Establishment and dynamics of the balsam fir seedling bank in old forests of northeastern Quebec

Sylvain Parent, Marie-Josée Simard, Hubert Morin, and Christian Messier

Abstract: This study examines balsam fir (*Abies balsamea* (L.) Mill.) recruitment in old fir stands. Studying the regeneration of these stands is essential to understand the regeneration dynamic of the species in the absence of stand-destroying disturbances. The objectives were (1) to obtain substrate–seedling associations for different age-classes and according to the presence or absence of adventitious roots; (2) to evaluate the contribution of the seed rain to seedling recruitment; (3) to re-examine age structures using the most appropriate method that minimizes estimation errors due to the presence of adventitious roots. A total of 90 quadrats (1 m^2) were established along transects. In each quadrat, subtrates were characterized (type and topography) and their area was estimated. All balsam fir seedlings (<50 cm tall) present in the quadrats were located, harvested whole (root and shoot), and described (age, height, presence of adventitious roots, etc). Fir seedlings were strongly associated with woody mounds covered with thin mats of mixed mosses and *Pleurozium shreberi* (Bird.) Mitt. but negatively associated with flat topography particularly dominated by *Hylocomium splendens* (Hedw.) B.S.G. The presence of adventitious root is related to seedling age more than substrate type or topography. The age structure is in agreement with seed production and disturbance regime.

Résumé : Cette étude examine la dynamique d'établissement des semis de sapin baumier (*Abies balsamea* (L.) Mill.) dans de vieilles sapinières. L'étude de la régénération de ces peuplements est essentielle à la compréhension de la dynamique de l'espèce en l'absence de perturbations qui dévastent la quasi-totalité des sapins matures. Les objectifs étaient (1) d'obtenir les patrons d'association semis–substrats selon la classe d'âge et la présence ou l'absence de racines adventives; (2) d'évaluer la contribution de la pluie de graines au recrutement; (3) d'établir la structure d'âges selon la méthode la plus appropriée qui tient compte des erreurs d'estimation attribuables à la présence de racines adventives. Quatre-vingt-dix quadrats (1 m^2) ont été délimités le long de transects. Dans chacun des quadrats, tous les lits de germination ont été caractérisés (type de substrat, topographie) et leur surface a été estimée. Tous les semis (<50 cm de hauteur) présents à l'intérieur des quadrats ont été localisés, récoltés en entier (incluant la racine) et décrits (âge, hauteur, présence de racines adventives etc.). Les semis étaient fortement associés aux substrats peu épais constitués d'un mélange de mousses, et de *Pleurozium shreberi* (Bird.) Mitt. couvrant les monticules et négativement associés à la mousse *Hylocomium splendens* (Hedw.) B.S.G. retrouvée principalement sur les topographies planes. La présence de racines adventives était reliée à l'âge des semis plutôt qu'au type de substrat ou à la topographie. La structure d'âges obtenue est en accord avec la production de graines et le régime de perturbation.

Introduction

The recruitment dynamics of balsam fir (*Abies balsamea* (L.) Mill.) has been extensively studied in the southern boreal forest of Canada where this species is widely distributed (Côté and Bélanger 1991; Osawa 1994; Morin and Laprise 1997; Kneeshaw and Bergeron 1999). Its distribution is shaped by a patchwork of gaps created by spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks occurring every 30 years or so (Morin et al. 1993; Morin 1994). Mature stands that are not totally devastated by the insect are often logged, burned by wildfire, or subject to major windthrow (Morin and Laprise 1990). Relatively undisturbed balsam fir stands exceeding 150 years of age are scarce. Studying the regeneration of these stands is nevertheless essential to understand the regeneration dynamic of the species in the absence of stand-destroying disturbances. The information gathered can also assist in the characterization of old growth stands. Moreover, these stands are ideal sites to study the initial recruitment of balsam fir because of the abundance of seed bearers and young seedlings.

A few of these old balsam fir stands are located in northeastern Quebec, Canada, in the black spruce (*Picea mariana* (Mill.) BSP) dominated boreal forest (Morin 1994). The forest floor, characteristic of these old balsam fir stands, consists of snags and logs in various states of decay covered by abundant moss communities dominated by *Hylocomium splendens* (Hedw.) B.S.G. Spatial variation in the density of newly germinated fir seedlings is mostly related to seed distribution (Duchesneau and Morin 1999). During the following 2 years, seedling distribution changes, resulting from the

Received 11 September 2001. Accepted 17 October 2002. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 17 March 2003.

S. Parent,[1] M.-J. Simard, and H. Morin. Département des sciences fondamentales, Université du Québec à Chicoutimi, Chicoutimi, QC G7H 2B1, Canada.
C. Messier. Université du Québec à Montréal, Département des sciences biologiques, C.P. 8888, succursale Centre-ville, Montréal, QC H3C 3P8, Canada.

