wider range of regeneration substrates than codominants (Knapp and Smith 1982; Klein et al. 1991; Kubota et al. 1994; Simard et al. 1998). Although the limited number of co-occuring tree species at these latitudes restrains analysis, higher *Abies* survival in understories is probably related to seed size.

Other research in our study area has shown that *Picea* and *Thuja* regeneration is particularly scarce under pure aspen stands compared with older, more coniferous stands (Kneeshaw and Bergeron 1996; Bergeron and Charron 1994). Aspen stands also have fewer nurse logs and coarse woody debris smaller in diameter (Simard et al. 1998; Hély et al. 2000). This study showed that during the year following a spring seeding, on analogous substrates, *Picea* and *Thuja* survivorship under aspen stands was not lower than under *Thuja*-dominated stands. Furthermore, on decaying logs, *Picea* and *Thuja* early survivorship was raised towards that of *Abies* regardless of stand type. If survivorship patterns are maintained, decaying logs would therefore increase *Picea* and *Thuja* dominance towards that of *Abies*. *Thuja* is also more likely to be killed by litterfall, suggesting that this most shade-tolerant species is to some extent less “understory tolerant” than the larger seeded *Abies* or *Picea* soon after germination. More detailed studies coupling understory microenvironmental descriptions with germination, survival, and predation are needed to evaluate the relative importance of microenvironmental variables and ultimately to modify forest management practices to enhance early seedling survival.

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