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Original article

Growth and mortality of trembling aspen (*Populus tremuloides*) in response to artificial defoliation

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ABSTRACT

To simulate the effects of forest tent caterpillar (FTC) defoliation on trembling aspen growth and mortality, an artificial defoliation experiment was performed over three years in young aspen stands of northwestern Quebec. Defoliation plots of 15 × 15 m were established on three sites, together with associated control stands of pure trembling aspen. In 2007, root collar diameters were measured and positions of all trees were mapped prior defoliation. Severe FTC defoliation was simulated for three successive years (2007–2009) by manually removing all leaves from all but 7–10% of the trees present in the defoliation plots. Yearly surveys of growth and mortality were conducted until 2010 to evaluate defoliation effects on defoliated as well as surrounding undefoliated trees. In absence of other factors, growth and mortality of trembling aspen decreased and increased, respectively, after defoliation. Our study further revealed that small diameter trees died after one year of artificial defoliation, while larger-diameter trees died after repeated defoliations. Distributions of tree mortality tended to be aggregated at small scales (<5 m), corroborating gap patterns observed in mature stands following FTC outbreaks. This experiment revealed that trembling aspen mortality can be directly attributed solely to defoliation. Repeated defoliations during FTC outbreaks have the potential to profoundly modify stand productivity and structure by reducing tree growth and increasing tree mortality in the absence of predisposing factors.

1. Introduction

In boreal deciduous and mixedwood forests of North America, the forest tent caterpillar (*Malacosoma disstria* Hübner) (FTC) is an important epidemic insect and voracious defoliator of various deciduous tree species, including trembling aspen (*Populus tremuloides* Michx.), which is its preferred host (Fitzgerald, 1995). With recurrence every 9–13 years (Cooke and Lorenzetti, 2006), FTC outbreaks last from 1 to 6 years (Cooke et al., 2009) and can occur as far as 54°N in Quebec (Huang et al., 2008). FTC defoliation reduces tree growth (Hildahl and Reeks, 1960; Hogg et al., 2002a) and stand productivity (Bergeron and Charron, 1994; Candau et al., 2002; Hogg and Schwarz, 1999). Such defoliation generally induces reallocation of trembling aspen carbohydrate reserves to produce photosynthetic tissues such as new leaves (Hogg et al., 2002b; Jones et al., 2004; Reichenbacker et al., 1996). Tree mortality that follows repeated FTC defoliations has been more frequently associated with predisposing, inciting and contributing factors (see Frey et al., 2004), such as climate (Hogg et al., 2008), stand age (Brandt et al., 2003; Sutton and Tardif, 2007), wildlife damage (Peterson and Peterson, 1992), wood-boring insects (Hogg et al., 2002a) or fungal pathogens (Brandt et al., 2003) rather than with FTC defoliation itself (Brandt et al., 2003; Candau et al., 2002; Churchill et al., 1964; Man and Rice, 2010; Moulinier et al., 2011).

Trembling or quaking aspen is the most widely distributed tree species in North America (Peterson and Peterson, 1992), if not globally. It is a fast-growing species that dominates early successional stages following a stand-replacing disturbance (Chen and Popadiouk, 2002) and is both nutrient-demanding and shade-intolerant (Burns and Honkala, 1990). Thus, trembling aspen is an important pioneer species in many boreal forest ecosystems, which provides wood products, wildlife habitat, carbon sequestration and many other appreciable resources and ecological services. Several studies have experimentally simulated insect defoliation in trembling aspen and hybrid poplars under controlled conditions to gain a better understanding of tree growth responses (Hodson, 1981; Kosola et al., 2001; Osier and Lindroth, 2004; Reichenbacker et al., 1996), effects on tree physiology, including stomatal

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conductance, leaf water potential, hydraulic conductance, nitrogen uptake, root demography and white tree ring formation (Gálvez and Tyree, 2009; Hart et al., 2000; Hogg et al., 2002b; Kosola et al., 2001), the effects of tree genotype (Osier and Lindroth, 2004; Reichenbacker et al., 1996), and individual insect performance and insect population dynamics (Kaitaniemi et al., 1999; Parry et al., 2003). Yet, few experiments have examined the effects of repeated defoliation during successive years (Kaitaniemi et al., 1999; Kosola et al., 2001) and none has documented the corresponding tree mortality.

