

# Missing growth rings at the trunk base in suppressed balsam fir saplings

Sylvain Parent, Hubert Morin, and Christian Messier

**Abstract:** Numerous researchers have suggested a causal relationship between low leaf biomass in suppressed trees and the lack of radial growth at the base of the trunk. The objective of this study was to verify this relationship with suppressed balsam fir (*Abies balsamea* (L.) Mill.) saplings found growing in an old-growth fir stand. A total of 29 saplings varying in height from 67 to 183 cm were uprooted. All saplings had adventitious roots. All terminal bud scars (TBS) found between the apex of the terminal leader and the trunk base (first adventitious root) as well as those found below ground were localized, and rings were counted between TBS along the aboveground trunk. Various morphological traits and the ratio of photosynthetic tissue dry mass (P, needles) to non-photosynthetic tissue dry mass (nP, aboveground stem) were used as an indicator of tree vigour. Between 3 and 33 rings counted along the aboveground trunk were missing at the trunk base. The number of missing rings at the base of the trunk was correlated with total height ( $r = 0.41$ ), height growth ( $r = -0.51$ ), radial growth ( $r = -0.44$ ), the P/nP ratio ( $r = -0.73$ ), and the proportion of live crown ( $r = -0.62$ ). Moreover, from 2 to 35 additional rings, missing at the trunk base, were found in the belowground section of trunk and these missing rings were associated with the adventitious roots phenomenon. In conclusion, suppressed firs had missing rings at the base of the trunk. When all of the missing rings were added to the number of rings counted at the base of the trunk, age estimates provided a different temporal pattern of recruitment compared with that obtained by solely counting rings at the base of the trunk. Stem analysis on the entire trunk is the best aging method for suppressed balsam fir saplings.

**Résumé :** De nombreux chercheurs ont suggéré un lien de causalité entre une réduction importante du feuillage dans l'arbre et le manque de cernes à la base du tronc. L'objectif de cette étude était de vérifier cette relation avec des gaulis de sapin baumier (*Abies balsamea* (L.) Mill.) supprimés croissant sous la voûte fermée d'une vieille sapinière. Un total de 29 gaulis dont la hauteur variait de 67 à 183 cm ont été récoltés. Tous les gaulis avaient des racines adventives. Les cicatrices d'écaillles du bourgeon terminal trouvées entre la flèche terminale et la base du tronc (première racine adventive) et celles sur la partie du tronc ensevelie dans l'humus ont été localisées. Les cernes ont été comptés entre les cicatrices d'écaillles du bourgeon terminal à partir de la base du tronc jusqu'à la flèche terminale. Les traits morphologiques et le rapport entre le poids sec des parties aériennes photosynthétiques (P, aiguilles) et le poids sec des parties aériennes non-photosynthétiques (nP, tiges) ont été utilisés comme indicateurs de vigueur du gaulis. Entre 3 et 33 cernes manquants à la base du tronc ont été localisés plus haut dans le tronc. Le nombre de cernes trouvés au-dessus de la base du tronc et manquants à la base du tronc était corrélé avec la hauteur totale ( $r = 0.41$ ), la croissance en hauteur ( $r = -0.51$ ), la croissance radiale ( $r = -0.44$ ), le rapport P/nP ( $r = -0.73$ ) et la proportion de cime vivante ( $r = -0.62$ ). De plus, entre 2 et 35 cernes additionnels manquaient à la base des troncs. Ces cernes manquants localisés dans la portion souterraine du tronc étaient associés à la formation des racines adventives. En conclusion, les gaulis supprimés de sapin baumier ont des cernes manquants à la base du tronc. La recherche de tous les cernes manquants permet d'obtenir une dynamique temporelle de recrutement très différente de celle obtenue en comptant uniquement les cernes à la base du tronc. L'analyse de tige sur toute la longueur du tronc est la meilleure méthode pour estimer l'âge de gaulis supprimés de sapin baumier.

## Introduction

In the Northern Hemisphere, a tree typically produces one growth ring a year. In general, ring counts at trunk base are

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**S. Parent<sup>1</sup> 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.

<sup>1</sup>Corresponding author (e-mail: Parentsb@netscape.net).

used to estimate the age of a tree (Telweski and Lynch 1991). The closer the trunk sample is to the true collar (the hypocotyl region), the more precise the age estimation (Telewski 1993; DesRochers and Gagnon 1997; Gutsell and Johnson 2002). However, if the tree has spent a large part of its life cycle under harsh growing conditions, growth rings could be missing at the base of the trunk (Bormann 1965; Kohyama 1980; Kohyama and Fujita 1981; Lorimer et al. 1999). Missing growth rings at the trunk base are considered a rare event so that any error in the estimation of the germination date of a tree can be minimized by cross-dating techniques (Schweingruber 1996; Bergeron 2000). However, if missing rings are numerous, establishing the chronosequence of suppressed trees is more difficult, and the sequence is difficult to match with the master chronosequence obtained

with non-suppressed or dominant trees in the canopy (Coleenutt and Luckman 1995; Lorimer et al. 1999). This can then lead to erroneous ecological interpretations (Riverain and Gagnon 1996; Parent et al. 2000, 2001).

