Natural root grafting in *Picea mariana* to cope with spruce budworm outbreaks

Roberto L. Salomón, Emilie Tarroux, and Annie DesRochers

Abstract: Spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks cause extensive mortality and growth reductions throughout boreal forests in eastern North America. As tree vulnerability to defoliation remains partially unexplained by tree and stand attributes, we hypothesized that root grafting might attenuate the negative impact of severe defoliation in tree growth. Two experimental sites in the Abitibi-Témiscamingue region dominated by black spruce (*Picea mariana* Mill.) were harvested and hydraulically excavated to study tree growth in 36 trees in relation to root grafting and the last spruce budworm outbreak using dendroecological methods. Root grafts reduced the negative effects of defoliation by maintaining stable growth in connected trees during epidemic periods. Among dominant trees, growth releases immediately after the outbreak were uniquely observed in grafted trees. Among suppressed trees, grafted trees tended to grow more than non-grafted trees when defoliation severity was the highest. Carbohydrate transfers through root grafts and enhanced efficiency to acquire resources may explain the better performance of grafted trees under scenarios of limited carbon supply. This study reinforces the growing body of literature that suggests root grafting as a cooperative strategy to withstand severe disturbances and highlights the key role of root grafting in stand dynamics to cope with periodic outbreaks.

Key words: black spruce (*Picea mariana*), insect defoliation, dendrochronology, root graft, tree growth.

Résumé : Les épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) sont la cause d'importantes réductions de croissance et de mortalité dans la forêt boréale de l'est de l'Amérique du nord. Comme la vulnérabilité des arbres à la défoliation reste en partie inexpliquée par les caractéristiques des arbres et des peuplements, nous avons posé l'hypothèse que le greffage racinaire pouvait atténuer l'impact négatif de défoliations sévères sur la croissance des arbres. Deux sites expérimentaux dominés par l'épinette noire (*Picea mariana* Mill.) ont été récoltés et excavés hydrauliquement dans la région de l'Abitibi-Témiscamingue afin d'étudier la croissance de 36 arbres en lien avec les greffes racinaires et la dernière épidémie de tordeuse par des méthodes dendroécologiques. Les greffes racinaires ont réduit l'effet négatif de la défoliation en maintenant une croissance plus ou moins stable des arbres greffés durant la période épidémique. Parmi les arbres dominants, la reprise de croissance suite à l'épidémie n'a été observée que pour les arbres greffés. Chez les arbres supprimés, les arbres greffés tendaient à avoir une meilleure croissance que les arbres non greffés quand la sévérité de l'épidémie était à son maximum. Les transferts de sucres par les greffes racinaires et l'amélioration de l'efficacité d'acquisition des ressources pourraient expliquer la meilleure performance des arbres greffés dans des conditions d'approvisionnement en carbone limitées. Cette étude renforce la théorie qui suggère le greffage racinaire comme une stratégie de coopération entre les arbres pour résister aux perturbations sévères et met en lumière le rôle des greffes dans la dynamique des peuplements pour faire face aux épidémies.

Mots-clés : épinette noire (*Picea mariana*), défoliation par les insectes, dendrochronologie, greffe racinaire, croissance des arbres.

Introduction

Spruce budworm (*Choristoneura fumiferana* Clem.) is the most damaging insect in boreal forests in eastern North America (Morin et al. 2007). Insect outbreaks have a periodicity of 30–40 years (Boulanger and Arseneault 2004; Boulanger et al. 2012) and cause extensive mortality, e.g., the latest spruce budworm outbreak destroyed up to 238 million m³ of softwood in Quebec (Boulet et al. 1996). Larval feeding on foliage can cause tree growth reductions above 40% (Krause and Morin 1999; Pothier et al. 2005) and, eventually, tree death. Canopy gaps are progressively filled by growth releases of surviving trees, and they trigger recruitment and post-outbreak colonization (Morin 1994). Therefore, spruce budworm outbreaks are widely recognized as main drivers of forest dynamics in eastern North America

(Morin et al. 1993, 2007; Morin 1994; Bouchard et al. 2007; Boulanger et al. 2012; Fierravanti et al. 2015).