Following severe disturbances (i.e., fire or clear-cutting) or the removal of apical dominance (Farmer, 1962), trembling aspen mostly regenerates via asexual reproduction through root suckering (Frey et al., 2004) from the residual root system of the previous stand. Suckers are produced on mother roots and, in turn, can develop their own roots to become independent trees (Brown and DeByle, 1987). Otherwise, suckers can remain interconnected their whole life through the common parental root system which they share (DesRochers and Lieffers, 2001a) and can interconnect with genetically different aspen clones through root grafting (Jelínková et al., 2009). Therefore, these clonal and physiological characteristics suggest that aspen stands could be considered as large physiological units of interconnected and genetically diversified trees (Jelínková et al., 2009) rather than individual trees or genetically uniform clones, as has been previously believed. Many would agree that interconnections between trees has great ecological significance (Moulinier et al., 2011), but few studies have clearly demonstrated the effects of root connections on tree physiology (see Tarroux and DesRochers, 2011 on Pinus banksiana). A recent experimental study of Baret and Desrochers (2011) did show, however, that interconnected suckers of trembling aspen could physiologically interact through root connections and even exhibit compensatory photosynthesis to support respiration costs of artificially defoliated suckers. Further, the contributions made by aspen suckers that are produced after disturbance can support respiration costs of the large parental root system upon which they grow, but high sucker densities and leaf area are required to maintain such important underground biomass (DesRochers and Lieffers, 2001b). When total leaf area of interconnected suckers becomes insufficient to compensate for respiratory costs of the communal root system (e.g., after defoliation), some suckers and a portion of the root system must therefore die off to balance the photosynthetic capacity of the aerial biomass (Chen and Popadiouk, 2002; DesRochers and Lieffers, 2001b). Given the dynamics associated with such interconnections in aspen stands, effects of simulated FTC defoliations on trembling aspen mortality and growth were investigated.

The first postulate was that, in absence of other influencing factors such as extreme weather events, insects, fungal pathogens, and mammals, differences in the response of mortality and growth that were expected between defoliated and control trees should be mostly attributable to defoliation itself. Our major hypothesis was that annual mortality of trembling aspen should increase, while growth should decrease, from the first to subsequent years of artificial defoliation. Defoliation was also expected to affect the response of undefoliated trees that were situated close and potentially interconnected to defoliated ones. Because of compensatory photosynthesis, such undefoliated trees were expected to exhibit increased growth after the first year of artificial defoliation. However, repeated defoliation should severely increase the imbalance between aerial and underground biomass of interconnected trees and should negatively affect both defoliated and undefoliated trees. As it is expected to be the case for defoliated trees, growth and mortality of undefoliated and surrounding trees were expected to decrease and increase, respectively, after multiple years of artificial defoliation. Finally, based on the distance between trees, the potential interconnection of trees through clonal establishment or root grafting could lead to aggregative mortality, as suggested from patterns of canopy gap formation described in young (Reinikainen et al., 2012) and mature stands (Kneeshaw and Bergeron, 1998; Moulinier et al., 2011). Our related hypothesis was that spatial mortality of trembling aspen observed following artificial defoliation should tend to be aggregative and, therefore, spatially correlated as opposed to random. To achieve these objectives, a three-year-long field experiment was conducted in young aspen stands of the boreal northwestern Clay Belt of Quebec, Canada.

2. Materials and methods

2.1. Study area

This study was conducted in the Harricana Teaching and Research Forest, which is located 150 km northeast of Rouyn-Noranda, northwestern Quebec (Fig. 1). Located on clay soils that originated from lacustrine deposits of the proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977), the study area is characterised by a flat landscape and low elevations (300 m). The continental climate has cold, dry winters and short, mild summers. The vegetation consists of discontinuous mixedwood forest that is dominated by trembling aspen, white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.) and jack pine (*Pinus banksiana* Lamb.).