Numerous researchers have indicated that balsam fir (*Abies balsamea* (L.) Mill.) is often difficult to age accurately, because it can grow in the understory for prolonged periods; these suppression periods can lead to the formation of narrow or missing rings (Moris 1948; Zarnovican 1981; Morin and Laprise 1997; Bergeron 2000; Kneeshaw and Claveau 2001). Studies done with branches or trunks indicate that a reduced photosynthetic capacity can cause frequent breaks in radial growth at the branch base or the trunk base (Bormann 1965; Kershaw et al. 1990; Roberts 1994). After several years of growth in the understory, fir crowns are often candelabra (seedlings) or umbrella (saplings) shaped (Davis 1991). These suppressed firs have only a small proportion of biomass in needles. Therefore, missing rings at the trunk base could be common in balsam fir regeneration. However, no study has related year-long breaks in radial growth (missing rings at the trunk base) with crown vigour of whole trees. The objectives of this study are (*i*) to confirm whether or not breaks in radial growth at the trunk base are frequent in balsam fir saplings that have grown for more than 10 years under a closed canopy and (*ii*) to determine if there is a relationship between missing rings at the trunk base and loss in vigour as measured by several growth parameters and crown morphological variables.

## Materials and methods

### Study site

The study took place in an old-growth conifer forest dominated by balsam fir ( $\geq 120$  years) located in northern Quebec, Canada ( $49^{\circ}46'N$ ,  $72^{\circ}42'W$ ). The study site is located in the black spruce (*Picea mariana* (Mill.) BSP) – feathermoss eco-climatic zone (region 12B, Thibault 1987). The selected stand dates back to 1841, and its structure was altered by two spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks, which started in ca. 1880 and 1909 (Morin 1994). The latest spruce budworm outbreaks (1944 and 1974) did not alter the structure of the forest (Morin 1994). The canopy is closed and dominated by mature firs averaging 16 m in height. About 10% of the basal area (DBH  $> 5$  cm) is composed of black spruce, white spruce (*Picea glauca* (Moench) Voss), and white birch (*Betula papyrifera* Marsh.). The forest floor is dominated by *Hylocomium splendens* (Hedw.) BSG moss. The density of the fir regeneration ( $< 2$  m in height) is estimated to be 83 000 seedlings/ha (Morin and Laprise 1997).

### Sampling

In the stand under study, suppressed fir saplings represent approximately 3% of the fir regeneration. These firs have a patchy distribution (S. Parent, personal observations). In the spring of 1999, a linear transect was oriented to cross the maximum number of patches. One sapling was selected at every 2–3 m along the transect. A total of 29 suppressed saplings were sampled. The selected saplings did not have any recent damage to the trunk or branches. In July of 1999, the proportion of incident light (photosynthetic photon flux

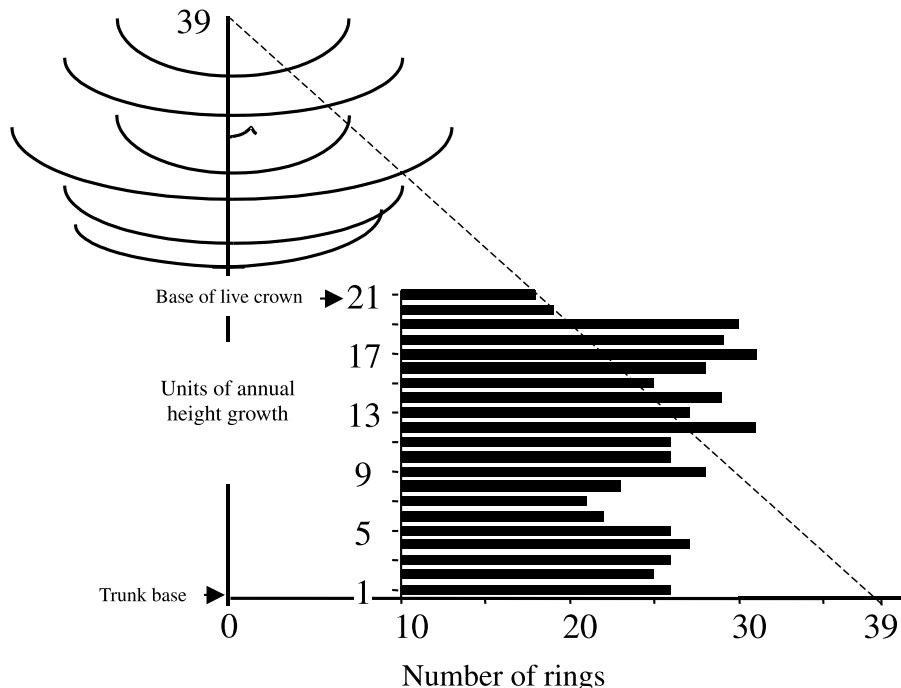
density (PPFD),  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) intercepted at the terminal leader was estimated under uniform cloud conditions using the method outlined by Parent and Messier (1996). In autumn, the selected saplings were harvested in their entirety including roots. In the laboratory, the trunk of each sapling was severed over the first living root (e.g., at the trunk base). Because of the asymmetry of the trunks, the diameter at the trunk base was calculated using the geometric mean. With a magnifying glass (40–100 $\times$ ), all aboveground and belowground (located below the trunk base) terminal bud scars (TBS) were precisely located and counted. A TBS is a small ridge that entirely encircles the trunk. It is a scar left by the fall of the scales protecting the bud of the terminal leader. Because balsam firs flush only once during a growing season, the trunk section between two TBS corresponds to a unit of annual height growth. Height growth was averaged over the last 5 years (HG<sub>1994–1999</sub>) according to measured height increments (from the terminal leader). Subsequently, the aboveground trunk of each sapling was cut into cross sections between each TBS (i.e., in the middle of each unit of annual height growth). Cross sections encompass two units of annual height growth separated by a single TBS, the bottom end having  $x$  rings and the upper end having (theoretically)  $x - 1$  rings. A few cross sections had two or three TBS when TBS were too close together to section precisely. Cross sections, branches, and needles were oven-dried separately ( $70^{\circ}\text{C}$ , 48 h). Belowground TBS were also counted to age the trunk section buried in humus (Parent et al. 2000).