The impact of spruce budworm defoliation on tree growth and mortality depends on several factors such as forest composition (Campbell et al. 2008; Colford-Gilks et al. 2012), site characteristics (MacKinnon and MacLean 2004), tree size (Bergeron et al. 1995), and tree age (Taylor and MacLean 2009). Tree vulnerability to outbreaks is crucial to predict forest dynamics and timber yield in boreal forests (Pothier et al. 2005; Bouchard et al. 2007; Morin et al. 2007); yet, knowledge on tree vulnerability is limited in comparison with our understanding of tree susceptibility to budworm outbreaks (Pothier and Mailly 2006; Campbell et al. 2008). Variability in tree growth and mortality following budworm defoliation remains largely unexplained; e.g., stand characteristics accounted for 40%

R.L. Salomón. Forest Genetics and Ecophysiology Research Group, E.T.S. Forestry Engineering, Technical University of Madrid (UPM), Ciudad Universitaria s/n 28040 Madrid, Spain.
E. Tarroux and A. DesRochers. Forest Research Institute, University of Quebec in Abitibi-Témiscamingue (UQAT), 341 rue Principale Nord, Amos, QC J9T 2L8, Canada.
Corresponding author: Roberto L. Salomón (email: roberto.salomon@upm.es).

of the variance in growth reduction in balsam fir (Bergeron et al. 1995; Campbell et al. 2008) and 47% of the total deviation in tree mortality in spruce and fir trees (Colford-Gilks et al. 2012). Similarly, the coefficient of determination between ring-width index and defoliation intensity was below 0.4 and 0.2 in fir and spruce trees, respectively (Pothier et al. 2005, 2012), suggesting a relatively weak relationship between defoliation and tree growth, especially for the latter species (Pothier et al. 2012). These observations point to overlooked factors that might influence tree performance to withstand budworm defoliation and could help to explain why some trees succumb to outbreaks whereas others survive.

Root grafting is a widespread phenomenon observed in many species, about 200 according to Graham and Bormann (1966). However, it might occur much more extensively given that it has received very little attention due to the difficulties to survey belowground tree attributes (Lev-Yadun 2011). Root connections could be beneficial under scenarios of limited carbon supply following outbreaks, as greater acquisition of resources and shared carbohydrate pools within physiologically integrated individuals (see Stone and Stone (1975) and Fraser et al. (2005, 2006) and references therein) could attenuate the negative impact of defoliation in tree growth and mortality. Root grafting is gaining attention as an adaptive strategy to face disturbances and environmental hazards, as cooperative behaviour could limit tree mortality and hinder establishment of new species (Eis 1972; Tarroux and DesRochers 2011). Nevertheless, despite the potential role of root grafting to cope with outbreaks, and more widely, in stand dynamics in boreal forests in eastern North America, there is no literature assessing the relationship between budworm outbreaks and root grafting.

In this study, we test the hypothesis of root grafting as a mechanism to survive budworm defoliation. We evaluated differences in stem growth between grafted and non-grafted trees following a spruce budworm outbreak. Dominant and suppressed trees were independently compared to avoid any related effect of tree dominance (Eis 1972; Baret and DesRochers 2011). Additionally, we assessed a potential temporal correlation between defoliation intensity and formation of root grafts. We excavated two sites dominated by black spruce (*Picea mariana* Mill.) that were severely defoliated by the last spruce budworm outbreak that affected the Abitibi-Témiscamingue region (Morin et al. 1993). We predicted that the negative effect of budworm outbreak on tree growth would be lessened in grafted trees in comparison with non-grafted trees and that suppressed trees would benefit to a greater extent, as they would be supported by connected dominant trees.

Materials and methods

Study site and fieldwork

The study was performed at two sites dominated by black spruce naturally regenerated and located in the western balsam fir – paper birch (*Abies balsamea* (L.) Mill. – *Betula papyrifera* Marshall) bioclimatic domain (Grondin et al. 1996), near Amos city (Abitibi-Témiscaminge region, Quebec, Canada; latitude, 48°34′N; longitude, 78°07′W). Mean annual precipitation during the last 30 years was 918 mm (670 mm of rainfall and 248 mm of snowfall), and mean daily temperature was 1.2 °C, with an average of 2334 degree days above 0 °C (Environment Canada 2010). Clayey soils and fine-grained sediments are associated with glaciolacustrine deposits from the maximum post-Wisconsonian extension of proglacial lakes Barlow and Objibway (10 100–8 000 years B.P.; Veillette 1994). Both stands were not subjected to any silvicultural treatment and originated from stand-replacing fires. Stand characteristics of the surveyed sites are shown in Table 1.

In total, 154 trees were felled and excavated in summer 2011, and 97 of them were alive. Dead trees were discarded, and 36 trees were selected for this study (18 trees per site). Twelve pairs of grafted trees and 12 non-grafted trees were selected (six pairs of grafted trees and six non-grafted trees per site). Sample size was

Table 1. Characteristics of two excavated plots dominated by black spruce naturally regenerated.

