Growth dynamics of successive post-fire cohorts of black spruce: Is site potential reduced?

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ABSTRACT

Black spruce is one of the main commercial species in boreal forests of North America. It usually forms large and single-species natural stands in eastern Canada, yet in recent years, parts of this area have undergone forest cover regression and the conversion of closed-crown forests to open lichen woodlands, partly due to successive disturbances and regeneration accidents. We studied two successive post-fire cohorts growing at the same site, for which a clear forest cover regression trajectory has already been demonstrated, to assess possible changes in the site potential. The Wilcoxon nonparametric test found significant differences in mean diameter and height growth between cohorts, compared by cambial age, generally with higher mean values for the most recent cohort. There were no indications of growth reduction between the previous and the current cohorts. This paper sets the ball rolling for a discussion on the pertinence of reforestation in this type of recently established open formation, where growth potential (as expressed by diameter and height) seems, at least, maintained.

Keywords: open lichen woodland, closed-crown forest, black spruce, successive disturbance, reforestation

RÉSUMÉ

L'épinette noire est l'une des principales espèces commerciales des forêts boréales de l'Amérique du Nord. Elle forme habituellement de vastes peuplements naturels monospécifiques dans l'est du Canada, même si, au cours des dernières années, une partie de ce territoire a subi une diminution de son couvert forestier et vu ses forêts denses converties en dénudés secs, notamment sous l'action des perturbations successives et des accidents de régénération. Nous avons étudié deux cohortes successives après feu poussant sur le même site et manifestant déjà une régression évidente du couvert forestier, afin d'évaluer les changements possibles dans le potentiel du site. Le test non paramétrique de Wilcoxon a relevé des différences significatives du diamètre moyen et de la croissance en hauteur entre les cohortes, sur la base de l'âge cambial, avec de plus fortes valeurs moyennes pour la cohorte la plus récente. On n'a pas observé de réduction de la croissance entre la cohorte précédente et celle d'aujourd'hui. Cet article veut lancer la discussion sur la pertinence de reboiser ce type de formation ouverte d'origine récente, dont le potentiel de croissance (sur la base du diamètre et de la hauteur) semble au moins s'être maintenu.

Monts clés : dénudés secs tapissés de lichen, peuplement fermé, épinette noire, perturbation successive, reboisement

Introduction

Black spruce is one of the main commercial species in boreal forests of North America (Gagnon and Morin 2001, Burton *et al.* 2003). Given its good mechanical properties and abundance, it is used for timber and fiber production (Burton *et al.* 2003, Krause *et al.* 2009). It usually regenerates naturally after disturbances, but when regeneration is insufficient it can be planted (Zasada *et al.* 1983, Gagnon and Morin 2001, Thiffault *et al.* 2004, Gauthier *et al.* 2009, Krause *et al.* 2009). Black spruce often forms large and single-species natural stands in eastern Canada, where the continuous spruce feathermoss forest covers the majority of the landscape between 49°N and 52°N (Gagnon 2001, Gagnon and Morin 2001, Mansuy *et al.* 2012). Yet some areas previously occupied by the closed-crown forest are being replaced by less dense wood savannah-like formations containing mainly lichens or ericaceous shrubs (Mallik 2003, Girard *et al.* 2008). The causes may be multiple, and primarily include successive disturbances resulting in the natural regression of forest cover (Gagnon 2001, Gagnon and Morin 2001, Girard *et al.* 2008, Mansuy *et al.* 2012). In Canada, more than half the

economic activity linked to forest products derives from the boreal forest (Burton *et al.* 2003). Moreover black spruce forests are unique to North America and so they have a value as elements of world biodiversity (Gagnon 2001, Gagnon and Morin 2001). Thus, better understanding the growth and regeneration of stands after forest cover regression is very important for forest managers and policy-makers in order to take informed decisions.