### Missing rings

All cross sections were sanded on each side; all rings (complete or incomplete) were counted using a binocular microscope (40–100 $\times$ ). In general, the maximum number of rings was counted on the largest transverse cut of the trunk. The theoretical taper assumes there is a one-ring difference between each adjacent TBS (Telewski and Lynch 1991). Missing rings were recorded at the trunk base if the number of rings counted above a given unit of annual height growth (i.e., above a given TBS) was equal to or greater than the number of rings below the TBS. As an example, in Fig. 1, two missing rings were deduced to occur at the trunk base, because at the third unit of annual height growth from the trunk base we measured 26 rings, while the cross section cut just below it had 25 rings (ring count). Finally, to confirm the presence of missing rings, ring width was measured for a series of contiguous cross sections located on each side of the terminal bud scar. Then, the radial growth curves were compared using cross-dating techniques (see DesRochers and Gagnon 1997).

In this study, sapling vigour was estimated by these variables: length of the terminal leader, height growth (HG<sub>1994–1999</sub>), radial growth (RG<sub>1994–1999</sub>), live crown ratio (length of the living crown divided by total height) an index of crown vigour for balsam fir saplings (Ruel et al. 2000), and photosynthetic/non-photosynthetic tissue (P/nP) ratio (needle dry mass divided by aboveground stem dry mass) based on the assumption that all these indexes are well correlated with both growth rate and productivity (Tilman 1988; Larcher 1995).

**Fig. 1.** Example of an abnormal taper of a suppressed fir sapling (from the trunk base to the base of the live crown). Bars show ring counts for each unit of height growth. The broken line indicates the expected number of rings for a normal taper. Note that the decrease in ring count between the 5th and the 7th and between the 18th and the 19th unit of annual height growth correspond to a lack of apical dominance during several years. Cross-dating techniques were used to match radial growth curves between these cross sections.



## Results

### Characterizing growth

Sapling characteristics are presented in Table 1. All the saplings have characteristics of suppression including weak height growth ( $7.3 \pm 6.5$  mm (mean  $\pm$  SD) for 1999), a live crown length of  $22 \pm 14\%$  of the total trunk height (%LC), weak radial growth ( $RG_{1994-1999}$ , width  $0.21 \pm 0.13$  mm), and a low ( $16 \pm 10\%$ ) P/nP.

Relationships between the different growth parameters are presented in Table 2. Of all the growth parameters, only height growth ( $HG_{1994-1999}$ ) was significantly correlated with the percentage of light measured (%PPFD) above the terminal leader (or apex). There was a strong positive correlation between P/nP and %LC ( $r = 0.80$ ,  $p < 0.001$ ). Sapling height was negatively correlated with P/nP and %LC. The correlations between P (needle dry mass),  $RG_{1994-1999}$ , and  $HG_{1994-1999}$  were moderate and positive. There was a positive correlation between  $HG_{1994-1999}$  and %LC or P/nP. However,  $RG_{1994-1999}$  was not correlated with %LC or P/nP. Finally, there was a strong correlation between diameter at the trunk base and non-photosynthetic biomass (nP) ( $r = 0.91$ ,  $p < 0.001$ ) as well as with total aboveground biomass (P + nP) ( $r = 0.90$ ,  $p < 0.001$ ).

### Missing rings

The number of rings counted at the trunk base varied between 23 and 67 ( $40 \pm 10$  rings). The number of TBS ( $39 \pm 8$ ) counted above the trunk base was not different from the mean number of rings counted at the trunk base ( $p = 0.700$ , paired  $t$  test), but the linear correlation between the number of rings counted at the trunk base and the number of terminal bud scars counted above the trunk base was not very

**Table 1.** Principal characteristics of harvested saplings.

	Minimum	Maximum	Mean $\pm$ SD
PPFD (%) <sup>a</sup>	3.24	17.9	7.83 $\pm$ 3.48
Height growth (mm in 2000)	1.15	21.6	7.37 $\pm$ 6.59
HG <sup>b</sup>	3.11	20.8	11.06 $\pm$ 5.44
Live crown (mm)	68	781	245 $\pm$ 41
Total height (mm)	672	1830	1165 $\pm$ 291
Diameter at trunk base (mm)	10.24	24.96	17.47 $\pm$ 3.79
RG <sup>c</sup>	0.04	0.54	0.21 $\pm$ 0.13
LC (%) <sup>d</sup>	4.43	61	22 $\pm$ 14
P/nP <sup>e</sup>	0.02	0.41	0.16 $\pm$ 0.10

<sup>a</sup>PPFD, photosynthetic photon flux density.

<sup>b</sup>HG, mean annual rate of height growth for 1994–1999.

<sup>c</sup>RG, mean annual rate of radial growth at the trunk base for 1994–1999.

<sup>d</sup>LC, length of the living crown compared with the total height.