Characteristic	Site 1	Site 2
Stand density (trees·ha⁻¹)	4727	2250
Dominant height (m)	13.3	18.6
Excavated area (m²)	110	200
No. of excavated trees	93	61
No. of excavated living trees	52	45
No. of grafted trees	34	35
Mean diameter (cm)	12.2±1.3	15.8±1.6
Mean tree age (years)	73.7±5.9	76.3±2.4

Note: The numbers of excavated trees, excavated living trees, and excavated grafted trees differ from the number of surveyed trees for this study (18 per site). Tree diameter (at ground level) and tree age refer to surveyed trees at the time of excavation in 2011, and values are presented as mean ± standard error.

limited by the number of non-grafted trees given that most excavated trees were grafted (see Table 1), and non-grafted trees in the edge of the excavated area were discarded. Non-grafted trees were selected according to their spatial location to confirm that their roots do not grow beyond the excavated area and do not form grafts. Each pair of grafted trees was composed of a dominant tree and a suppressed tree to evaluate different responses to defoliation depending on tree size (see Baret and DesRochers (2011)). Of the 12 non-grafted trees, six trees were dominant and six were suppressed. Trees were felled with a chainsaw, and cross-sectional disks were cut at ground level (0 m) and at breast height (1.30 m) for age determination. To allow hydraulic excavation of the root systems, plots were located near a pond, and a forestry water pump (Mark III, Wajax, Lachine, Quebec) was used to expose the root systems. The excavated areas covered 110 and 200 m² (Table 1). Sketches depicting trees, roots, and grafts were drawn by hand. Detailed protocols for hydraulic excavation and field sampling can be found in Tarroux and DesRochers (2010).

Laboratory work

Cross-sectional disks were air-dried and progressively sanded (80–400 grit paper) to clearly reveal growth rings. Razor blades and white chalk were punctually used for better accuracy in particularly problematic sections. Root grafts were dissected with a bandsaw to examine their anatomy, and uniquely functional intraspecific grafts, involving morphological union of cambium, phloem, and xylem (Graham and Bormann 1966), were considered for analyses. To estimate the period of graft formation within each pair of grafted trees, the first and the last years of graft formation were determined among several root disks along the root graft, as in Tarroux and DesRochers (2010). Cross-sectional disks at ground level were used for ring-width measurements, and disks at breast height were used to cross-date and validate tree age in case of aberrant features (e.g., eccentric growth and missing or discontinuous growth rings). Ring-width series from the center pith to the outermost ring of each disk were measured on four radii (when possible) using a unislide measuring table (Velmex Inc., Bloomfield, New York) interfaced with a computer. The first measurement radius was positioned at 22.5° from the longest cross-sectional disk radius, and the three consecutive measurement radii were perpendicular to the first one (Zarnovican 1985). COFECHA (Grissino-Mayer 2001) and TSAPWin (RINNTECH, Engineering and Distribution, Heidelberg, Germany) programs were used to verify tree-ring radial growth series. Ring-width chronologies were standardized using ARSTAN (Grissino-Mayer 2001) to minimize related effects of tree size and age, which were out of the scope of this research.

Statistical analyses

Spruce budworm outbreak and root grafting intensity

To detect the last budworm event at the study sites, the OUTBREAK program was used (v.1.50; Holmes and Swetnam 1996). The program

identifies occurrence of spruce budworm attacks in series of annual tree-ring width measurements and quantifies the length and severity of the outbreak for each tree. A control non-host chronology based on three naturally regenerated jack pine (*Pinus banksiana* Lamb.) stands located near the experimental plots (Tarroux and DesRochers 2010) was used to detect growth reductions due to spruce budworm by comparison of radial growth curves between host and non-host species. The percentage of grafted trees was calculated as the cumulative percentage of trees that started to form root grafts (and remained connected) over the 12 pairs of grafted trees. The number of grafts being formed was calculated as the yearly frequency of graft formation among grafted trees.

Effect of dominance status and root grafting on tree growth

Statistical analyses were performed in R (v.3.1.1), and model assumptions were tested and verified. To analyse how tree growth was affected by the outbreak according to tree status, we compared tree growth before, during, and after the 1970s outbreak between dominant and suppressed trees. First, as the period of maximum defoliation intensity lasted 6 years, cumulative radial growth of the 6 years before, during, and after the outbreak was compared using a linear mixed model with the lme function in the nlme library (Pinheiro et al. 2008). Linear mixed models differentiate between fixed and random effects to consider the error structure for longitudinal, clustered, or repeated measurements. Tree status (dominant or suppressed), period (before, during, and after the outbreak), and their interaction were fixed as categorical factors (model CUM_STATUS). To avoid sacrificial pseudoreplication error (data from different experimental units are used as independent replicates and pooled in the same analysis; Hurlbert 1984), radii were nested within their corresponding tree, and trees were nested within their corresponding site and were considered as random factors. Backward selection tested the model containing all the variables (global model) and removed the least significant variable until all variables included in the model were significant ($p < 0.05$). Second, we studied yearly radial growth using a linear mixed model with the lme function and the lmer function in the lme4 library (model YEAR_STATUS; Bates et al. 2014), in which tree status, year, and their interaction were fixed as categorical factors. Radii, trees, and sites were nested random factors. Because sampled trees were not even aged, only the time span since the emergence of the youngest tree was considered (from 1967 to 2011). The temporal series were split into shorter temporal sets of 5 years to avoid a qualitative factor with 45 categories. As yearly growth values are not independent from one another (growth of year t is affect by growth of year t–1), a first-order autoregressive correlation structure was used (Grissino-Mayer 2001; Pinheiro et al. 2008). To detect growth differences between dominant and suppressed trees within single years, contrasts were performed using the glht function in the multcomp library (Hothorn et al. 2008).