2.2. Experimental design

Three 8-year-old pure stands of healthy aspen were selected at the onset of the 2007 growing season. They were similar in terms of soil type, topography, drainage class, tree age and density, and had originated from clear-cuts made in December 1998. All stands that had regenerated from these cuts were manually brushed in 2006 to remove competitive vegetation (mostly *Alnus* spp.), thereby minimising effects of interspecific competition on future growth and mortality of aspen. The three stands were spaced about 600 m apart.

The experiment was considered a randomised block design with repeated measures (years) and four treatments within each block: artificially defoliated trees (ArtDefol); control undefoliated trees within artificial defoliation plots (CtrlTrees); control undefoliated trees in an undefoliated buffer zone surrounding the artificially defoliated plots (CtrlBuff); and a control plot (undisturbed trees in an adjacent plot within a block; CtrlPlot).

In each of the three stands, one ArtDefol plot and one CtrlPlot were assigned, with the paired plots forming a statistical block. The plots (Appendix A) were about 25 m apart and measured 15 by 15 m (225 m^2). One edge of the plots was next to the logging road and facing south to allow for similar light incidence in each block. The three remaining sides of the plots were formed by the regenerated stands, with no change in stem densities and which acted as a buffer zone. On three sides of the ArtDefol plots, the first 5 m of the buffer zone were considered as CtrlBuff.

The artificial defoliation treatment was repeated over three successive years (2007, 2008, 2009), and consisted of clipping the leaves from all but 7–10% of the trees. The unclipped trees in the ArtDefol plots, termed CtrlTrees, were located close to the center of each of the nine 5 by 5 m sub-plots composing a plot. Artificial defoliations were completed during the last two weeks of June, about when the leaves had reached full expansion, which is consistent with the timing of maximum food intake by FTC under natural conditions (Hodson, 1941). To further mimic natural