<sup>e</sup>P/nP, ratio of photosynthetic/non-photosynthetic tissue for the aboveground biomass only, e.g., above the trunk base.

strong ( $r = 0.55$ ,  $p < 0.001$ ; results not shown). Height growth was extremely slow and frequently inhibited for all saplings examined. For all saplings, stem analysis from the terminal leader to the base of the live crown did not reveal any missing rings. On the other hand, stem analysis from the trunk base to the base of the live crown revealed the presence of several rings (<0.1 mm) located above the trunk base (Fig. 1) that were missing at the trunk base. As indicated in Fig. 1, the number of rings counted in a given cross section was frequently lower than the number of rings counted in the cross section located just one terminal bud

**Table 2.** Degree of Spearman correlation characterizing the growth of saplings.

	P	nP	P+nP	HG	RG	DTB	Height	LC	P/nP
PPFD	0.44ns	0.38ns	0.34ns	0.51**	0.11ns	0.12ns	0.08ns	0.22ns	0.23ns
P		0.59***	0.70***	0.73**	0.49**	0.55**	0.02ns	0.54***	0.72***
nP			0.98***	0.55**	0.43**	0.91***	0.73***	0.77ns	-0.07ns
P+nP				0.60***	0.44**	0.90***	0.63***	0.02ns	0.05ns
HG					0.60***	0.42*	0.13ns	0.48***	0.50***
RG						0.41**	0.08ns	0.30ns	0.28ns
DTB							0.64***	0.11ns	-0.10ns
Height								-0.47**	-0.54**
LC									0.80***

**Note:** Variables are as defined in Table 1. DTB, diameter of the trunk base. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ ; ns, not significant ( $p > 0.05$ ).

scar (unit of annual height growth) above it, indicating an abnormal taper along the trunk.

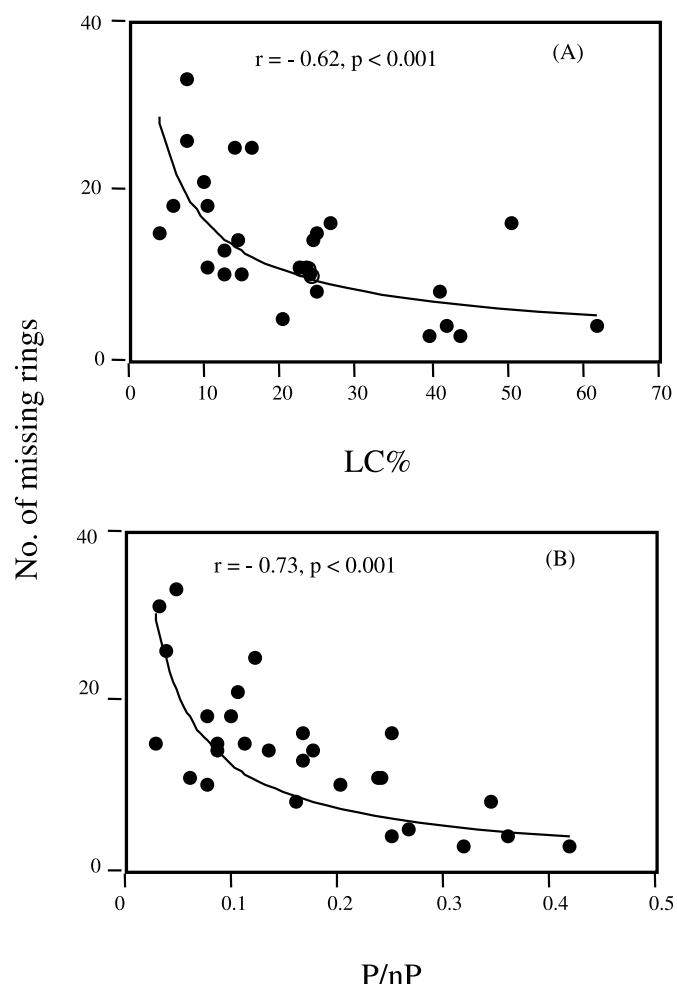
From 3 to 33 additional rings found along the trunk were missing at the trunk base. The number of missing rings at the trunk base was not correlated with the number of rings at the trunk base ( $r = -0.35$ ,  $p > 0.05$ ), nor with the number of terminal buds scars counted from the trunk base to the terminal leader ( $r = 0.29$ ,  $p > 0.05$ ), nor with the diameter at trunk base ( $r = 0.01$ ,  $p = 0.99$ ). Correlations were significant between the number of missing rings and total height ( $r = 0.41$ ,  $p = 0.02$ ), HG<sub>1994–1999</sub> ( $r = -0.51$ ,  $p = 0.003$ ), or RG<sub>1994–1999</sub> ( $r = -0.44$ ,  $p = 0.002$ ). Strong correlations were found between the number of missing rings at the trunk base and the percentage of live crown ( $r = -0.62$ ,  $p < 0.001$ ), or the P/nP ratio ( $r = -0.73$ ,  $p < 0.001$ ) as shown in Figs. 2A and 2B, respectively.

### Age of saplings

Parent et al. (2000) indicated that counting all terminal bud scars on the entire trunk provides a better age estimate for balsam fir seedlings than ring count at the shoot–root interface (similar to the trunk base in our study). In Fig. 3, the number of terminal bud scars counted on the entire trunk (i.e., including the belowground trunk) is compared with the number of rings counted at the trunk base (Fig. 3A, age 1), with the total number of rings above the trunk base (age 2 = age 1 + missing rings found in the aboveground trunk; Fig. 3B), and the age obtained by adding age 2 with bud scars on the belowground trunk (Fig. 3C, age 3). For all saplings, age 3 was most accurate rather than adding bud scars on the aboveground trunk + bud scars on the belowground trunk (Fig. 3, x axis). The best age estimate (age 3) is provided by stem analysis, because bud scars could be missing on the aboveground trunk (see Fig. 1) and on the belowground trunk since the hypocotyl region of these saplings is missing.