To assess the influence of root grafting on tree growth in relation to the outbreak, dominant and suppressed trees were separately analysed to concentrate the analysis on the differences between grafted and non-grafted trees within the same stratum. To compare cumulative and yearly growth between grafted and non-grafted trees, linear mixed models were similarly adjusted to CUM_STATUS and YEAR_STATUS by substituting the categorical factor tree status by grafting presence (grafted or non-grafted) in both dominant (CUM_DOM and YEAR_DOM) and suppressed (CUM_SUP and YEAR_SUP) trees.

Results

The last spruce budworm outbreak negatively affected tree growth in the 1970s, reaching a maximum of infested trees between 1973 and 1978 (up to 86%; Fig. 1). Among the 12 pairs of grafted trees,

the cumulative percentage of grafted trees increased from 42% to 58% during the period of maximum defoliation (Fig. 1). The yearly percentage of infested trees was directly related to the number of grafts being formed during the same year (Pearson's correlation = 0.429; $p = 0.002$). This correlation progressively improved considering lagged regressions up to 7 years (Pearson's correlation = 0.649; $p < 0.001$).

Dominant and suppressed trees established at the same time ($p = 0.23$), and tree basal diameter before the outbreak (1972) was similar between dominant and suppressed trees ($p > 0.05$). Eventually, dominant trees were bigger than suppressed trees at the time of excavation in 2011 ($p < 0.001$), with the mean tree radius at ground level being 93.2 ± 5.4 mm and 46.9 ± 4.5 mm (mean ± standard error) for dominant and suppressed trees, respectively. The cumulative radial growth of the 6 years before, during, and after the outbreak was not influenced by tree status (dominant or suppressed) or its interaction with the surveyed period ($p > 0.05$). Growth decreased during the outbreak and increased after it ($p < 0.001$). Results on yearly radial growth before, during, and after the outbreak corroborate the results obtained for cumulative growth (Fig. 2). Yearly radial growth decreased from 1973 to 1978, with the maximum growth reduction encountered in 1976; immediately after the outbreak, radial growth increased to levels from before the outbreak (Fig. 2). Suppressed trees showed significant growth reductions from 1990 to 2005 ($p < 0.05$; Fig. 2; Supplementary Table S1[1]).

Among dominant trees, cumulative growth of grafted trees showed no decrease during the outbreak ($p = 0.487$), and a significant growth increase was observed after it ($p = 0.016$; Fig. 3a). Contrarily, cumulative growth decreased during the outbreak for dominant non-grafted trees ($p < 0.001$), and remained constant after the outbreak ($p = 0.119$; Fig. 3a). Differences in cumulative growth between dominant grafted and non-grafted trees within the same period were not observed (Fig. 3a); however, non-grafted trees tended to have higher growth before the outbreak ($p = 0.067$). Yearly growth of dominant grafted trees was lower than the growth of dominant non-grafted trees in 1971 and 1972 (Fig. 4a; Supplementary Table S2[1]), whereas it was similar during and immediately after the outbreak. Growth of grafted trees increased to higher rates than non-grafted trees in 1988 and 1989, whereas non-grafted trees showed higher growth in 2007 (Fig. 4a).

Among suppressed trees, cumulative growth of grafted trees remained roughly constant before, during, and after outbreak (Fig. 3b). Cumulative growth of non-grafted trees was significantly lower during outbreak event compared with before the defoliation ($p < 0.001$; Fig. 3b). Within the same period, cumulative growth of suppressed grafted and non-grafted trees was similar (Fig. 3b); however, grafted trees tended to have higher growth during the outbreak ($p = 0.083$). Differences in yearly radial growth between grafted and non-grafted trees within the suppressed stratum were only significant in 1990 when grafted trees exhibited larger growth than non-grafted trees (Fig. 4b; Supplementary Table S2[1]).

Discussion

Root grafts to cope with outbreaks

Despite the fact that grafted and non-grafted trees were even sized prior to the outbreak, cumulative growth of grafted trees remained roughly stable during the outbreak relative to predisturbance values, whereas non-grafted trees suffered growth reductions for both dominant and suppressed statuses. Furthermore, cumulative growth of dominant grafted trees was released immediately after the outbreak, whereas growth of dominant non-grafted trees after the outbreak did not increase relative to the outbreak period. These results suggest that root grafts attenuate the effect of insect defoliation in tree growth. Grafted trees can share resources, namely water and

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0121.