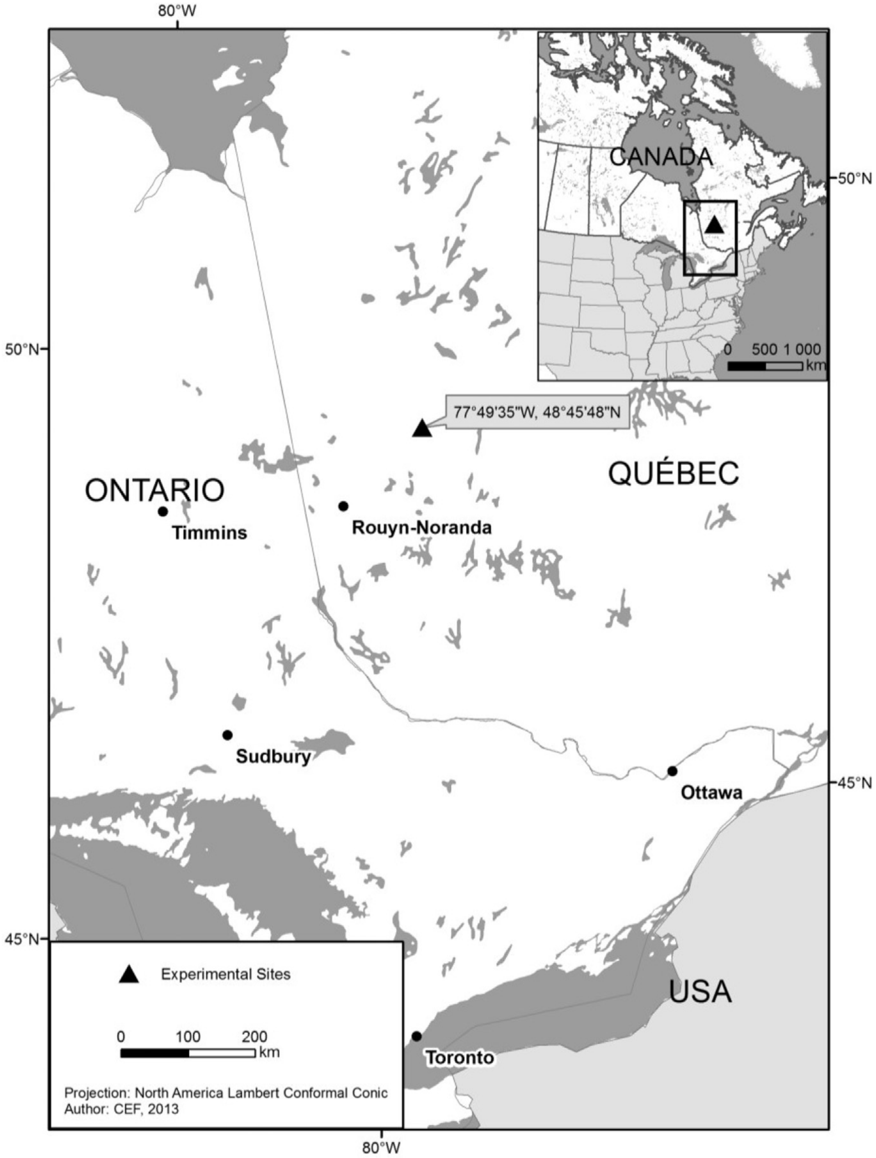

Fig. 1. Location of the experimental sites within the northwestern Clay Belt of Quebec (Canada).

defoliation by the insect, petioles were left intact on branches. Clipped leaves were removed from the plots and discarded. Under natural conditions, undigested leaf material would normally return to the ground as frass, which serves as a source of microbial inoculum and nutrients that can promote soil processes and plant growth (Frost and Hunter, 2004; Kagata and Ohgushi, 2012). Given that the clipped material had not undergone processing through insect guts, and that we could not find in the literature what confounding effect might have resulted from leaving the clipped material in place, we chose to remove it.

2.3. Data collection and analyses

Root collar diameter of all trees was measured in the plots at the onset of each growing season in 2007, 2008, 2009, and 2010. These measurements allowed us to calculate root collar diameter growth for 2007, 2008 and 2009 for all trees that were alive in the subsequent year. All dead trees were noted, measured, and mapped each year.

Linear mixed-effect models (Pinheiro et al., 2008; Pinheiro and Bates, 2000) were performed to analyse annual mortality rate, root collar diameter growth, and root collar diameter of dead trees as a function of treatment, year, and their interaction, i.e., treatment × year. Log-transformation was performed on the response variables (annual mortality rate, root collar diameter growth, and root collar diameter of dead trees) to satisfy assumptions of normality and homoscedasticity. Block was considered as a random effect in the annual mortality model, and trees were considered as nested within blocks for the growth and diameter models. Mixed models were fitted in R version 2.10.1 (R Development Core Team, 2010), using the *lme* function of the *nlme* (Pinheiro et al., 2008) and the *lmer* function of the *lme4* (Bates, 2008) packages, respectively.

To determine spatial patterns of tree mortality in ArtDefol plots, the positions of all trees within the treatments were recorded to the nearest 10 cm at the onset of the experiment. Then, O-ring function analyses (Wiegand et al., 1999; Wiegand and Moloney, 2004) were performed to determine the presence of spatial patterns in tree mortality. Based on point-to-point distances, the O-ring function allows the analysis of spatial distributions without explicit knowledge of the process driving them. The $O(r)$ function calculates the density of points in a ring of a given radius (r) centered on each point (trees). The prediction of a random distribution (null hypothesis of complete randomness) is tested by simulating a random process with the Monte Carlo method (Dale, 1999). O-ring function can be use to describe point patterns with two types of points (e.g., trees dying in different years); the O-ring function $O_{12}(r)$ which is the modified pair-correlation function $g_{12}(r)$ estimates the expected density of points of pattern 2 at a distance r from an arbitrary point of pattern 1. In the present study, the O-ring procedure was used to test spatial associations between years of mortality (2007–2008, 2008–2009, 2007–2009). Spatial analyses were conducted in R, using the Spatstat package (Baddeley and Turner, 2005).