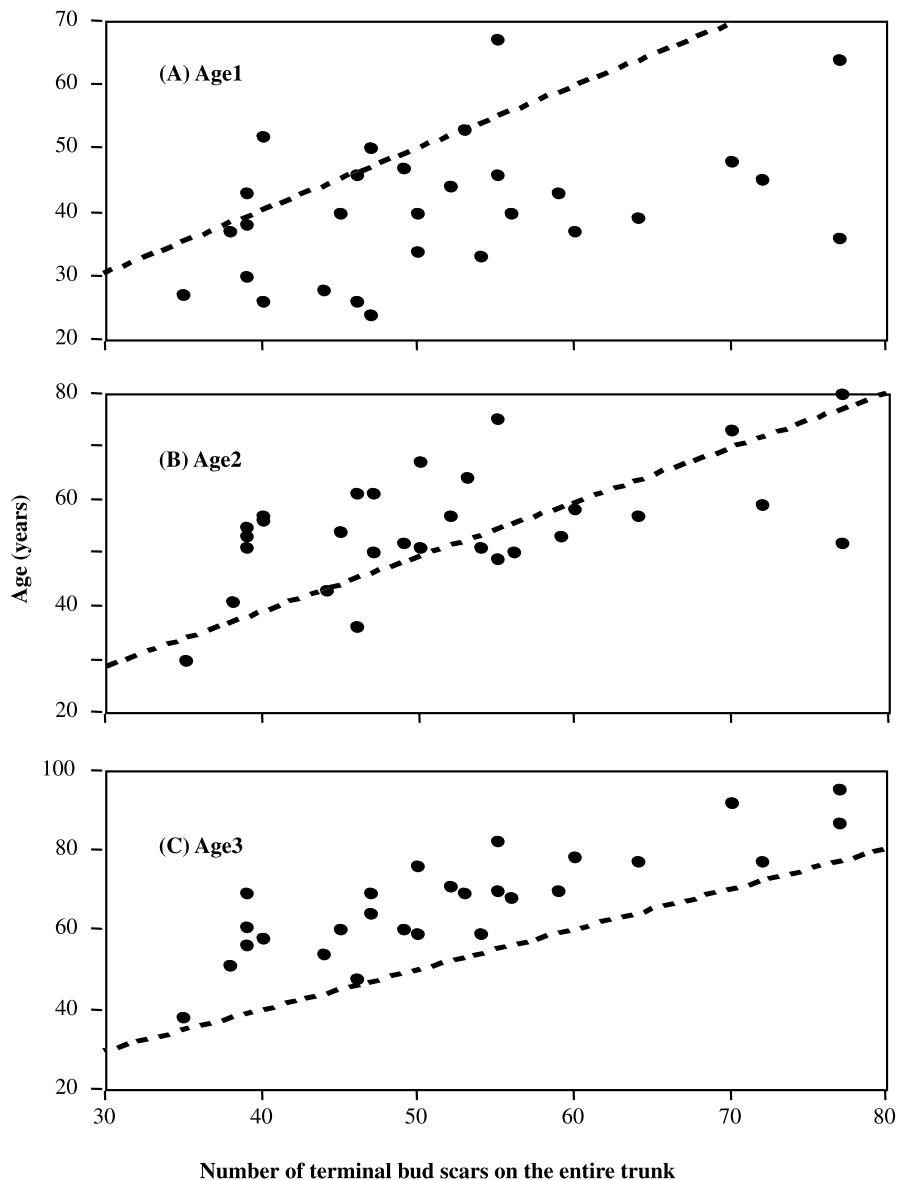
The mean age of the sapling population estimated by the number of rings at the trunk base (age 1) is  $41 \pm 10$  years. This estimate increases to  $55 \pm 10$  years by adding all the aboveground missing rings (age 2) and further increases to  $67 \pm 13$  years by adding the years included in the buried trunk in humus (belowground TBS count) (age 3). In Fig. 4, the age estimates shown in Fig. 3 are presented as frequency histograms along a time scale, and spruce budworm outbreaks are outlined. According to these histograms, all the saplings recruited before the last spruce budworm outbreak,

**Fig. 2.** Relation between the number of missing rings at the trunk base and the live crown ratio (A) and the P/nP ratio (B). Spearman's  $r$  and the  $p$  value for the correlation are given.



which lasted from 1974 to 1985. Figures 4A and 4B suggest that 33% of the saplings were recruited during the preceding spruce budworm outbreak (1944–1955), while Fig. 4C reveals a much longer recruitment period. According to the best age estimate (i.e., age 3) (which is still minimal because hypocotyls were absent), only 3 of 29 saplings were recruited during the 1944–1955 outbreak and 5 of 29 recruited during the 1908–1923 outbreak.

**Fig. 3.** Scatterplot comparing the age of saplings obtained by counting the number of terminal bud scars counted on the entire trunk ( $x$  axis) with (A) the number of rings counted at the trunk base (age 1), (B) the total number of rings above the trunk base (age 2 = age 1 + missing rings found in the aboveground trunk), and (C) the age obtained by adding bud scars on the belowground trunk to age 2 (age 3). The broken line indicates where  $x = y$ .