[1]Corresponding author (e-mail: Parentsb@netscape.net).

 doi: 10.1139/X02-194

spatial variation in the suitability of seedbeds, decayed logs being the most favourable substrate (Duchesneau and Morin 1999). However, high mortality during the first 5 years can obscure early substrate associations such that analysing the distribution of older seedlings is sometimes necessary to determine what seedbeds are safe regeneration sites (Schupp 1995). In dense closed stands, where understory light rarely exceeds 15% of full light, light is a poor predictor of seedling location and growth (Parent 2002). However, variations in seed production will likely modulate seedling abundance. Although the contribution of mast years is acknowledged, there is little empirical evidence supporting the idea in balsam fir stands.

Recent work has demonstrated that balsam fir seedlings and saplings often develop adventitious roots (Parent et al. 2000). Adventitious roots increase understory survival (Parent 2002). However, it is not known at what age the formation of these roots starts and if seedlings with adventitious roots are more abundant in particular substrates. Moreover, the formation of adventitious roots is accompanied by a reverse taper phenomenon, i.e., the number of annual growth rings decreases from the presumed collar (the trunk base) to the true collar (hypocotyl region). Consequently, counting annual rings at any level on the trunk would not be reliable, and age structures of fir seedlings, particularly those found in northeastern Quebec (Morin and Laprise 1997), could be partially or totally erroneous (Parent et al. 2000, 2001). Therefore, age structures have to be redone, and factors contributing to recruitment have to be re-evaluated according to the best age estimates.

The first objective was to obtain substrate–seedling associations for different age-classes (determined using the most appropriate aging method) and according to the presence or absence of adventitious roots to determine which substrate best favours seedling establishment and adventitious root formation. The second objective was to evaluate the contribution of the seed rain to seedling recruitment. The third objective was to re-examine age structures (Parent et al. 2000, 2001).

Study area

The study area is about 100 km northeast of Lake Saint-Jean (49°48′N, 72°35′W) in the province of Quebec, Canada. The area is in the black spruce – feathermoss ecoclimatic domain (Thibeault 1987). It is also classified as part of the Boreal Shield ecozone, more specifically in the Central Laurentians ecoregion (Ecological Stratification Working Group 1995). The mean annual temperature recorded at the closest meteorological station is –0.7°C ranging from –19°C in January to 15.8°C in July, and the mean annual precipitation is 421.7 cm with 356.6 cm falling as snow (Environment Canada 1992). Spruce budworm outbreaks have been less severe in this domain than in the balsam fir dominated ecozone (Morin 1994). Consequently, many balsam fir stands located in the area are composed of dense mature trees with very few large gaps.

Our study was conducted in three of the four stands studied by Morin and Laprise (1997) and Duchesneau and Morin (1999). One site has been excluded (site 4*b*) because we judged it was too open and too wet to represent average balsam fir stands. This site presents an abundant *Sphagnum* sp. cover on the forest floor, a condition associated with poor soil drainage, which is rather untypical of balsam fir dominated stands (Parent and Messier 1995; Morin 1994; Roy et al. 2000). The three balsam fir stands chosen are 2–8 km apart and are dominated by mature balsam fir trees (15 m tall). Although these stands were subject to spruce budworm outbreaks of variable intensities (Morin 1994), all stands are similar in their vertical and spatial structure. Stem density (DBH = 2.5 cm) ranges from 1675 to 17 150 stems·ha^{-1}. Each stand forms a closed canopy with 88–96% of the stems being balsam fir. The basal area of these firs (including dead stems) ranges from 80 to 91% of the total basal area (Duchesneau and Morin 1999). Black spruce, white spruce (*Picea glauca* (Moench) Voss), and paper birch (*Betula papyrifera* Marsh.) represent altogether only 10% of the basal area. Understory plants and spatial structure were not affected by the last budworm outbreak (1970–1985) (Morin and Laprise 1997). The moss layer is dominated by *Hylocomium splendens*, in association with *Pleurozium shreberi* (Bird.) Mitt. and *Ptilium crista-castrensis* (Hedw.). The plant community in these stands is similar to the balsam fir – white birch type of the more southern balsam fir – white birch zone (Grandtner 1966). Stands are located on a moderately drained sandy till.

Materials and methods

The sampling was done in the fall of 1998. Each stand was visited and the area of undisturbed canopy was estimated to locate three transects per stand. In each of the three stands, 30 quadrats (1 m^2) were delimitated at regular intervals (8 m) along the transects. In each quadrat, substrates were delimited and characterized (moss species, topography, depth to mineral soil or woody debris) and their area was draw on paper (1:10 scale). A total of 870 balsam fir seedlings smaller than 50 cm in height were present in the quadrats. The exclusion of taller firs has little impact on results, since under closed balsam fir stands 85–95% of the fir regeneration does not reach 20 cm in height (Côté and Bélanger 1991; Morin and Laprise 1997). These firs were located and harvested whole (root and shoot). Each seedling was measured (height, diameter, annual height increments, hypocotyl lenght), aged by counting the number of terminal bud scars on the entire trunk (Parent et al. 2000) and the presence of adventitious roots was noted. Height and annual height increments are actually measures of trunk length and elongation when seedlings are more or less prostate. For seedlings with adventitious roots, the belowground part starts at the first adventitious root. These are the only seedlings with belowground terminal bud scars. Hypocotyl length extends from the start of the primary roots to the first leaves. Seed traps installed at regular intervals (for details, see Duchesneau and Morin 1999) have been emptied regularly since 1994. Logistic regression and contingency tables were used to evaluate the effect of seedling age and rooting substrate on the presence or absence of adventitious roots. Substrate–seedling associations were determined by χ^2 analysis specifying expected frequencies according to the area covered by the substrate (Scherrer 1984). This analysis was done with SPSS® software (SPSS, Inc. 1993) while all other