Fire is an important ecological factor, together with insect outbreaks and, more recently, forest cuts, shaping the growth and distribution of many boreal forest trees (Sirois and Payette 1989, Greene *et al.* 1999, Johnstone and Chapin 2006). Black spruce is generally considered to be well but not perfectly adapted to fire through semi-serotinous cones (Gagnon and Morin 2001, Johnstone *et al.* 2009). Tree establishment is usually very rapid, starting from the second year following fire and being mainly completed within five years (St-Pierre *et al.* 1992, Des-Rochers and Gagnon 1997, Charron and Greene 2002, Fantin and Morin 2002, Johnstone *et al.* 2004). Continued tree establishment at low levels is possible, as the stand ages, but later cohorts show high rates of mortality (Sirois and Payette 1989,

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Johnson *et al.* 1994, Gutsell and Johnson 2002, Johnstone *et al.* 2004). Actually, tree establishment is expected to decrease with time since fire, given that adequate mineral soil and humus seedbeds become increasingly rare and the number of viable seeds in the aerial bank decreases, while competition by ericaceous shrubs increases (Greene *et al.* 1999, Gagnon 2001). Many factors can affect the success of post-fire regeneration and may lead to insufficient re-establishment and the conversion of closed-crown forests to less dense stands, like lichen woodlands (Simard and Payette 2005).

Spruce budworm (*Choristoneura fumiferana* [Clem.]) is the second most important ecological factor influencing black spruce forest dynamics and growth, especially in the eastern part of North America (Greene *et al.* 1999, Simard and Payette 2005). Spruce budworm may hamper regeneration of black spruce for up to 20 years following a severe outbreak, reducing the seed bank in the canopy (Simard and Payette 2005). Indeed, the insects may kill the upper part of the canopy, where the majority of cone-bearing branches are located (Begin and Filion 1999), or directly prevent the formation of new cones by feeding on megastrobili before they mature into cones (Schooley 1980, Prévost *et al.* 1988). Luckily, in the absence of fire, the reduction of seed production is not usually a problem for black spruce regeneration, which can count on pre-established seedlings and layers growing in the understory of mature stands (Gagnon 2001, Gagnon and Morin 2001, Gauthier *et al.* 2009). However, if a forest fire occurs before the aerial seed bank is re-established, killing pre-established trees, this may severely limit the regeneration of black spruce forests. Thus, successive disturbances with a too-short time lag, like an insect outbreak followed by wildfire a few years later, may lead to the regression of the forest cover and the formation of an open lichen woodland (Payette *et al.* 2000, Jasinski and Payette 2005, Simard and Payette 2005, Girard *et al.* 2009). An increasing number of observations suggest that once these formations have replaced the closed-crown forest, the new stand does not evolve to a closed-crown forest naturally (Dussart and Payette 2002, Jasinski and Payette 2005, Girard *et al.* 2009, Côté *et al.* 2012). Dussart and Payette (2002) suggested two main causes of the regression from closed-canopy forests to open lichen woodlands: the limited density of advance regeneration, not compensated by adequate seedling establishment; and weak growth of black spruce.

Recently, Mansuy *et al.* (2012) described three types of stable open lichen woodlands in the eastern boreal forest of Canada: those of climatic origin, north of the 52° parallel in the taiga forest; those due to strong edaphic constraints; and those originated by successive disturbances. In the latter, poor regeneration is mainly a result of insufficient viable seeds and favourable seedbeds. Over the last 50 years, 9% of a vast area, between 70°W and 72°W and the southern and northern limit of the closed-crown boreal forest zone (47°N and 52°N, respectively) has been replaced by lichen woodlands, which may be an alternative stable state, preventing a natural re-densification of these sites (Riverin and Gagnon 1996, Jasinski and Payette 2005, Hébert *et al.* 2006, Girard *et al.* 2008, Côté *et al.* 2012). However, as many of these sites were previously occupied by closed-crown forests (Simard and Payette 2005, Girard *et al.* 2008, Mansuy *et al.* 2012), it is now important to know if these sites, resulting from the natural conversion of closed-crown black spruce forests to open lichen woodlands, have maintained the potential to sustain adequate tree growth. This knowledge is key to understanding if reforestation of these sites could be

a viable strategy for combating natural deforestation (Hébert *et al.* 2006, Gaboury *et al.* 2009, Mansuy *et al.* 2012, Tremblay *et al.* 2013). Considerations other than timber yield should also be taken into account, e.g., the importance of maintaining the continuous spruce feathermoss forests, which are concentrated in the eastern part of Canada, for their biodiversity and socio-economic values (Gagnon and Morin 2001, Burton *et al.* 2003, Gaboury *et al.* 2009).