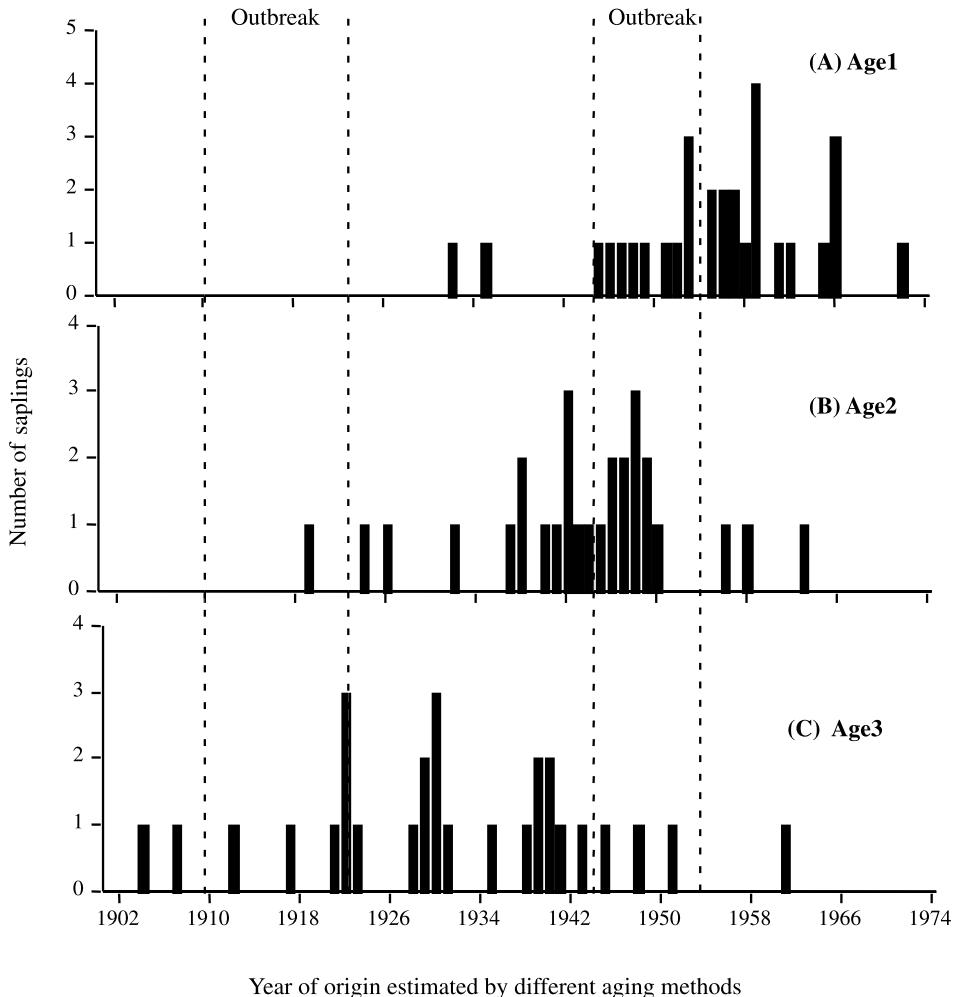
## Discussion

Our study of suppressed balsam fir saplings demonstrates that missing rings are not necessarily rare events, because we found missing rings in all 29 saplings investigated. Year-long breaks in radial growth at the trunk base can be consecutive and repeated at least 33 times in an 80-year horizon. Bormann (1965) found at least 12 missing rings at the trunk base of suppressed white pine (*Pinus strobus* L.) saplings, and reported that Tuberville and Hough (1939 in Bormann 1965) noted 28 missing rings in an older white pine. Lorimer et al. (1999) found about 20 missing rings in sugar maple (*Acer saccharum* Marsh.), which is more shade tolerant than white pine. In Japan, Kohyama (1980) noted that several rings are frequently missing at the trunk base of sup-

pressed *Abies mariesii* Mast. saplings. All these observations suggest that any tree species that grows under suppressed conditions can cease producing annual growth rings at the trunk base (Telewski and Lynch 1991; Kozlowski and Pallardy 1997).

Results presented in Fig. 2 suggest possible dynamic mechanisms explaining the non-producing rings at the trunk base for suppressed fir saplings. Under a light-limiting canopy, the annual growth of suppressed fir saplings continuously accumulates non-photosynthetic biomass (respiring tissues), which should gradually limit resources available for the production of new foliage (Waring 1987). This phenomenon might be the main factor responsible for the senescence of trees in deep shade (Waring 1987; Givnish 1988, 1995). When leaf biomass does not produce enough carbon to sup-

**Fig. 4.** Age structures of saplings when age is estimated by (A) the number of rings counted at the trunk base (age 1 in Fig. 3A), (B) total ring count, i.e., including all additional rings found along the aboveground trunk (age 2 in Fig. 3B), (C) total ring count plus belowground TBS count (age 3 in Fig. 3C). Note that during the last century, three spruce budworm outbreaks were recorded in the area during the following periods: 1908–1923, 1944–1955, and 1974–1985 (Morin 1994).