3. Results

During the three years of the experiment, the annual mean temperature at the closest meteorological station (Berry Lake; 48°85′N, 78°38′W) was consistent among years (1.05 °C, 1.29 °C, and 1.1 °C in 2007, 2008 and 2009, respectively; Environment Canada, 2010) but was higher than the mean for the previous 30 years (0.73 ± 0.21 °C, 1977–2006). Total annual precipitation in the second (2008) and third (2009) years of the experiment (867 and 911 mm, respectively; Environment Canada, 2010) was consistent with the mean of the previous 30 years (886 ± 20 mm) but was higher than the annual total of 2007 (729 mm).

3.1. *Tree mortality*

The mortality surveys indicated that the number of dead trees in Artdefol was higher in each year than in any other treatments (Table 1). Only one of the 67 unclipped CtrlTrees located within the ArtDefol plots died. This death occurred in 2009 after three years of artificial defoliation (Table 1).

Analysis of annual tree mortality demonstrated that mortality in ArtDefol was higher than in Ctrlplot, CtrlBuff, and CtrlTrees since the first year of artificial defoliation (Table 2, Fig. 2a). Annual mortality of defoliated trees increased significantly after the second ($P < 0.01$) and third ($P < 0.01$; Table 2) years of artificial defoliation. Mortality in CtrlBuff was similar to Ctrlplot for each year of the experiment (Table 2, Fig. 2a). The cumulative mortality rate in ArtDefol reached 36.3% at the end of the second year of applying artificial defoliation and almost doubled (71.1%) at the end of the third year (Fig. 2b).

3.2. *Tree growth*

In all treatments, mean root collar diameter growth of live stems was higher in 2008 than in 2007 and 2009, except in CtrlTrees where annual growth increases in 2008 and 2009 were similar (Fig. 3). In each year, the growth of Artdefol trees was lower than in any of the other treatments (Table 3, Fig. 3) and was the lowest reported after three successive years of artificial defoliation (0.11 cm). Root collar diameter growth after the first year of artificial defoliation was 40–50% lower in ArtDefol plots than in the other treatments and this difference increased to 60% and 75% after the second and third years of defoliation, respectively, compared to CtrlBuff and CtrlPlot. Root collar diameter growth in CtrlBuff was similar to that in CtrlPlot) but tended to be greater in the first (2007) and second (2008) years of the experiment (Fig. 3). CtrlTrees exhibited higher root collar diameter growth, which was 35 and 88% greater in 2008 (0.77 cm) and 2009 (0.78 cm), respectively, than in CtrlPlot (Fig. 3).

Table 1
Summary data for the number of trembling aspen present in each block and associated treatments, and for the associated number of dead trees in each year of defoliation (shown in parentheses for years 2007, 2008 and 2009). Treatments were defined as follow: artificial defoliation (ArtDefol), control buffer (CtrlBuff), control plot (CtrlPlot) and control trees (CtrlTrees).

Block	ArtDefol	CtrlTrees	CtrlBuff	CtrlPlot
1	290 (36,110,89)	31 (0,0,1)	469 (14,15,12)	350 (11,11,18)
2	258 (18,66,91)	18 (0,0,0)	438 (15,14,12)	339 (7,12,21)
3	200 (9,43,77)	18 (0,0,0)	285 (6,1,4)	266 (3,7,7)

Table 2
Parameter estimates and associated standard errors with t- and p-values from linear mixed-model analysis describing annual mortality of trembling aspen. The models considered the effects of treatment and year, and the interaction between these two factors. P-values in bold are associated with parameters significant at $P < 0.05$. Treatments were defined as follow: artificial defoliation (ArtDefol), control buffer (CtrlBuff), control plot (CtrlPlot) and control trees (CtrlTrees). Reference level was Control plot and year 2007.

