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Balsam fir (*Abies balsamea*) establishment dynamics during a spruce budworm (*Choristoneura fumiferana*) outbreak: an evaluation of the impact of aging techniques

Sylvain Parent, Hubert Morin, and Christian Messier

Abstract: The effects of recurrent spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks on balsam fir (*Abies balsamea* (L.) Mill.) mortality have been extensively studied in Canada. Most studies report substantial seedling recruitment of balsam fir during outbreaks when reproductive trees are dying. According to previous research, this contradiction could be due to inaccuracies in the conventional aging method. Counting the maximum number of growth rings found at the tree base would significantly underestimate tree age. Counting terminal bud scars found on the entire trunk, including buried stem, would give a more accurate tree age. In this study, we compare recruitment dynamics obtained for aging seedlings in two balsam fir populations (about 500 km apart) using (*i*) the conventional method and (*ii*) bud scar counts. For both populations, the conventional method shows substantial recruitment during adult mortality, while the second aging technique reveals reduced recruitment during the epidemic phase of the spruce budworm outbreak.

Résumé : Les effets des épidémies de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) sur la mortalité des sapinières boréales (*Abies balsamea* (L.) Mill.) ont été largement documentés au Canada. La plupart des études rapportent un important recrutement de semis de sapin durant une épidémie alors que meurent les sapins matures. Selon la recherche auparavant, cette contradiction serait due à l'inexactitude de la méthode conventionnellement utilisée pour estimer l'âge des semis. Le décompte du nombre maximal de cernes de croissance à la base du tronc sous-estimerait de façon importante l'âge réel des semis. Le compte des cicatrices d'écailles du bourgeon terminal sur tout le tronc, incluant la partie enfouie de la tige, serait une méthode plus appropriée. La présente étude compare la dynamique du recrutement de deux populations de semis de sapin baumier lorsque l'âge est estimé (*i*) par la méthode conventionnelle et (*ii*) par le compte des cicatrices d'écailles du bourgeon terminal sur tout le tronc. Environ 500 km séparaient les deux populations. Dans les deux cas, la méthode conventionnelle révèle des structures d'âge discordantes avec la mortalité des adultes. Par contre, les structures d'âge obtenues avec l'autre méthode indiquent une réduction du recrutement des semis durant la période épidémique.

Introduction

The effects of recurrent spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks on balsam fir (*Abies balsamea* (L.) Mill.) mortality in eastern North America have been extensively studied (Baskerville 1975; Blais 1983; MacLean 1984; Bergeron et al. 1995). Outbreaks have occurred every 30 years or so during the last century (Morin 1994) and balsam fir populations have maintained themselves owing to the species establishment (germination and growth) success in understories and the resultant formation of an abundant seedling bank (Ghent 1958; Côté and Bélanger 1991; Morin and Laprise 1997).

During an outbreak, spruce budworm larvae prefer feeding on floral buds than vegetative buds and foliage (Powell 1973; Schooley 1978). Mature firs will die after 4 or 5 years of severe defoliation (Maclean 1984). Knowing that the viability of dispersed seeds does not exceed 1 year (Houle 1992), it is surprising to notice that many studies report massive seedling recruitment during the epidemic phase of outbreaks when seed trees are dying and few seeds are produced

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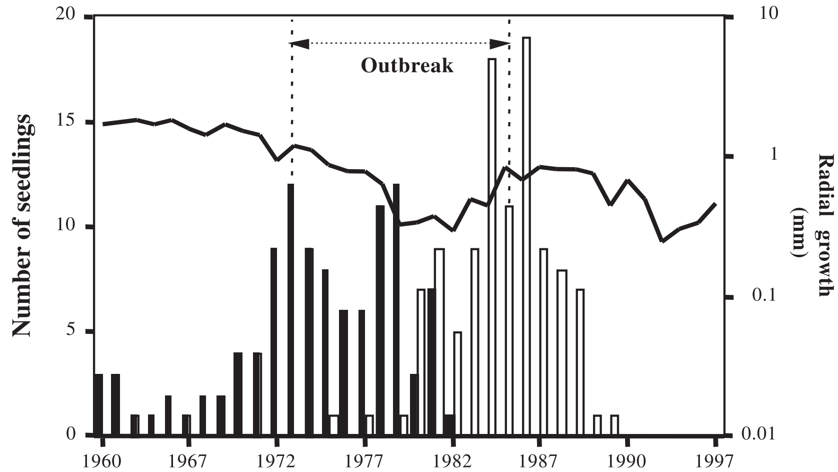
Fig. 1. Age structure of balsam fir regeneration (n = 157) sampled in the Lake Duparquet stand. Age was determined by counting the number of terminal bud scars on the entire stem, including the belowground section (solid bars), and by counting the maximum number of growth rings at tree base (open bars). Solid line shows the mean radial growth of five white spruce trees.