Fig. 1. Grafting occurrence in two excavated sites dominated by black spruce, and spruce budworm outbreak intensity quantified by the percentage of defoliated trees. Percentage of infested trees was obtained using the OUTBREAK program comparing tree-ring series between host (black spruce) and non-host (jack pine) species. The percentage of grafted trees is calculated as the cumulative percentage of trees that started to form root grafts (and remained connected) over the 12 pairs of grafted trees. The number of grafts being formed exhibits the yearly frequency of graft formation among grafted trees.
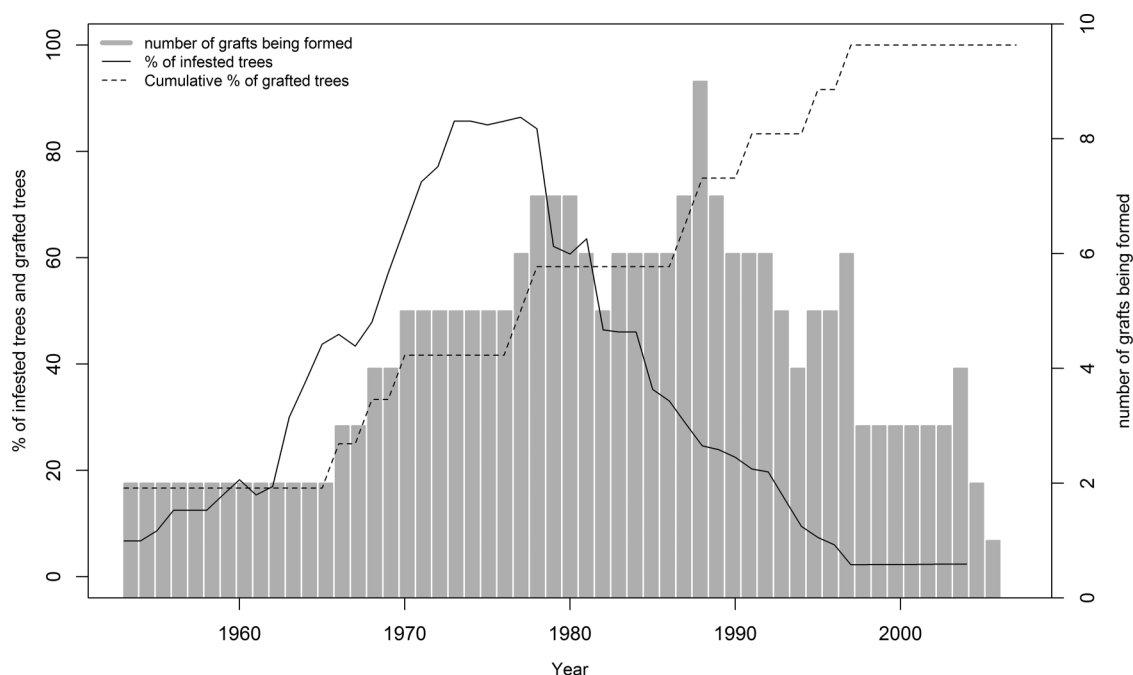