	Value	SE	DF	t-value	p-value
Intercept	1.098	0.224	22	4.893	**<0.01**
ArtDefol	1.027	0.242	22	4.240	**<0.01**
CtrlTrees	−1.097	0.242	22	−4.536	**<0.01**
CtrlBuff	0.235	0.242	22	0.972	0.34
2008	0.325	0.243	22	1.343	0.19
2009	0.638	0.243	22	2.634	**0.01**
ArtDefol × 2008	0.981	0.342	22	2.865	**<0.01**
CtrlTrees × 2008	−0.584	0.342	22	−1.707	0.11
CtrlBuff × 2008	−0.325	0.342	22	−0.950	0.35
ArtDefol × 2009	1.264	0.324	22	3.693	**<0.01**
CtrlTrees × 2009	−0.780	0.324	22	−2.277	**0.03**
CtrlBuff × 2009	−0.157	0.324	22	−0.460	0.65

Note: DF, degree of freedom.

3.3. *Diameter of dead trees*

The trees that died in ArtDefol were increasingly larger, and significantly so, in each consecutive years (Table 4, Fig. 4). The root collar diameter of trees that died in 2007 was 1.8 cm, 2.5 cm in 2008 and 3.3 cm in 2009. In contrast, the root collar diameters of dead trees were similar across years (1.6–2 cm) in CtrlPlot and CtrlBuff treatments. Root collar diameters of trees dead in 2008 and 2009 were larger at the onset of the experiment (Fig. 4) and root collar diameters of trees dead in 2007 did not differ between treatments (ArtDefol, CtrlPlot and CtrlBuff; Fig. 4, Table 4). The sole dead tree observed in the CtrlTrees treatment had a root collar diameter of 2.8 cm (data not shown).

3.4. *Spatial mortality patterns*

Maps of defoliation plots (Fig. 5; Appendix B and C) illustrate the distribution of dead trees for each year of the experiment as well as that of trees still alive in 2010. Mortality in 2007 and 2008 in ArtDefol 1 showed a significant and positive association (statistical attraction) at 3–4 m, and in 2008 and 2009, at 1.5–2 m (Fig. 6a). Patterns of mortality in 2007 and 2008 in ArtDefol 2 (Fig. 6b) also showed a positive association at scales ≤ 2 m (1–1.5 m). Mortality in ArtDefol 3 (Fig. 6c) was spatially randomly distributed among years, although the spatial aggregation of mortality in 2008 and 2009 was close to significance at a scale close to 2 m.

4. Discussion

Artificial defoliation had significantly decreased trembling aspen growth. During each of the three successive years of artificial defoliation, trees had been deprived of their photosynthetic

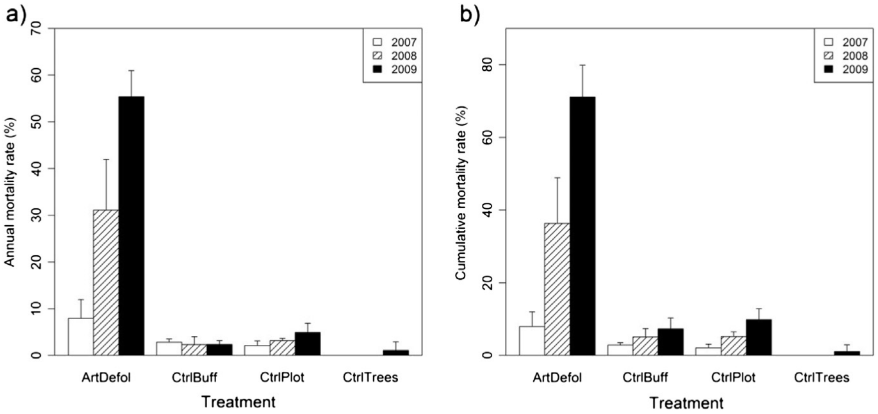

Fig. 2. Annual mortality rates (a) and cumulative mortality rates (b) (mean ± SE) of trembling aspen during 3 successive years of artificial defoliation (2007, 2008, 2009) in each of the four experimental treatments defined as follow: artificial defoliation (ArtDefol), control buffer (CtrlBuff), control plot (CtrlPlot) and control trees (CtrlTrees).