(Déry et al. 2000; Kneeshaw and Bergeron 1999; Morin and Laprise 1997; Parent and Messier 1995; Côté and Bélanger 1991; Marchand 1991; Batzer and Popp 1985). In these studies, seedling age has been evaluated by counting the maximum number of growth rings at the tree base or by counting the number of terminal bud scars from the apex to the tree base, at the forest floor level. Osawa (1994) has estimated the age of fir seedlings growing in Maine, U.S.A., by counting the number of terminal bud scars on the entire length of the trunk, including bud scars located below forest floor level. The Osawa (1994) study is one of the few reporting a decrease in fir recruitment during a spruce budworm outbreak. Recently, Parent et al. (2000) have demonstrated that counting the maximum number of growth rings at tree base can frequently and significantly underestimate seedling age. In the understory, seedling growth is often accompanied by a gradual burial of the base of the trunk in humus. This phenomenon favours the development of adventitious roots and reverse taper in the embedded section of the trunk, i.e., a reduction of the diameter and of the number of growth rings towards the true collar (hypocotyl) located below ground in humus (see also DesRochers and Gagnon 1997). With time, the number of annual height growth increment becomes clearly superior to the maximum number of growth rings at tree base. Therefore, counting the number of terminal bud scars on the entire trunk (including the embedded section) gives a better estimation of seedling age. In this study, we compare recruitment dynamics obtained by estimating tree age using the conventional method (Morin and Laprise 1997; Kneeshaw and Bergeron 1999) to those obtained by counting bud scars on the entire trunk section (Osawa 1994; Parent et al. 2000) for two balsam fir populations located about 500 km apart. Each seedling population was recruited in a mature balsam fir stand that was infested by spruce budworm larvae during the last outbreak.

Methods

The first study site was located near Lake Duparquet, in Abitibi, Que. (48°30′N, 79°27′W). The stand was composed of a mixture of mature black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), and white birch (*Betula papyrifera* Marsh.) reaching heights of 14–16 m. Between 1974 and 1986 a spruce budworm outbreak killed all mature balsam firs (Morin et al. 1993), thus creating a heterogeneous mosaic of canopy gaps varying in size and shape (Parent and Messier 1995). An abundant balsam fir regeneration (43 000 seedlings/ha) has grown on the sphagnum moss (*Sphagnum* spp.) covering the forest floor.

In the stand, a 60 × 70 m quadrat was delimited, enclosing the same balsam fir seedling population studied by Parent and Messier (1995). Two or three firs (<2 m height) were harvested in their entirety, with roots, every 5 m (x and y axis of the quadrat) and brought to the laboratory. Terminal bud scars and hypocotyl (true collar) were located by examining the entire trunk (including belowground section) with a binocular microscope (40–100×). The trunk base, or presumed collar (sensu Parent et al. 2000), was located above the first living root (>0.7 mm in diameter). Discs were sampled every 3 cm above and below the presumed collar until a maximum number of growth rings was obtained (Morin and Laprise 1997; Kneeshaw and Bergeron 1999).

White spruce trees are defoliated by the spruce budworm during an outbreak. The attack reduces radial growth but rarely results in tree death (Blais 1983; Morin et al. 1993). To evaluate the presence and intensity of the defoliation by the budworm in the stand, five white spruce trees (>14 m height) were harvested and a disc was sampled below each crown. Discs were polished with fine sand paper (up to 400 grit) and the width of all growth rings, from the pith to the bark, was measured along two rays following the usual technique (Morin and Laprise 1990).

The second study site was located about 500 km east of the first one in the Montmorency forest owned by Université Laval, near Québec (47°20′N, 71°30′W). Balsam fir stands located in this area were also damaged to varying degrees by the spruce budworm outbreak that occurred between 1974 and 1986. However, aerial sprayings of insecticide significantly reduced the severity of the outbreak in the Montmorency forest (Marchand 1991). Seedlings were harvested in a closed forest dominated by balsam fir trees (12–14 m tall) established after a clearcut done between 1941 and 1944. Selected seedlings (<50 cm tall) were located in five quadrats (4 m^2) randomly on a 15 × 15 m grid. The age of seedlings was determined using the conventional methods described above.