In a recent article, Côté *et al.* (2012) demonstrated a gradual reduction in tree density and stocking and the formation of open lichen woodland, studying three cohorts established following successive disturbances on a site. The study demonstrated the regression of the forest cover but did not answer a fundamental question about the possible variation of the site potential. A sign of possible loss of site potential was a decrease in the number of merchantable trees (diameter at breast height over 10 cm) from the first to the second cohort, which had a stocking (i.e., proportion of the area actually occupied by trees) of only 25%, which is close to the lower limit for a closed-crown forest (Côté 2004, Côté *et al.* 2012). The aim of the present research was thus to compare the growth of trees growing at this site to assess possible reduction of growth following successive disturbances. The interest of using this particular site was based on the exceptionality of the data available (i.e., the study of three successive cohorts at the same site; Côté *et al.* 2012). The site was initially a closed-crown stand in the range of the continuous spruce feathermoss forest of Quebec, Canada (Côté *et al.* 2012). This paper presents data on the growth of trees of the two most recent cohorts established on the site after successive disturbances.

Material and Methods

Study site

The study site (49°59'N, 71°59'W) was a recently burned 25-ha lichen-spruce woodland located in the southern closed-crown boreal forest zone of eastern Canada, 125 km northeast of Dolbeau-Mistassini, in the Saguenay-Lac-St-Jean Region of Quebec (Fig. 1). Two fires burned the site, the first in 1920 and the last in 1995 (estimated through fire scars and historical data, see Côté *et al.* 2012 for more details). At the time of the initial sampling (1997), remnants of a first tree cohort (Cohort 1) established prior to the 1920 fire were found within the forest floor, buried under the lichen mat, generally at a state of decomposition not allowing growth analysis (Côté *et al.* 2012). All the three tree cohorts (i.e., trees established before the 1920 fire, trees established between 1920 and 1995 fires and trees established after the 1995 fire) were present on the site and were the object of a previous research on black spruce forest cover regression after successive disturbances (i.e., spruce budworm outbreaks followed closely by stand-replacing fires; Côté *et al.* 2012). For the present study, only trees pertaining to the second and third cohorts were used, due to the state of degradation of the first cohort. In 1997, the standing dead trees of the second cohort (Cohort 2, established after the 1920 fire) were sampled, while young living trees established after the 1995 fire (Cohort 3) were sampled in 2012. Samples were analyzed to assess diameter and height growth, in order to evaluate possible changes in tree productivity following successive disturbances, by comparing the two cohorts.

The area was part of the black spruce-feather moss bioclimatic domain (Robitaille and Saucier 1998). The site was dominated by black spruce, with a small presence of jack pine

Fig. 1. Location of the study site in the province of Quebec (Canada) at the heart of the closed-crown forest.

plots were at 70-m intervals, except for the first line, on which one parcel was not in a burnt area (Fig. 2). Each circular plot had an area of 100 m² (1/100 ha or 5.64-m radius), where ecological observations were performed according to the methods in Saucier *et al.* (1994) (Fig. 2). Using these plots, the tallest (dominant) standing dead tree of Cohort 2 was sampled for stem analysis (Zarnovican 1985), totaling 41 trees (one for each circular plot).

For stem analysis, stem discs were taken at 0 m (at ground height), 1 m, 1.3 m (at breast height), 2 m and then at 1-m intervals up to the last complete metre of the stem. Stem discs were dried and sanded in order to ease the observations with a binocular at 100×. Annual growth rings were counted on each disc and diagnostic rings (e.g., light, frost and incomplete rings) were identified. Growth curves were built measuring ring widths of each disc along two opposite radii with WinDendro and WinStem software (Regent Instrument Inc.) (Guay *et al.* 1992). Measurements had 0.002-mm precision.

and had a black spruce stocking level varying from 25.6% (Cohort 2) to 11.5% (Cohort 3) (see Côté *et al.* 2012 for more details). The ground was covered by lichens (mainly *Cladonia* species.). The shrub layer was mostly composed of ericaceous species, such as *Kalmia angustifolia* L. and *Rhododendron groenlandicum* (Oeder) Kron and Judd. (Payette *et al.* 2000, Côté *et al.* 2012). The site had an average altitude of 420 m a.s.l. with low topographical variation. It developed on thick and undifferentiated glacial till deposits. The soil was a podzol with a discontinuous hardened layer (i.e., hardpan). The drainage of the site was estimated to vary from good (76% of the sampled area) to moderate (the remaining 24%), according to Saucier *et al.* (1994).