Table 1. Chi-square analysis of seedling rooting substrate or topography class specifying fixed expected frequencies according to the area covered by the substrate or topography class.

	Cases observed	Cases expected	Residual	χ^2	P
Substrate					
Hylocomium	279	405.9	–126.9		
Pleurozium	164	91.4	72.5		
Mixed moss	320	192.2	127.7		
Litter + moss	106	179.4	–173.4		
Total	869			212.305	<0.001
Topography class					
Flat	411	655.6	–224.6		
Woody mound	368	120.6	247.3		
Other mound	91	93.7	–2.7		
Total	870			598.302	<0.001

tests were done using JMP® software (SAS Institute Inc. 1996). Analysis of variance was performed to compare mean values for the continuous variables measured. Multiple comparisons where performed with Tukey–Kramer HSD test.

Results

Substrate–seedling associations

The observed frequency distribution of seedlings per substrate class differed significantly for the distribution expected according to the area covered by the substrate classes, indicating substrate–seedling associations were significant (Table 1, $P < 0.001$). These associations were constant for the three age-classes analysed (1–4, 5–8, and >8 years old, details not shown). Associations show seedling density is higher in mixed-moss communities and *P. schreberi* moss (Fig. 1*a*) and also on the woody-mound topography class (Fig. 1*b*). Seedlings found in mixed-moss communities, *P. schreberi* moss, and on woody mounds are located in thinner moss than on flat surfaces or other mounds (Fig. 2). Bryophyte communities on woody mounds occupied only 13.8% of the forest floor area, although 42.3% of all seedlings were found in this topography class (Fig. 1*b*). Bryophyte communities on woody mounds were frequently dominated by *P. schreberi*. This moss was also found on flat topography where it forms mats approximately three times thicker (12.2 ± 0.3 cm; mean ± SD) than on woody mounds (4.6 ± 0.2 cm). Only 25% of seedlings associated with *P. schreberi* were found on flat topography.

Hylocomium splendens is the most dominant moss on the forest floor. *Hylocomium splendens* substrate occupied more than 47% of the area (Fig. 1*a*) and 50–90% of flat topography (results not shown). Flat topography occupied 75% of the forest floor area (Fig. 1*b*). *Hylocomium splendens* forms the thickest mats (18 ± 3 cm) (Fig. 2*a*). *Hylocomium splendens* was also found on woody mounds where it forms thinner mats (12.7 ± 0.6 cm) than on flat topography (20.53 ± 0.36 cm) (one-way ANOVA, $P < 0.001$). Pits were not included in the analysis because they cover little area and have few seedlings.

Seedling growth

Seedling height averaged 6.4 ± 6.3 cm (median 5.0 cm) and 98% were smaller than 25 cm. Some characteristics of seedling growth are presented in Table 2, and values are compared among substrate and topography classes. On average, height growth in 1998 and mean height growth for the first 4 years after germination was ca. 1 cm·year^{-1}. We found that, on average, height growth in 1998 was slightly but significantly higher in *H. splendens* than in other substrates. We found no significant effect of topography class on height growth in 1998. Similar results were found analysing height growth during the first 4 years after germination. Hypocotyls were, on average, significantly longer in *H. splendens* substrate and on flat topography than on woody mounds or other mosses (Table 2).

Adventitious roots

Adventitious root formation, leading to the observation of belowground terminal bud scars, starts at about 6 years of age (Fig. 3). Less than 1% of seedlings younger than 5 years of age had adventitious roots compared with 85% of seedlings exceeding 7 years of age. In fact, there was a strong correlation between the total number of terminal bud scars (TBS) counted on the entire trunk and the number of TBS counted on the belowground section of trunk ($r = 0.85$; $P < 0.001$, Pearson correlation test). The presence of adventitious roots is related to seedling age more than to substrate type or topography (Table 3). Although there is a significant association with *H. splendens* moss substrate, this is due to the interaction with seedling age (Table 3). We found a very weak relationship between the depth of the organic mat and the number of TBS counted on the belowground section of trunk $R^2 = 0.018$; $P < 0.001$), and on the entire trunk $R^2 = 0.08$; $P < 0.001$).