structures and consequently suffered from short growing seasons. Such short growing seasons that are caused by early defoliation have been reported to decrease tree growth and xylem production (Jones et al., 2004). Reduction of root collar diameter growth that was observed after the first year of artificial defoliation was more pronounced than has been previously observed for radial and diameter growth in artificial defoliation studies (Jones et al., 2004; Kosola et al., 2001; Reichenbacker et al., 1996). Such differences in growth may result from variation in defoliation intensity in contrast to the complete defoliation executed in the present study; partial defoliation has been shown to increase the photosynthetic rate of residual leaves and compensate for the loss of foliage (Bassman and Dickman, 1982; Hart et al., 2000; Reichenbacker et al., 1996). Root collar diameter growth reduction that was observed after the second and third years of artificial defoliation, however, compares well with radial growth reductions that have been reported after repeated defoliation during FTC outbreaks in mature trembling aspen stands (Hildahl and Reeks, 1960; Hogg et al., 2002a, 2008; Man et al., 2008). Our experiment confirmed growth reduction in trembling aspen as early as the first year of defoliation, and corroborated that FTC outbreaks, depending on their severity, duration and extent, can represent an important contributor to productivity loss at the tree-, stand-, and landscape-levels (Bergeron and Charron, 1994; Hogg et al., 2002a; Man and Rice, 2010).

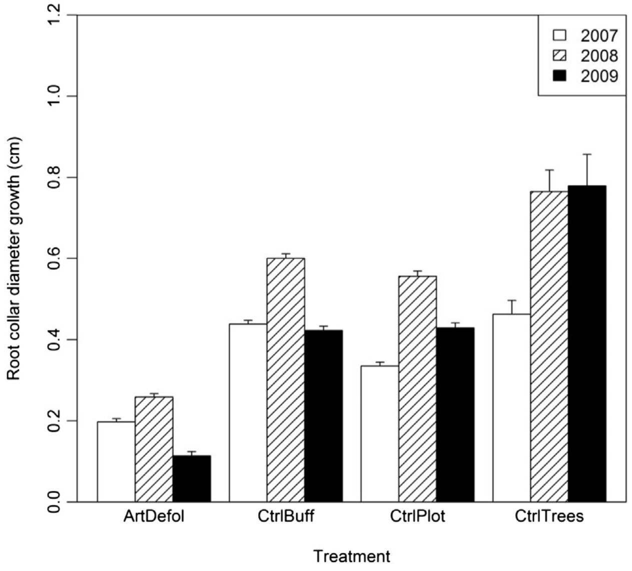

Fig. 3. Trembling aspen root collar growth (mean ± SE) in 2007, 2008 and 2009 for all living trees in each of the four experimental treatments defined as follow: artificial defoliation (ArtDefol), control buffer (CtrlBuff), control plot (CtrlPlot) and control trees (CtrlTrees).

The increase in the growth of undefoliated trees (CtrlTrees) that were located within defoliated plots (ArtDefol) was contrary to our expectations. We expected that these trees would bear most of the expenses of supporting the connected root system. Apparently, this is not the case. This result suggests that growth releases may be observed in natural stands when some trees are defoliated and some are not, such as when FTC populations are initially increasing during an incipient outbreak. Of course, such increases in growth have been shown as a result of an increase in canopy opening and light availability with gap formation (McCarthy, 2001). The increase in available light that resulted from leaf removal could have contributed to improve the overall photosynthetic activity and carbohydrate production (Pothier and Prévost, 2002) of the remaining undefoliated trees within defoliation plots. This positive growth response of undefoliated trees could also be due to compensatory photosynthesis that is induced through root connections with defoliated trees (Baret and Desrochers, 2011). Compensatory photosynthesis of undefoliated trees is expected to support the respiratory cost of the parental root system shared by trees. Such mechanisms enhance carbohydrate availability for interconnected trees (connected undefoliated and defoliated neighbours) and could confer advantage to undefoliated trees, particularly if defoliated trees and part of the common parental root system died following defoliation (DesRochers and Lieffers, 2001b). Furthermore, tree mortality induced by defoliation could enhance resource uptake by undefoliated and connected trees if the roots of dead trees continue to occupy the soil and maintain their activity (DesRochers and Lieffers, 2001a).