The climate was continental, with cool, short summers and long, cold winters. Data were obtained from the closest weather station (Chute-des-Passes, 49°54'N, 71°15'W). Mean annual precipitation was about 978 mm (of which 261 mm as snow) for the period 1951 to 1980 (more recent data are available only for a much more distant weather station), with precipitations mainly occurring between June and September. Mean annual temperature was -0.2°C, with the coldest and warmest months being January (average temperature of -18.4°C) and July (average temperature 15.5°C) (Environnement Canada 1982, Côté *et al.* 2012).

Sampling of Cohort 2 (1997)

During the autumn 1997, 41 circular plots were established at 70-m intervals along eight lines spaced 70 m apart, to evaluate tree stocking (Côté *et al.* 2012). To be retained the plots had to be located in burnt areas. The resulting 41

Raw tree-ring data were used for tree diameter analyses, in order to preserve the influence of age on tree growth. Through stem analysis, diameter at ground height (DGH) and height curves of Cohort 2 were reconstructed for each sampled tree (Herman and DeMars 1970). Annual increments and cumulated values of diameter and height were used for the analyses. The Carmean method, considered the most precise to estimate annual height increments from stem analysis data, was used (Carmean 1972, Krause *et al.* 2009).

Fig. 2. Aerial photograph showing the limits of the study site and the distribution of the sampling points used in 1997 (Cohort 2) and 2011 (Cohort 3).

Sampling of Cohort 3 (2012)

In July 2012 (16 years after the most recent fire), the 41 circular plots sampled in 1997 were located in the field using GPS data and wooden stakes left as position markers. In each plot, the two tallest living trees from Cohort 3 were extracted from the soil, conserving a part of the root system in order to establish the position of the root collar. Tree height was measured from the root collar to the final complete annual shoot (i.e., that of 2011). Of the two sampled trees per circular plot, only the tallest (dominant) was used for further analyses. The age of the tree was estimated by counting growth rings on a disc taken as near as possible to the root collar (average distance between the disc and the root collar 8.3 cm). Only trees established from seed after the 1995 fire were retained. Pre-established seedlings and layers were dismissed after being identified through observation of 1) the number of annual internodes on the stem, 2) the structure of the root system, or 3) the number of growth rings at the root collar (once in the lab). This resulted in a total of 39 trees, since one plot was avoided because it was located in a wet area of the site, where alder had established after the last fire, and another in which the two dominant trees taken in the field had established before and survived the 1995 fire.

For each tree of Cohort 3, the year of establishment was estimated as the year corresponding to the innermost ring counted at the root collar. For both cohorts, cambial age of individual trees was calculated as the difference between the year corresponding to each measure and the estimated year of establishment, allowing for comparison of trees of the same age. For example, cambial age zero corresponded to a measurement taken on each tree the first year of their respective establishment. We believe this way of looking at data is acceptable when dealing with even-aged stands (i.e., the majority of trees established within the same 20-year age class) with a low density (where competition for space is absent or reduced).

Annual diameter increment near the root collar was measured, after sanding the wood disc, using WinDendro software to measure two opposite radii, avoiding reaction wood (Guay *et al.*

1992). Cumulated diameter was calculated cumulating successive annual increments in diameter. For Cohort 3, annual height increment was reconstructed using the bud scar method (Krause *et al.* 2009), i.e., measuring the distance between terminal bud scars on young seedlings. Sometimes it was not possible to measure the first height increments at the base of the seedling because the bud scars were not evident; in most cases the initial annual increment was not known. The cumulated height was estimated as the sum of annual increments, using the distance between the root collar and the bud scar at the base of the first measured annual increment, as the starting value of the cumulated height. For this reason the first annual increment was measured only the year following the first value of cumulated height.

Statistical analyses

The values of cumulated and annual increments for diameter at ground height (DGH) and height of Cohort 2 and Cohort 3 were compared graphically and statistically, by cambial age. Annual height increment and cumulated height of Cohort 2 and Cohort 3 were compared using the non-parametric Wilcoxon rank-sum test (considered robust for not normally distributed data) with the NPAR1WAY procedure in SAS (SAS 2003). This is acceptable, even if the bud scar method is considered more precise than the Carmean method, since their estimations are comparable (Krause *et al.* 2009). The annual and cumulated diameter of the two cohorts were compared in the same manner with a Wilcoxon rank-sum test.