Fig. 2. Yearly radial growth of dominant and suppressed trees in the excavated sites. The surveyed period was split in temporal sets of 5 years. The vertical shaded area indicates the outbreak period (1973–1978). Growth estimates and standard errors are depicted. Symbols indicate a significant difference between dominant and suppressed trees: ***, <0.001; **, <0.01; *, <0.05; •, <0.1.
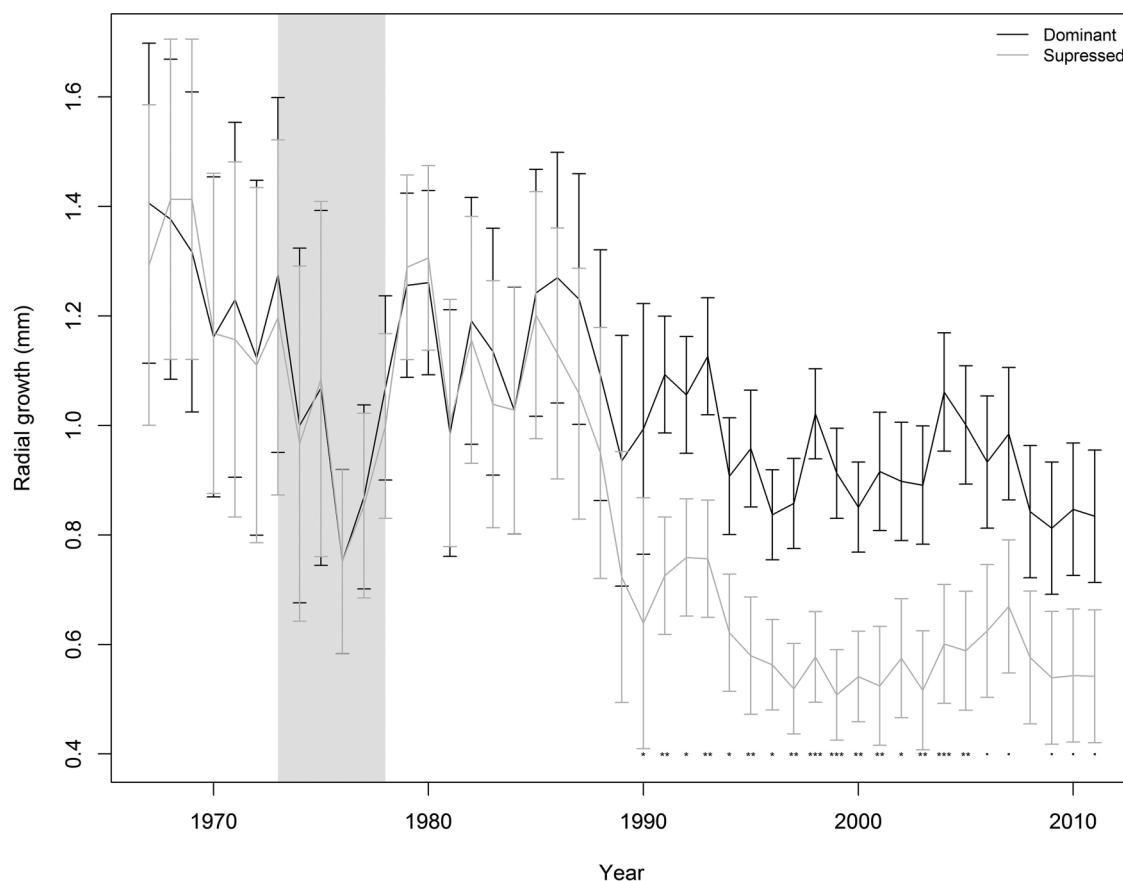
Fig. 3. Cumulative radial growth of grafted and non-grafted trees among (*a*) dominant and (*b*) suppressed statuses before (from 1967 to 1972), during (from 1973 to 1978), and immediately after (from 1979 to 1984) the outbreak. Different lowercase letters indicate significant differences ($p < 0.05$) in cumulative growth across the surveyed periods and between grafted and non-grafted trees.
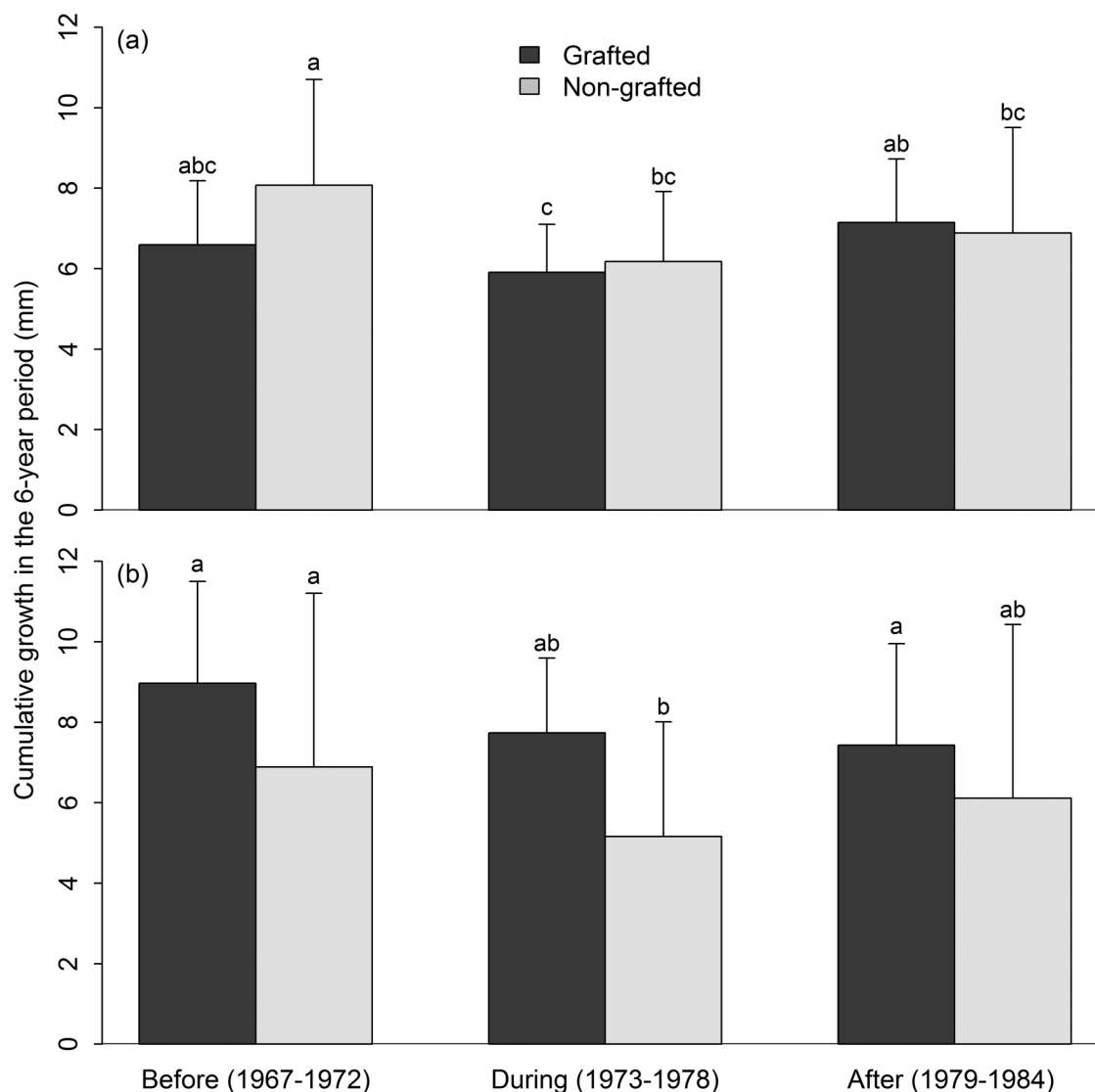
nutrients (Stone and Stone 1975; Fraser et al. 2006), and communal root systems allow maximum efficiency to capture and distribute resources among connected trees that may lead to increased stem growth (Tarroux and DesRochers 2010). Moreover, as carbohydrates can be transferred through root grafts, larger and shared carbohydrate pools may contribute to the better performance of grafted trees to face outbreaks after carbon depletion that firstly occurs in non-grafted trees (see fig. 1 in Fraser et al. (2006)). An attenuated effect of budworm outbreak in grafted trees supports the hypothesis that common functioning of genetically distinct individuals can overcome the death of weaker trees (Basnet et al. 1993; DesRochers and Lieffers 2001; Fraser et al. 2005, 2006; Tarroux et al. 2010) as a competitive strategy to impede recruitment of different species (Tarroux and DesRochers 2011). Consistently, graft formation lagged behind the outbreak by up to 7 years, suggesting that defoliation might be the underpinning trigger of graft formation in black spruce (Loehle and Jones 1990). However, this is not necessarily a cause–effect relationship, and manipulative tests may help to further examine this idea.