Results and discussion

In the Lake Duparquet area, the last spruce budworm out-

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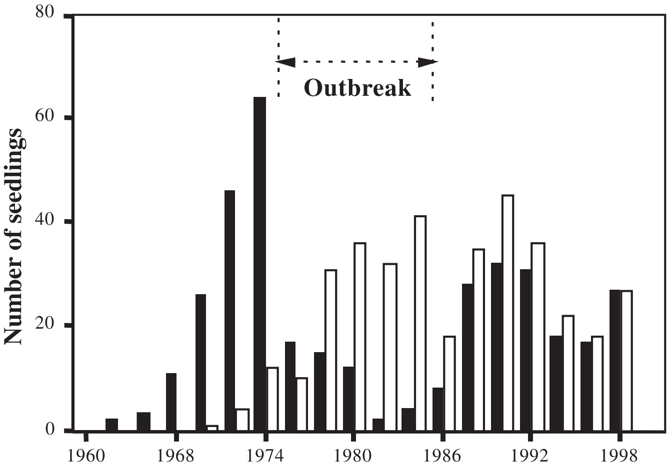
Fig. 2. Age structure of balsam fir regeneration (*n* = 368) sampled in the Montmorency stand. Age was determined by counting the number of terminal bud scars from tree base to apex (open bars) and by counting the number of terminal bud scars on the entire stem, including the belowground section (solid bars). Seedlings ranged from 3 to 52 cm in height (mean 15.5 ± 8.7 cm).



break lasted from 1970 to 1982. Most trees died between 1980 and 1981 (Morin et al. 1993; Bergeron et al. 1995). The radial growth of the white spruce trees that survived the outbreak started showing signs of reduction around 1970, with the smallest rings being those of 1978–1981, followed by a return to average growth after 1982 (Fig. 1, solid line). Therefore, the radial growth pattern observed on white spruce is in agreement with the spruce budworm chronology estimated in the area.

Seedlings harvested in the Lake Duparquet stand measured from 17 to 186 cm in height. The age structure obtained by counting the maximum number of growth rings (Fig. 1, open bars) was normal and centered on 17 ± 4.58 years. According to this age structure, some seedlings established during the epidemic phase of the outbreak, while 75% of the seedlings recruited after the outbreak, that is after 1982. Seedlings harvested in the stand located in the Montmorency forest averaged 13 ± 6.6 years (maximum 29 years) according to conventional ring count. As in the Lake Duparquet site, results suggest there is substantial recruitment during the spruce budworm outbreak. Age structures on both study sites are inconsistent with current knowledge of budworm feeding behaviour, seed tree mortality during the outbreak, and seed viability (Powell 1973; Schooley 1978; Morin et al. 1993). Nevertheless, this type of recruitment dynamic corroborates other studies done in the Lake Duparquet area (Kneeshaw and Bergeron 1999; Galipeau et al. 1997; Bergeron and Charron 1994), in the Montmorency forest (Côté and Bélanger 1991; Marchand 1991; Déry et al. 2000), and in the United-States (Batzer and Popp 1985), using the same methodology for determining tree age. However, for both populations sampled, the second age structure obtained by counting terminal bud scars (Figs. 1 and 2, solid bars) differs from the first age structure and is in agreement with a severe reduction of the reproductive potential of the species after the epidemic (Osawa 1994). In the Lake Duparquet stand, according to the second age structure, seedlings were older, more than 25% established before the outbreak and recruitment completely ceased after 1982. In the Montmorency stand, the second age structure is bimodal and reveals an important decrease in fir recruitment during the outbreak period (1975–1985) (Fig. 2). Compared with the Lake Duparquet population, there is some recruitment during the outbreak followed by an increase in recruitment after 1985, because some mature firs survived the epidemic owing to the aerial sprayings of insecticide.

Approximately 85% of the fir seedlings sampled in the Montmorency forest had their hypocotyl, and therefore, age could be determined with maximum precision (see Parent et al. 2000). However, only 25% of the seedlings sampled in the Lake Duparquet stand still had their hypocotyls, so the method was more imprecise there. Locating all bud scars was not easy, and moreover, counting bud scars on the entire stem still only gives the minimum age of seedlings (Osawa 1994). If precise ages could be reliably done, results may reveal even less recruitment during the outbreak than reported here.

Although the age structure obtained by counting terminal bud scars on the entire stem does not provide us with an exact aging of the seedling population, it tends to present a more consistent picture than that obtained with the traditional method of counting growth rings at the tree base. This study lends further support to the suggestion by Parent et al. (2000) that counting growth rings at tree base can lead to erroneous interpretations of temporal establishment dynamics in balsam fir population and so determining age through terminal bud scars over the entire stem should provide more accurate interpretations of tree establishment dynamic in the boreal forest.

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