Seedling recruitment

Hypocotyls could be observed and located on 96.4% of seedlings, therefore enabling precise age determination (see Parent et al. 2000). The age structure of fir seedlings estimated by counting all terminal bud scars present on the entire trunk is presented in Fig. 4. From 1948 to 1998, seedling numbers decrease with seedling age forming a jagged in-

Fig. 1. Percent area of forest floor covered by (*a*) substrate or (*b*) topography and percent seedlings found on a given substrate or topography class. Asterisks indicate that observed seedling numbers are significantly (***, $P < 0.001$; **, $P < 0.01$) lower or higher than expected according to the area of forest floor covered by substrate or topography. Note that pits were not included in the analysis because they cover little area and have few seedlings. Classes are not divided by substrate and topography because observed numbers would fall below the minimum required by the analysis.

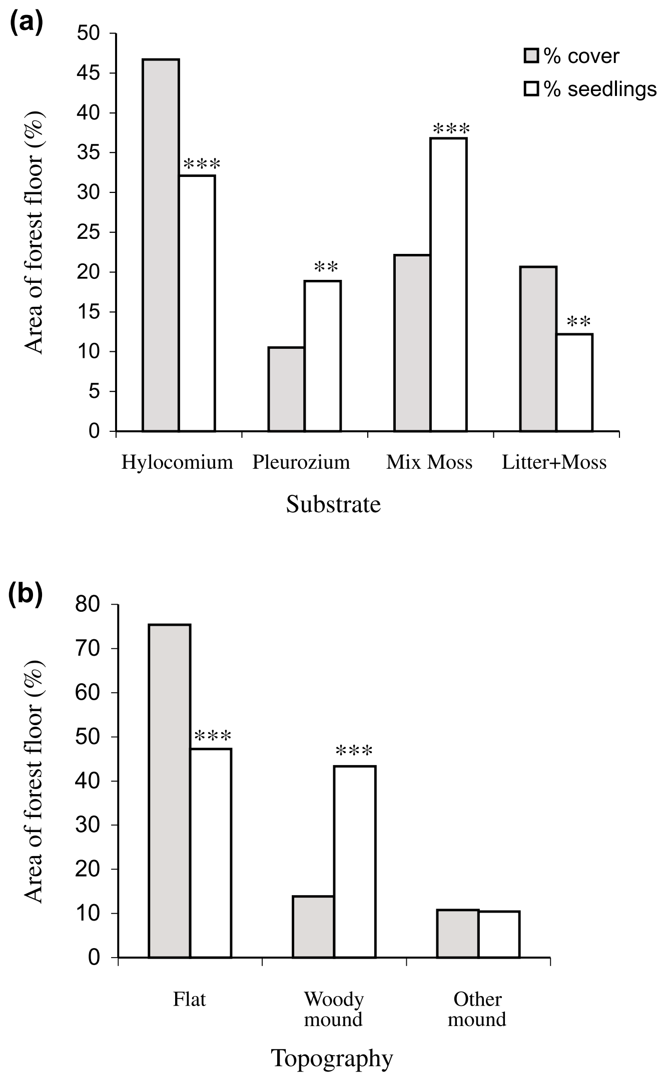
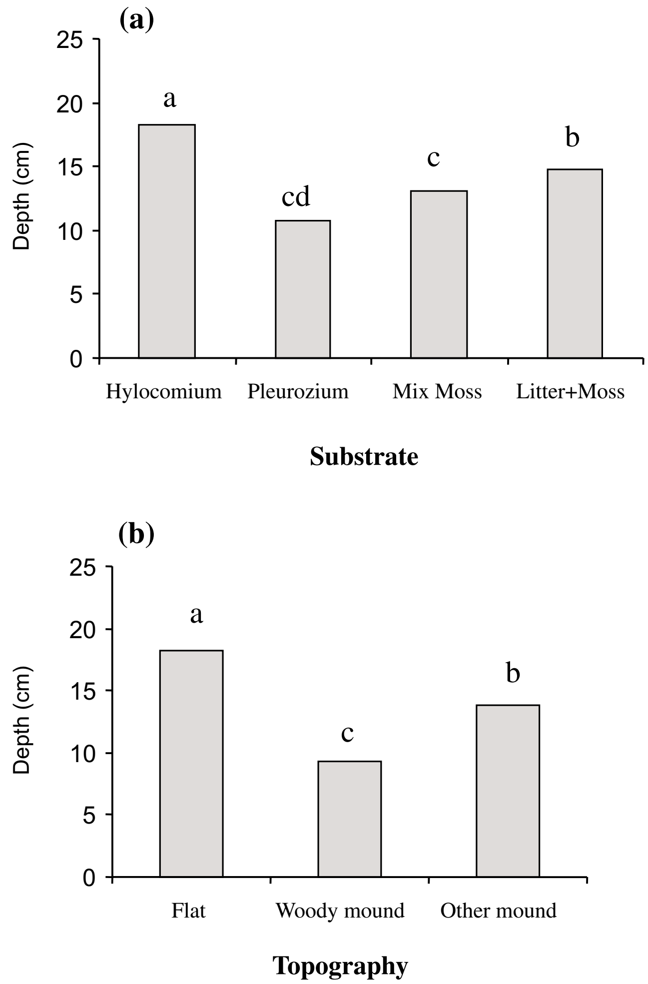