Results

Age structure

The age distribution of the sampled trees is presented in Fig. 3a. For Cohort 2, trees established 5 to 29 years after fire (Fig. 3b). The majority of trees (39/41, 95%) established in the first 20 years following the fire, reaching a plateau, with only two of our sampled trees establishing between 1940 and 1950 (Fig. 3a

Fig. 3. Age structure and percentage of establishment of the two cohorts, as a function of time after fire (years).

and 3b). However, these results should be taken with caution, due to methodological problems in age estimation when sampling at the stump. The majority of trees from Cohort 3 (>85%) established in the first five years following the fire in 1995 (Fig. 3b). Only five trees (13%) established thereafter, with the last in 2002, seven years after the fire (Fig. 3a and 3b).

Comparison of measurements between Cohorts 2 and 3 according to cambial age

Mean annual increment in DGH for Cohort 2 increased, with a sigmoidal trend typical of juvenile growth, starting from 0.9 mm at year 0 and reaching its maximum around year 34, with a 4.5 mm increment, which was maintained up to 39 years of age (Fig. 4, top left panel). It then started decreasing and stabilized around year 53 at 2.9 mm/year up to a cambial age of 66 years. For Cohort 3, mean annual DGH increment increased steadily, surpassing that of Cohort 2 from the fourth year of cambial age and reaching its maximum, 3.9 mm/year, at the end of the time series, at cambial age 15 (Fig. 4, top left panel). Cumulated DGH of Cohort 3 remained slightly lower than that of Cohort 2 up to cambial age 6, starting with a value of 0.6 mm at age 0 and reaching a maximum at age 13 (27.5 mm). The decrease in mean cumulated DGH for cambial age 14 and 15 is likely an artifact due to the small number of samples at the end of the series (less than five) and their smaller diameters (Fig. 4, right panel). This problem is common to the end of all the series studied. At age 13, the cumulated DGH for Cohort 2 was only 17.8 mm, thus almost 10 mm smaller than that for Cohort 3.

Mean annual height increment for Cohort 3 increased from the first year, starting from 0.07 m/year (similar to Cohort 2) and reaching its maximum, 0.20 m/year at cambial age 13 (more than double that of Cohort 2 at the same cambial age).

After an initial period of limited increase, the mean cumulated height of Cohort 2 started to increase more steadily from cambial age 14, exceeding 8.3 m by cambial age 50 and reaching 11.3 m at cambial age 66 (Fig. 5, top right panel). For Cohort 3, the cumulated height always showed higher values than that of Cohort 2, reaching 1.7 m at cambial age 13, when Cohort 2 had a cumulated height of only 1.1 m (Fig. 5, top right panel).

The results of the Wilcoxon test for the comparison of annual and cumulated height growth between the two cohorts are reported in Table 1. From cambial age 4 up to cambial age 14, Cohort 3 had significantly higher annual and cumulated increments in height than Cohort 2. The differences for cambial age 15 were not significant very likely because of the too-small number of samples for Cohort 3 (Table 1). Similarly, the difference in annual increments and cumulated diameter between the two cohorts was generally significant, with higher values for Cohort 3 from the cambial age 5 and 7, respectively (Table 1).

Using stem analysis data, the mean stem volume for Cohort 2, 75 years after the 1920 forest fire, was estimated at more than 70 dm³ and projected to be almost 160 dm³ at 100 years after the fire (data not shown, Côté 2004). If the stand density increased to values near that of nearby closed-crown stands, then we could expect volume yields comparable to that of commercial black spruce stands in the region (about 100 m³/ha, see Parent 1999, as cited in Côté 2004).

Discussion and Conclusions

The growth of two successive tree cohorts, at a site previously occupied by a closed-crown forest, was studied to assess possible changes in the site potential following fire and spruce budworm disturbances. The loss of site potential, relative to nearby sites occupied by the closed-crown forest, is sometimes

Fig. 4. Annual increment in diameter at ground height (DGH, mm/year) and cumulated DGH (mm) plotted against cambial age (years). The points are means with 95% confidence intervals (not reported for the end of the series where there were less than five samples). The number of samples for the two cohorts is reported below each panel.