port the carbon demands of the entire tree, growth rings are not produced at the trunk base (Bormann 1965; Marchand 1984). Similar arguments have been suggested to explain lack of ring production at the base of the lowest branches in the crown of *Pseudotsuga menziesii* (Mirb.) Franco (Kershaw et al. 1990), and *Abies lasiocarpa* (Hook.) Nutt. (Roberts 1994). Therefore, absent rings at the trunk base in suppressed fir saplings revealed a physiological stress probably due to a severe reduction of sapling vigour resulting from a long period of growth under low light conditions (Bormann 1965; Kohyama 1980; Marchand 1984; Kershaw et al. 1990; Roberts 1994; Lorimer et al. 1999). It is also possible that severe defoliation during outbreaks can cause missing rings at the trunk base in suppressed fir saplings (Krause and Morin 1995, 1999). However, we believe that this factor is minor, because the last three spruce budworm outbreaks have not severely affected our study stands; additionally, small trees are generally defoliated less by insects than dominant firs (Morin 1994). Other factors could include the particular environmental conditions of the old balsam fir stand studied, such as low temperature or low nutrient avail-

ability. Therefore, our results suggest that there exists a threshold of sapling vigour or productivity (expressed by the P/nP ratio) under which the annual growth ring is not formed at the trunk base.

Models of sapling mortality under closed canopy suggested that consecutive years without ring production close to the trunk base lead to sapling death (Kobe et al. 1995; Kobe and Coates 1997). Our method was not designed to estimate how many years a suppressed fir sapling may not produce rings at the trunk base before it dies. However, our observations suggest that suppressed firs may not produce rings at the trunk base or not allocate enough carbon to form apparent rings at the trunk base during at least eight consecutive years (see additional rings located at the 16th and 17th unit of annual height growth in Fig. 1). At least four (*Pinus strobus*; Bormann 1965) and 11 (*Pinus radiata* Donn. Ex D. Don; Harris 1952, in Bormann 1965) consecutive years without rings production have been noted in pines. The observed consecutive years without ring production at the trunk base suggest a local dormancy of cambial activity during several years. Therefore, some physiological factors reg-

ulating radial growth at the trunk base, such as ethylene production or other endogenous growth regulators may be altered by a severe reduction of photosynthetic capacity (Kozlowski and Pallardy 1997). Because new rings at the trunk base may represent an important carbon investment for the whole sapling (Kohyama 1991; Cannell and Dewar 1994; Enquist and Niklas 2000), it is possible that the capacity of a suppressed sapling to cease radial growth at the trunk base minimizes carbon allocation to non-photosynthetic biomass (Givnish 1995). This carbon can presumably be allocated to more important organs such as fine roots and needles with a limited life cycle rather than the production of growth rings at the trunk base (Krause and Morin 1995). In this case, consecutive years without rings production at the trunk base would be an efficient mechanism of persistence in deep shade by limiting carbon requirements for respiration and, hence, maintaining a positive carbon budget at the whole plant level (Tilman 1988; Givnish 1988).

### Age of saplings

All the saplings examined in this study had adventitious roots, and their true collar (hypocotyl region) was absent, probably decomposed over time or accidentally cut off during harvest. It was, therefore, impossible (*i*) to confirm the origin of the sapling (seed or layer) and (*ii*) to count all terminal bud scars (TBS) on the trunk and all rings formed since germination (Parent et al. 2000, 2001). Although estimating the age of fir saplings was not our main goal, we found that the count of terminal bud scars on the entire trunk did not provide a good age estimation of suppressed fir saplings, because there were too many units of annual growth missing above and below (lack of the hypocotyl region) the trunk base. In fact, to estimate the minimum age of suppressed balsam fir saplings (% live crown  $\pm$  0.22 on average in our study), it is necessary to find the missing rings located in the aboveground part of the trunk as well as those located in the belowground trunk section. Belowground missing rings are related to the formation of adventitious roots (LeBaron 1945; Kohyama 1983; DesRochers and Gagnon 1997; Parent et al. 2000; Parent and Morin 2002). The formation of adventitious roots favours a reverse taper in the embedded section of the trunk that is a reduction of diameter and of number of growth rings from the trunk base to the hypocotyl region. Consequently, estimating the age of suppressed fir requires a complete stem analysis on the entire trunk. This method is time consuming. However, taking into account all the missing rings at trunk base, the small saplings studied (<2 m tall) were not only older than expected, some almost 100 years old, but their recruitment dynamics were very different from that obtained by solely counting the rings at the trunk base (see Fig. 4).

### Conclusion

Missing rings are frequent and numerous in suppressed balsam fir saplings. Two types of rings are missing at the trunk base. The first type (aboveground missing rings) is strongly related to the high reduction in sapling vigour expressed by the percent live crown or the P/nP ratio, while the second type (belowground missing rings) is associated to the formation of adventitious roots (see DesRochers and Gagnon

1997; Parent et al. 2000). Our study agrees with the idea that aboveground missing rings could be the direct result of a carbon shortage caused by a reduction in the photosynthetic to non-photosynthetic ratio (Bormann 1965; Marchand 1984; Roberts 1994). Therefore, we suggest that the numerous rings missing at the trunk base (aboveground and belowground), which minimize carbon allocation to non-photosynthetic organs, play an important role in the high shade tolerance of balsam fir regeneration. According to our study, stem analysis on the entire trunk is the best aging method for suppressed balsam fir saplings.