Fig. 2. Mean thickness of the moss or litter layer for each (*a*) substrate or (*b*) topography class. Means with the same letter are not significantly different at $\alpha = 0.05$.



verse J-shape. From 1987 to 1998, we observe three sequences of 4 years with similar variations in seedling numbers. These sequences begin with peak seedling counts followed by a decrease of 70% or more, followed by an increase to 30–45% of the peak value, and finally a low count (<15%). Annual variations in seedling numbers could be related to seed production during the previous year for the period of seed collection (1999–1996) (Fig. 5). No regular temporal variations in seedling numbers are observed from 1986 to 1948.

Variations in seedling numbers during the last spruce budworm outbreak (1974–1985) are different than during the following years. From 1977 to 1982, seedling numbers decreased until the end of the outbreak. After the outbreak, there was a marked increase in seedling numbers, but the observed pattern is not regular until 1988.

Discussion

Substrate–seedling associations

In these old stands, seed bearers are abundant and the spatial distribution of seeds is random (Duchesneau and Morin 1999). However, our results show a strong association between fir seedlings (all age-classes) and substrates dominated by thinner moss species on woody mounds. Therefore, feather mosses on woody mounds are not only good safe sites for germination and survival during the first 2 years (Duchesneau and Morin 1999) but also for long-term survival in the understory. Many researchers recognize that mounds provide more heat, minimize herbaceous and bryophyte competition, and accumulate less litter that may kill 1-year-old seedlings (Place 1955; Harmon and Franklin 1989; Houle 1992; DeLong et al. 1997). Our results indicate that thin organic mats (more frequent on woody mounds) have a positive effect on conifer establishment (Place 1955; St-Hilaire and Leopold 1995; Simard et al. 1998). Bryophyte communities forming thin mats facilitate the penetration of seedling roots into the moist humus layer. Moreover water

Table 2. Seedling growth (mean ± standard deviation) in different substrate and topography classes.

	Hypocotyl length (mm)	Mean height growth for the first 4 years (mm)	Height growth in 1998 (mm)
All seedlings	31.81±6.17	8.57±2.8	8.30±3.5
Substrate			
Hylocomium	32.54±0.38a	9.11±0.2a	9.49±0.3a
Pleurozium	30.41±0.51b	7.69±0.3b	8.33±0.4b
Mixed moss	31.63±0.34bc	8.61±0.2c	7.56±0.3c
Litter + moss	32.68±0.61c	7.85±0.3b	7.09±0.5b
*P**	0.0035	0.001	0.001
Topography			
Flat	32.66±0.64a	8.65±0.2a	8.12±0.3a
Woody mound	30.64±0.32b	8.65±0.2a	8.24±0.3a
Other mound	33.03±0.64a	7.98±0.4a	8.46±0.6a
*P**	0.001	0.2953	0.8489

Note: Means with the same letter are not significantly different at $\alpha = 0.05$.
**P* values for whole ANOVA models.

Table 3. Chi-square values for the logistic regression analysis testing the effect of substrate type, topography, and seedling age on the presence of adventitious roots.

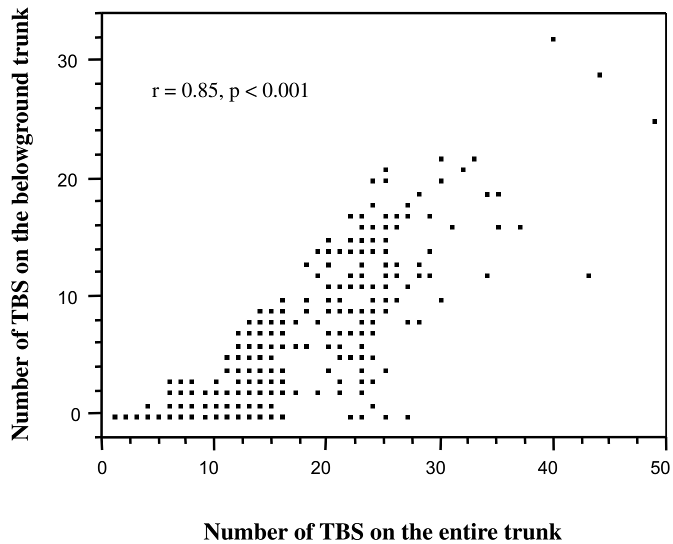
Effect	df	Wald's χ^2	*P*
Substrate type	3	4.741	0.192
Topography	2	2.075	0.3544
Seedling age	1	72.19	<0.0001
Substrate type × topography	6	6.332	0.3870
Substrate type × seedling age	3	2.729	0.4352
Topography × seedling age	2	1.403	0.4959

Note: The third-order interaction could not be tested without yielding unstable parameter estimates.

fluctuations during the summer may be lessened by water contained in the subjacent substrate, particularly decayed wood (Knapp and Smith 1982; Nakamura 1992; Cornett et al. 1997). Thin bryophyte layers are also warmer, which increases root growth (Van Cleve et al. 1983; Farmer 1997; Eckstein 2000).