Fig. 5. Annual increment in height (m/year) and cumulated height (m) plotted against cambial age (years). The points are means with 95% confidence intervals (not reported for the end of the series where there were less than five samples). The number of samples for the two cohorts is reported below each panel.

used as an argument to explain the persistence of stable open lichen woodlands and against their reforestation, without making necessary distinctions based on their origin (e.g., regeneration accident or climatic and edaphic constraint; Côté *et al.* 2012, Mansuy *et al.* 2012). In our research, trees of the most recent cohort (Cohort 3) showed a rapid establishment following fire, and relatively strong growth, without clear signs of growth reduction before the year of sampling. Compared to trees of the initial cohort (Cohort 2), their diameter and height growth were higher, except maybe for the first few initial years of tree establishment, in which they were generally similar. Thus, trees from this open lichen woodland derived from a closed-crown forest do not seem to have a severe reduction in growth potential following the disturbances at their origin. Given the demonstrated conservation of the site potential and the fact that the number of merchantable trees in Cohort 1 was higher than those in Cohort 2 (data not shown, see Côté 2004), it is likely that this site already sustained a volume yield per hectare higher than that currently observed in the field (Cohort 3). Thus, a hypothesis may be advanced, i.e., that the site can sustain again such a timber yield and that regeneration accidents limiting tree establishment do not affect site potential. If our findings are confirmed elsewhere, they may have important implications for reforestation strategies and management policies. For example, our results may contribute to the debate on the possibility and interest of reforestation in these areas to maintain closed-crown forest continuity, for the socio-economic importance of timber sector in Quebec and as means of mitigating climate change through CO₂ fixation by trees.

Spruce budworm outbreak may affect both tree recruitment and growth. Stands regenerated during epidemic periods were

less productive than those established during periods without severe defoliation (Krause *et al.* 2009). This may partly explain the reduced growth of Cohort 2, which was affected by spruce budworm outbreaks during the 1970s and 1980s (data, by calendar year, not shown), however it cannot explain the differences between cohorts during the juvenile phase (Morin and Laprise 1990).

A possible clue is the different age structures of the two cohorts. Cohort 3 showed rapid establishment following a negative exponential, generally in agreement with conifer establishment following fire (St-Pierre *et al.* 1992, Fantin and Morin 2002, Johnstone *et al.* 2009), while Cohort 2 establishment appeared to be more gradual (Fig. 3). However, for black spruce, apparent delayed tree establishment may be due to methodological difficulties in exactly estimating tree age from adult trees. These difficulties may arise from slow growth in the juvenile phase, growth suppression and the formation of adventitious roots along the stem as the depth of the moss layer covering the forest floor increases with stand age and the soil subsides under mature tree weight (St-Pierre *et al.* 1992, DesRochers and Gagnon 1997). Growth suppression due to competition for light is not likely for Cohort 2, since its stocking and density was already very low for a mature stand (less than 30% and less than 1100 stems per hectare, respectively; Côté *et al.* 2012). Nonetheless, using the growth rate presented for black spruce in Gutsell and Johnson (2002), the errors associated with sectioning at ground height (e.g., 30 cm above root collar, Cohort 2) rather than the below-ground root collar (Cohort 3) can be roughly estimated as an underestimation of about five to 10 years for Cohort 2, relative to the more precise estimates (root collar and branch whorl count) of Cohort 3. DesRochers and Gagnon (1997) also

Table 1. Results of the Wilcoxon rank-sum test on differences in height and diameter at ground height (DGH) between cohorts, as a function of cambial age

Cambial age	Difference in annual height increment (m-year ⁻¹) (Cohort 3– Cohort 2)	Difference in cumulated height (m) (Cohort 3– Cohort 2)	Difference in annual DGH increment (cm-year ⁻¹) (Cohort 3– Cohort 2)	Difference in cumulated DGH (cm) (Cohort 3– Cohort 2)
0	NA ^a	0.05***	-0.34***	-0.34***
1	0.00	0.00	-0.24*	-0.63***
2	0.01	-0.01	-0.18	-0.81*
3	0.03***	0.02	0.03	-0.77
4	0.04***	0.06**	0.15	-0.63
5	0.05***	0.11***	0.41*	-0.22
6	0.06***	0.18***	0.68***	0.46
7	0.07***	0.25***	1.00***	1.46*
8	0.08***	0.32***	1.09***	2.55**
9	0.08***	0.40***	1.23***	3.78***
10	0.08***	0.48***	1.55***	5.35***
11	0.09***	0.54***	1.71***	6.94***
12	0.08***	0.59***	1.66***	8.52***
13	0.11***	0.61***	1.76***	9.71***
14	0.08** ^a	0.49*	1.51* ^a	7.70 ^a
15	0.05 ^a	0.29 ^a	1.85* ^a	2.10 ^a

Significant differences are reported with the following notation: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. When there are no asterisks, the difference is not significant.