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### References

- Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology*, **81**: 1500–1516.
- Bormann, F.H. 1965. Changes in the growth pattern of white pine trees undergoing suppression. *Ecology*, **46**: 269–277.
- Cannell, M.G.R., and Dewar, R.C. 1994. Carbon allocation in trees: a review of concepts of modelling. *Adv. Ecol. Res.* **25**: pp. 60–103.
- Colenutt, M.E., and Luckman, B.H. 1995. The dendrochronological characteristics of alpine larch. *Can. J. For. Res.* **25**: 777–789.
- Davis, W.C. 1991. The role of advanced growth in regeneration of red spruce and balsam fir in east centre Maine. *In Proceedings of the Conference on Natural Regeneration*. Edited by C.M. Simpson. Canadian Forest Service, Fredericton, N.B. pp. 157–168.
- DesRochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? *Can. J. For. Res.* **27**: 1263–1267.
- Enquist, B.J., and Niklas, K.J. 2001. Invariant scaling relations across tree-dominated communities. *Nature (London)*, **410**: 655–660.
- Givnish, T.J. 1988. Adaptation to sun vs. shade: a whole plant perspective. *Aust. J. Plant. Physiol.* **15**: 63–92.
- Givnish, T.J. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. *In Plant stems: physiology and functional morphology*. Edited by B.L. Gartner. Academic Press, New York. pp. 3–49.
- Gutsell, S.L., and Johnson, E.A. 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. *J. Ecol.* **90**: 153–166.
- Kershaw, J.A., Maguire, D.A., and Hann, D.W. 1990. Longevity and duration of radial growth in Douglas-fir branches. *Can. J. For. Res.* **20**: 1690–1695.
- Kneeshaw, D.D., and Claveau, Y. 2001. Comment — Effects of adventitious roots on age determination in balsam fir regeneration. *Can. J. For. Res.* **31**: 1292–1295.
- Kobe, R.K., and Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in

- shade tolerance of eight species of northwestern British Columbia. *Can. J. For. Res.* **27**: 227–236.
- Kobe, R.K., Pacala, S.W., and Silander, J.A., Jr. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* **5**: 517–532.
- Kohyama, T. 1980. Growth pattern of *Abies mariesii* sapling under conditions of open-growth and suppression. *Bot. Mag. (Tokyo)*, **93**: 13–24.
- Kohyama, T. 1983. Seedling stage of two subalpine *Abies* species in distinction from sapling stage: a matter-economic analysis. *Bot. Mag. (Tokyo)*, **96**: 49–65.
- Kohyama, T., and Fujita, N. 1981. Studies on the *Abies* population in Mt. Shimagare. I. Survivorship curve. *Bot. Mag. (Tokyo)*, **94**: 55–68.
- Kozlowski, T.T., and Pallardy, S.G. 1997. Physiology of woody plants. 2nd ed. Academic Press, New York.
- Krause, K., and Morin, H. 1995. Changes in radial increment in stems and roots of balsam fir (*Abies balsamea* (L.) Mill.) after defoliation by spruce budworm. *For. Chron.* **71**: 747–754.
- Krause, K., and Morin, H. 1999. Root growth and absent ring in mature black spruce and balsam fir, Quebec, Canada. *Dendrochronologia*, **16–17**: 21–35.
- Larcher, W. 1995. Physiology plant ecology. 3rd ed. Springer, New York.
- LeBarron, R.K. 1945. Adjustment of black spruce root system to increasing depth of peat. *Ecology*, **26**: 309–311.
- Lorimer, C.G., Dahir, S.E., and Singer, M.T. 1999. Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. *Plant Ecol.* **143**: 189–202.
- Marchand, P.J. 1984. Dendrochronology of a fir wave. *Can. J. For. Res.* **14**: 51–56.
- Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the Boreal Zone of Quebec. *Can. J. For. Res.* **24**: 730–741.
- Morin, H., and Laprise, D. 1997. Seedling bank dynamics in boreal balsam fir forests. *Can. J. For. Res.* **27**: 1442–1451.
- Moris, R.F. 1948. How old is a balsam fir tree? *For. Chron.* **24**: 106–110.
- 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., and Messier, C. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. *Can. J. For. Res.* **26**: 151–154.
- Parent, S., and Morin, H. 2002. Reply — Effects of adventitious roots on age determination in balsam fir regeneration. *Can. J. For. Res.* **32**: 1296–1300.
- 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.
- Riverain, S., and Gagnon, R. 1996. Dynamique de la régénération d'une pessière à lichen dans la zone de la pessière noire à mousset, nord du Saguenay-Lac-Saint-Jean (Québec). *Can. J. For. Res.* **26**: 1504–1509.
- Roberts, S.D. 1994. The occurrence of non-ring producing branches in *Abies lasiocarpa*. *Trees*, **8**: 263–267.
- Ruel, J.-C., Messier, C., Doucet, R., Claveau, Y., and Comeau, P. 2000. Morphological indicators of growth response of coniferous advance regeneration to overstorey removal in the boreal forest. *For. Chron.* **76**: 633–641.
- Schweingruber, F.H. 1996. Tree ring and environment dendroecology. Swiss Federal Institute for Forest, Snow, and Landscape Research, Berne, Switzerland.
- Telewski, F.W. 1993. Determining the germination date of woody plants: a proposed method for locating the root/shoot interface. *Tree-Ring Bull.* **53**: 13–16.
- Telewski, F.W., and Lynch, A.M. 1991. Measuring growth and development of stems. In *Techniques and approaches in forest tree ecophysiology*. Edited by J.P. Lassoie and T.M. Hinckley. CRC Press, Boca Raton, Fla. pp. 504–554.
- 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.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J.
- Waring, R.H. 1987. Characteristics of trees predisposed to die. *Bioscience*, **37**: 569–574.
- Zarnovican, R. 1981. À propos de l'âge du sapin baumier et de sa détermination. *Can. J. For. Res.* **11**: 805–811.