Hylocomium splendens is a competitive moss and tends to form thicker mats than *P. schreberi*. The lower establishment success of fir seedlings on *H. splendens* could also be explained by its particular growth form. This moss is composed of annual branched segments (1–2 cm in length) forming stepladders (Okland 1995). In dense communities these segments form a net-like barrier, which traps fallen fir seeds. According to Nakamura (1992) when seeds germinate on the surface of these segments, the newly germinated seedling may suffer from water stress caused by high moisture fluctuations, and fir hypocotyls might not be long enough for the taproot to reach the moister humus layers. Secondly, when seeds geminate below this canopy of *H. splendens* segments, the germinant can be smothered by the faster-growing moss (Hörnberg et al. 1997; S. Parent, personal observation). Seedlings found in *H. splendens* moss had slightly longer hypocotyls, suggesting that the seedling etiolated more in these thick moss mats. Abnormal

Fig. 3. Relation between seedling age, as determined by counting the number of terminal bud scars (TBS) present on the entire trunk, and the age of the trunk embedded in humus, as determined by the number of terminal bud scars counted on the belowground trunk from the first adventitious root to the belowground hypocotyl. Adventitious root formation leads to the observation of belowground terminal bud scars.



hypocotyl elongation is often caused by low light (von Arnim and Deng 1996). Seedlings with longer hypocotyls are generally more slender and therefore more susceptible to drought or physical damage (Peterson and Facelli 1992; Simard 1999). Nevertheless, our results suggest, as found by Nakamura (1992) and Hörnberg et al. (1997), that the presence of thick *H. splendens* moss does not favour the establishment of conifer seedlings. Moreover, it is recognized that *H. splendens* is a more competitive moss for space than *P. schreberi* (Jonssen and Esseen 1990; Hörnberg et al. 1997).

Adventitious roots

According to our results, adventitious root formation starts early in the life cycle (ca. 6 years of age) and increases with seedling age. With time, the lower part of the trunk is imbedded in humus, and the aboveground part of the trunk moves away from the germination point. In fact, most seedlings older than 7 years had a prostate trunk creeping at ground level. Often the aboveground trunk was younger (lower terminal bud scar counts) than the belowground section. Results show that 85% of seedlings exceeding 7 years of age had adventitious roots.

Recruitment dynamics

Adventitious root formation leads to false age determination according to ring counts, and this phenomenon has greatly modified records of temporal recruitment dynamics (Parent et al. 2001). In our study, age determinations are more reliable, and seedling age distribution is characteristic of undisturbed stands where recruitment is continuously occurring and early death rates are high (Barbour et al. 1987). Although we only have 5 years of seed collection, results indicate that yearly variation in seedling abundance strongly depends on temporal variations in viable seed production.

Fig. 4. Age structure of balsam fir seedlings. Limits of the spruce budworm outbreak are from Morin (1994). The total area sampled is 90 m^2.

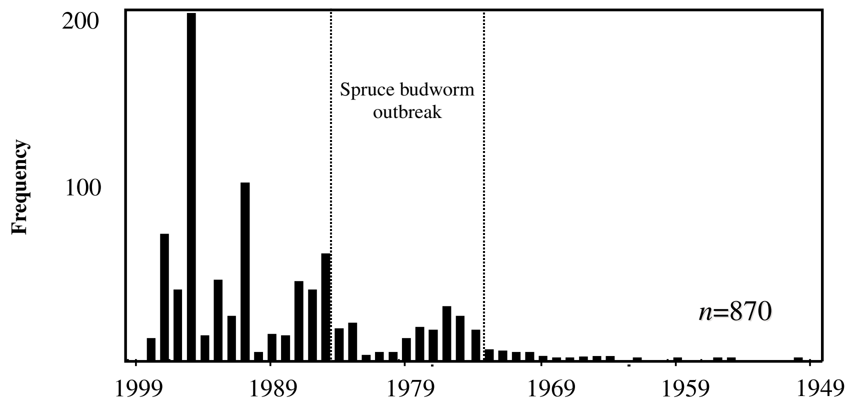
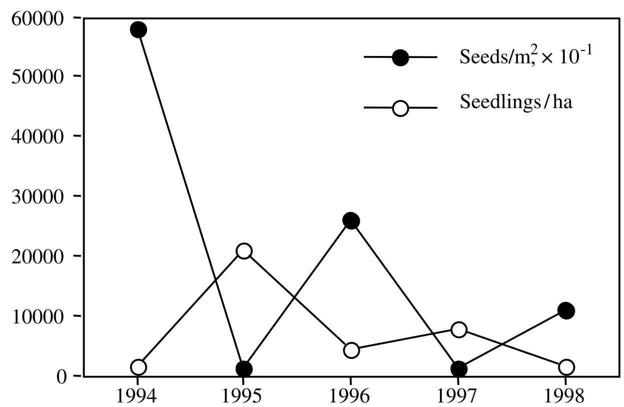


Fig. 5. Mean seed production per square metre (×10^{-1}) (●) and number of seedlings per hectare (○) that germinated the same year according to bud scar counts. Note that most balsam fir seeds germinate in the year following their dissemination. Although only 4 years of data can be included, seedling numbers and seed production the previous year are correlated (Pearson's ρ = 0.98).