^a Number of observations for Cohort 3 < 5; NA = no observations

observed on average 10 additional growth rings below ground level. In our study, trees from Cohort 2 may have already passed the phase of tree establishment generally characterised by small but rapidly increasing height and diameter increments in absolute value. So, for the 15 years compared with the Wilcoxon test, the unobserved initial annual increments of Cohort 2 may have been even smaller than those considered, accentuating observed differences. Given that uncertainties in height estimation should be much more limited than those for age, when we compare the two cohorts by cambial age correcting for the five to 10 years of age underestimation for Cohort 2, it could be expected that at a given age trees of Cohort 2 may have had even lower heights than those observed. Thus, our estimates of Cohort 2 height may have been optimistic. The possible underestimation of tree ages for Cohort 2 also means that tree establishment may have been rapid and mainly concentrated in the first decade following fire, similar to Cohort 3. Thus, other factors than differences in the age structure (with potential different competition by ericaceous shrubs) should be invoked.

Factors that may help explain the differences in growth of the two cohorts include climate warming and increased N deposition. The usually strong response to N fertilization has confirmed that N-limitation is widespread in vast areas of the boreal forest (Vitousek and Farrington 1997, Hyvonen *et al.* 2008, de Vries *et al.* 2009). One of the main inputs to the N cycle in the boreal forest comes from atmospheric N depositions which are estimated to be around 4–6 kg N·ha⁻¹·year⁻¹ over this area (Ouimet and Duchesne 2009). Given that these inputs have increased over the last century due to anthropogenic activities (Galloway *et al.* 2004, Ouimet and Duchesne 2009, Schlesinger 2009), this can partly explain the difference in growth between the two cohorts (one established in the early 1920s and the other in the late 1990s). In favour of this hypothesis, in a survey of Swedish forest response to increased N depositions, Binkley and Hogberg (1997) report that growth increased by about

30% from the 1950s to 1990s. Comparing sites from northern and southern Sweden, higher N depositions in the southern Norway spruce stands were estimated to be responsible for an increase in tree biomass of 2.0±1.0 kg·m⁻² of C (Hyvonen *et al.* 2008). According to Reich *et al.* (2006), both N availability and low temperatures limit boreal forest growth. In our opinion, the combination of climate warming and higher N availability due to the cumulative amount of N retained in the soil following increased N depositions and the stimulation of N mineralization expected under warmer soils (Rustad *et al.* 2001, Campbell *et al.* 2009) may have acted synergistically to foster early growth of the most recent cohort relative to that of the one established after the 1920 fire. In an experiment combining heating and fertilization, Norway spruce stem growth showed a 25% increase relative to the average growth preceding the treatment (Strömgren and Linder 2002).

This study showed that growth of two successive black spruce cohorts in an open lichen woodland was not reduced following compound disturbances, which resulted in forest cover regression. It is difficult to explain the difference in juvenile growth between the two studied cohorts with a single variable and methodological problems make their comparison subject to some uncertainties. Nonetheless, no sign of growth reduction were evident from Cohort 2 to Cohort 3. Moreover, taking into account a possible underestimation of about 10 years of cambial age for Cohort 2, the difference between the two cohorts would be even increased, in favour of Cohort 3. This paper sets the ball rolling for a discussion on the pertinence of reforestation in this type of open formation, where growth potential is, at least, maintained. Some scientists oppose the reforestation of these areas, citing the low growth of these sites and the short fire return interval. However, there is limited understanding and many uncertainties related to changes in growth of boreal trees subject to successive disturbances and climate change and the management approach we could use (Gaboury *et al.* 2009,

Mansuy *et al.* 2012). According to some authors, scarification may be used to favour tree regeneration, reduce conifer growth check by ericaceous species and ensure the return of productive closed-crown forest stands (Thiffault *et al.* 2004, 2012; Thiffault and Jobidon 2006; Veilleux-Nolin and Payette 2012; Tremblay *et al.* 2013). Afforestation trials may help resolve these issues in a straightforward way. We look forward to the results of this type of experiments, which have been underway in the Saguenay-Lac-St-Jean region of eastern Canada since the early 2000s.

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