Notwithstanding, significant differences between grafted and non-grafted trees were not observed before, during, or immediately

after the outbreak, indicating a moderate influence of root grafting in tree growth in response to defoliation. In any case, it is worth noting that during the epidemic period (1973–1978), weaker trees that eventually became suppressed tended to have greater growth if grafted ($p = 0.083$). This significance level ($\alpha = 0.10$) might be reasonable to detect actual differences given the limited sample size in this study, constrained by methodological difficulties related to the excavation of forest soils. Similarly, limited sample size also reduces the likelihood that a significant result reflects an actual effect, and differences observed in this study should be taken with caution.

On the other hand, although root grafting seems favourable to persist under frequent outbreak regimes, drawbacks of root grafting in stem growth were detected under more favourable conditions, i.e., prior to outbreak and after stand recovery, when carbon supply was not curtailed by insect defoliation. Among dominant trees, yearly growth reductions of grafted trees were observed immediately before (1971 and 1972) and long after (2007) the outbreak. Tarroux and DesRochers (2011) observed that during periods of root graft formation, grafting tended to reduce radial growth in jack pines as root grafting is an energetically costly process. Carbon invest-

Fig. 4. Differences in yearly radial growth between grafted and non-grafted trees among (*a*) dominant and (*b*) suppressed statuses. The surveyed period was split in temporal sets of 5 years. The vertical shaded area indicates the outbreak period (1973–1978). Growth estimates and standard errors of the contrasts are depicted. Symbols indicate a significant difference between grafted and non-grafted trees: **, <0.01; *, <0.05; •, <0.1.