Balsam fir seeds do not persist more than 1 year on the forest floor (Houle and Payette 1991). Variations in seedling numbers therefore suggest that when spruce budworm predation is negligible, good seed production occurs every 2 years. These results are consistent with studies indicating that balsam fir produces sizeable viable seed crops at 2-year intervals (Frank 1990), possibly due to carbohydrate replenishment (Morris 1951).

Spruce budworm outbreaks affect seedling demography because larvae prefer feeding on floral buds than on vegetative buds or foliage (Powell 1973; Osawa 1994; Parent et al. 2001). Most mature firs survived the last outbreak in the area (Morin 1994) and results show that a substantial number of seedlings became established during the last outbreak. However, aging errors are still possible, particularly for old and very suppressed seedlings, and results indicate the reproductive potential of the trees has been reduced during the outbreak (1978–1984). Morin and Laprise (1997) also reported a progressive decrease in fir recruitment in the area, from 1978 approximately. Although these authors used ring counts to estimate seedling age, underestimations caused by this method (Parent et al. 2000) were probably low for the first decade, because their sampling has been done at the end of the outbreak (D. Laprise, personal communication, 1986) and seedlings younger than 10 years have few adventitious roots. Immediate recovery of seedling recruitment after the outbreak has been observed only in a few stands in the area (Morin and Laprise 1997). However, similar demographic patterns, indicating reduced seedling recruitment during the outbreak and rapid recovery afterwards, have been reported in other studies. In the later studies, several mature firs had survived the outbreak and seedlings were also aged by counting terminal bud scars on the entire trunk (Osawa 1994; Parent et al. 2001).

Conclusion

In old stands, balsam fir seedlings are not randomly distributed on the forest floor. Logs are covered by thinner moss mats, which favour initial recruitment, and this association is maintained through time. After ca. 6 years of growth, the formation of adventitious roots appears unconditional to substrate types. Using the appropriate aging method, we obtained an age structure in agreement with seed production and disturbance regime.

Acknowledgments

We sincerely thank Sébastien Audet and Danielle Laprise for their technical and field assistance. Precious comments were provided by Dr. Anne Légère. This study was financed by the Sustainable Forest Management Network, the Consortium de recherche sur la forêt commerciale à Chicoutimi, and le Groupe de recherche forestière interuniversitaire (GREFi).

References

Barbour, M.G., Burk, J.H., and Pitts, W.D. 1987. Terrestrial plant ecology. Benjamin/Cummings Publishing, Menlo Park, Calif.

Côté, S., and Bélanger, L. 1991. Variations de la régénération préétablie dans les sapinières boréales en fonction de leurs caractéristiques écologiques. Can. J. For. Res. **21**: 1779–1795.

Cornett, M.W., Reich, P.B., and Puettmann, K.J. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer–deciduous forests. Écoscience, **4**: 353–364.

DeLong, H.B., Lieffers, V.J., and Blenis, P.V. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. **27**: 1452–1457.

Duchesneau, R., and Morin, H. 1999. Early seedling demography in balsam fir seedling banks. Can. J. For. Res. **29**: 1502–1509.

Eckstein, R.L. 2000. Nitrogen retention by *Hylocomium splendens* in a subartic birch woodland. J. Ecol. **88**: 506–515.

Ecological Stratification Working Group. 1995. A national ecological framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa–Hull. Report and national map at 1 : 7 500 000 scale.

Environment Canada. 1992. Sommaire météorologique mensuel, Chibougamau–Chapais, janvier–décembre 1992. Meteorological Service of Canada, Environment Canada, Ottawa, Ont.

Farmer, R.E., Jr. 1997. Seed ecophysiology of temperate and boreal zone forest trees. St-Lucie Press, Delray Beach, Fla.

Frank, R.M. 1990. *Abies balsamea* (L.) Mill. Balsam fir. *In* Silvics of North America. Vol. 1. Conifers. U.S. Dep. Agric. Agric. Handb. 654.

Grandtner, M.M. 1966. La végétation forestière du Québec méridional. Presses de l'Université Laval, Québec, Que. pp. 219–220.

Harmon, M.E., and Franklin, J.F. 1989. Tree seedlings on logs in *Picea–Tsuga* forests in Oregon and Washington. Ecology, **70**: 48–59.

Houle, G. 1992. The reproductive ecology of *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in the Tantaré Ecological Reserve, Québec. J. Ecol. **80**: 611–623.

Houle, G., and Payette, S. 1991. Seed dynamics of *Abies balsamea* and *Acer Saccharrum* in a deciduous forest of Northeastern North America. Am. J. Ecol. **78**: 895–905.

Hörnberg, G., Ohlson, M., and Zarckrisson, O. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. Can. J. For. Res. **27**: 1015–1023.

Jonsson, B.G., and Essen, P.-A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. J. Ecol. **78**: 924–936.

Knapp, A.K., and Smith, W.K. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Can. J. Bot. **60**: 2753–2761.

Kneeshaw, D.D., and Bergeron, Y. 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. Écoscience, **6**: 214–222.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Québec. Can. J. For. Res. **24**: 730–741.

Morin, H., and Laprise, D. 1990. Analyse dendrochronologique d'une sapinière issue d'un chablis dans la zone boréale, Québec. Can. J. For. Res. **20**: 1753–1758.

Morin, H., and Laprise, D. 1997. Seedling bank dynamics in boreal balsam fir forests. Can. J. For. Res. **27**: 1442–1451.

Morin, H., Laprise D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region Québec. Can. J. For. Res. **23**: 1497–1506.

Morris, R.F. 1951. The effects of flowering on the foliage production and growth of Balsam fir. For. Chron. **27**: 40–57.

Nakamura, T. 1992. Effect of bryophytes on survival of conifer seedlings in subalpine forests of central Japan. Ecol. Res. **7**: 155–162.

Okland, R.H. 1995. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. I. Demography. J. Ecol. **83**: 697–712.

Osawa, A. 1994. Seedling responses to forest canopy disturbance following a spruce budworm outbreak in Maine. Can. J. For. Res. **24**: 850–859.

Parent, S. 2002. Stratégies de croissance en sous-bois chez les semis du sapin baumier. Ph.D. thesis, Université du Québec à Montréal, Montréal, Que.

Parent, S., and Messier, C. 1995. Effets d'un gradient de lumière sur la croissance en hauteur et la morphologie de la cime du sapin baumier régénéré naturellement. Can. J. For. Res. **25**: 878–885.

Parent, S., Morin, H., and Messier, C. 2000. Effects of adventitious roots on age determination in Balsam fir (*Abies Balsamea* (L.) Mill.) regeneration. Can. J. For. Res. **30**: 513–518.

Parent, S., Morin, H., and Messier, C. 2001. Balsam fir (*Abies balsamea*) establishment dynamics during a spruce budworm (*Choristoneura fumiferana*) outbreak: an evaluation of the impact of aging technique. Can. J. For. Res. **31**: 373–376.

Peterson, C.J., and Facelli, J.M. 1992. Contrasting germination and seedling growth of *Betula alleghaniensis* ans *Rhus typhina* subjected to various amounts and types of plant litter. Am. J. Bot. **79**: 1209–1216.

Place, I.C.M. 1955. The influence of seedbed conditions on the regeneration for spruce and balsam fir. Canada Department of Northern Affairs, Natural Resources Forestry Branch, Ottawa, Ont. Bull. 117.

Powell, G.R. 1973. The spruce budworm and megasporangiate strobilie of Balsam fir. Can. J. For. Res. **3**: 424–429.

Roy, V., Ruel, J-C., and Plamondon, A.P. 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetland. For. Ecol. Manage. **129**: 253–267.

SAS Institute Inc. 1996. JMP® start statistics: a guide to statistical and data analysis using JMP® and JMP IN® software. Duxbury Press, Belmont, Calif.

Scherrer, B. 1984. Biostatistique. Gaëtan Morin ed., Boucherville, Que.

Schupp, E.W. 1995. Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. Am. J. Bot. **82**: 399–409.

Simard, M.-J. 1999. L'établissement initial de la régénération résineuse en sous-bois dans le sud-ouest de la forêt boréale québécoise et l'influence du substrat forestier. Ph.D. thesis, Université du Québec à Montréal, Montréal, Que.

Simard, M.-J., Bergeron, Y., and Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci. **9**: 575–582.

SPSS, Inc. 1993. SPSS® base system syntax reference guide release 6.0. SPSS, Inc., Chicago, Ill.

St-Hilaire, L.R., and Leopold, D.J. 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. Can. J. For. Res. **25**: 261–269.

Thibault, M. 1987. Les régions écologiques du Québec méridional. Deuxième approximation. Carte. Service de la recherche, ministère de l'Énergie et des Ressources du Québec, Québec, Que.

Van Cleve, K., Dyrness, C.T., Viereck, L.A., Fox, J., Chapin, F.S., III, and Oechel, W. 1983. Taiga ecosystems in interior Alaska. Bioscience, **33**: 39–44.

von Arnim, A., and Deng, X.-W. 1996. Light control of seedling development. Annu. Rev. Plant. Physiol. Plant. Mol. Biol. **47**: 215–243.