ment for graft constitution and callus formation might contribute to reduce growth of grafted trees immediately before and long after defoliation, when outbreak may not compromise tree growth. Furthermore, carbohydrate supply from dominant to suppressed connected trees — and even grafted stumps and roots without aerial counterparts (DesRochers and Lieffers 2001; Tarroux and DesRochers 2010; Tarroux et al. 2010; Salomón et al. 2016) — might also constrain stem growth of dominant grafted trees under favourable conditions. In this line, vertical development of stems and crowns to compete for aboveground resources might be unnecessary among trees extensively and horizontally connected, and so non-competitive forces may govern growth dynamics among physiologically connected individuals (Basnet et al. 1993; Baret and DesRochers 2011) favouring carbon allocation to storage. A conservative carbon economy may reduce tree growth under favourable conditions (see Wiley and Helliker (2012), but see Palacio et al. (2014)); however, in the long term, it could be beneficial to cope with budworm outbreaks, hence reflecting a trade-off between aboveground performance and persistence among grafted trees. In summary, reduced growth of dominant grafted trees not constrained by budworm defoliation might be partially explained by (*i*) carbon investment in graft formation, (*ii*) carbon donation to maintain suppressed grafted trees, and (*iii*) a conservative strategy of carbon storage.

Budworm outbreak and stand dynamics

Balsam fir and white spruce (*Picea glauca* (Moench) Voss) are commonly the preferred hosts of the spruce budworm (Morin et al. 2007); even so, the last outbreak in Quebec caused defoliation of 55 million ha of black spruce stands (Fierravanti et al. 2015). In the surveyed sites, 85% of the black spruces were defoliated between 1973 and 1978, reaching rates of defoliation as high as in fir-dominated forests, with maximum growth reductions in 1976. Our results corroborate the closest study performed in Lac Duparquet (Abitibi region, Quebec) in white spruce in which important growth reductions occurred between 1973 and 1977 (Morin et al. 1993). Similarly, insect defoliation in black spruce were noticed by dendrochronology and photointerpretation in lakes Libéral and Onatchiway between 1976 and 1979 (Krause and Morin 1999) and in Lac Lamandonis around 1980 (Bouchard et al. 2007). At a wider spatial scale, this event corresponds to the well-documented last spruce budworm outbreak in Quebec in the 20th century (e.g., Morin et al. 1993, 2007; Krause and Morin, 1999; Bouchard et al. 2007; Simard et al. 2008; Boulanger et al. 2012; Fierravanti et al. 2015).

Tree mortality following periodic outbreaks results in canopy gaps that govern recruitment dynamics and tree growth patterns in boreal forests in eastern Canada (Morin 1994; Bouchard et al. 2007). In the surveyed sites, significant growth reductions during

the outbreak and growth releases immediately after it were observed in both dominant and suppressed trees. Before the outbreak, trees that would become dominant and suppressed at the time of excavation (2011) were even sized, but the outbreak might have triggered differential growth between them. As the impact of budworm defoliation in stand development lengthens far beyond the outbreak (Colford-Gilks et al. 2012), differential growth between potential dominant and suppressed trees (1990–2005) lagged 12 years behind the period of highest outbreak intensity (1973–1978). Accordingly, the post-outbreak impact in balsam fir has been observed to persist during wide temporal spans, e.g., 6 years in relation to tree growth (Pothier et al. 2005) and 11–15 years (Taylor and MacLean 2009) and up to 35 years in relation to tree mortality (MacLean and Andersen 2008). Enhanced carbon allocation to storage (Salomón et al. 2016) and use of starch reserves to fuel metabolism over periods of limited carbon supply (Bhupinderpal-Singh et al. 2003; Aubrey et al. 2012) and to resprout in cases of canopy dieback is the life strategy of species subjected to frequent disturbance regimes (Bond and Midgley 2001). In the specific case of black spruce, the use of starch reserves by roots can extend over time for up to 6 years, as demonstrated by radiocarbon signatures ($\Delta^{14}C$; Czimczik et al. 2006; Schuur and Trumbore 2006). Thus, a conservative allocation pattern of carbohydrates in black spruce could contribute to the delayed effect of defoliation in stem growth that eventually led to the current stand structure.

Beyond the outbreak, yearly growth of dominant grafted trees was higher relative to dominant non-grafted trees in 1988 and 1989; subsequently, growth of suppressed grafted trees was higher relative to suppressed non-grafted trees in 1990. As similarly observed in lodgepole pine after manipulative shading (Fraser et al. 2006), suppressed grafted trees may have benefited from the preceding (and comparatively enhanced) growth of dominant grafted trees by carbohydrate transfer from higher to lower strata, i.e., carbon source and sink, respectively. Again, the positive effect of root grafting in stem growth was observed after several years of limited carbon supply, coinciding with the first symptoms of carbon depletion exhibited by suppressed trees.

Conclusions

Root grafts slightly attenuated the negative effects of defoliation in black spruce during and immediately after spruce budworm outbreak. Moreover, graft formation lagged behind insect defoliation by 7 years, suggesting that root grafting might be fostered under scenarios of limited carbon supply. Root grafting may be a cooperative strategy to face insect defoliation, and it might play an important role in stand dynamics in areas subjected to periodic outbreaks. The classic concept of trees as discrete identities competing for light and soil resources should be revisited.

Acknowledgements

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