Although aspen mortality following FTC defoliation has been generally associated with predisposing, inciting and contributing factors (Brandt et al., 2003; Frey et al., 2004; Hogg et al., 2002a, 2008), our study clearly showed a strong relationship between artificial defoliation and aspen mortality in the absence of other co-factors such as climate (precipitation, temperature and wind), extreme weather events, insects (woodborer, leaf miner and roller), pathogenic wood decay fungi including root rots (i.e., Armillaria spp.), polypores (Phellinus spp.), cankers (Hypoxylon spp.) and mammals (small rodents and moose), none of which were observed during the three years of the experiment. Our results revealed that tree mortality occurred as soon as after one year of artificial defoliation in young and healthy stands not submitted to stressful

Table 3
Summary of the linear mixed-model regression analysis of annual root collar diameter growth. Treatment, year, and the interaction between the two factors were considered as explanatory factors. Treatments were defined as follow: artificial defoliation (ArtDefol), control buffer (CtrlBuff), control plot (CtrlPlot) and control trees (CtrlTrees). Reference level was Control plot and year 2007.

	Value	SE	DF	*t*-value	*p*-value
Intercept	0.275	0.026	7572	10.45	**<0.01**
ArtDefol	−0.101	0.011	7572	−9.81	**<0.01**
CtrlTrees	0.095	0.026	7572	3.67	**<0.01**
CtrlBuff	0.075	0.009	7572	8.24	0.64
2008	0.139	0.007	7572	19.62	**<0.01**
2009	0.044	0.007	7572	6.12	**<0.01**
ArtDefol × 2008	−0.098	0.011	7572	−8.27	**<0.01**
CtrlTrees × 2008	0.030	0.023	7572	1.39	**<0.01**
CtrlBuff × 2008	−0.039	0.009	7572	−4.19	0.34
ArtDefol × 2009	−0.138	0.015	7572	−8.96	**<0.01**
CtrlTrees × 2009	0.120	0.028	7572	4.32	**<0.01**
CtrlBuff × 2009	−0.068	0.009	7572	−7.06	0.56

Note: DF, degree of freedom.

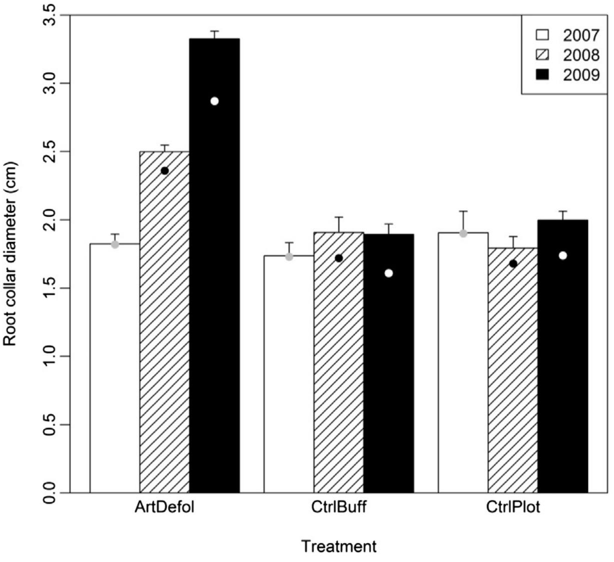

Fig. 4. Root collar diameter (mean ± SE) of dead trees in 2007, 2008 and 2009 for each of the three experimental treatments defined as follow: artificial defoliation (ArtDefol), control buffer (CtrlBuff) and control plot (CtrlPlot). Dots (grey, black and white) represent the 2007 root collar diameter of trees that were dead in 2007, 2008 and 2009.].

environmental conditions. The pronounced rates of trembling aspen mortality observed after repeated artificial defoliation may result from the incapacity of interconnected trees to sustain respiratory requirements of the total aerial and underground biomass (Desrochers et al., 2002; DesRochers and Lieffers, 2001b). The diameter and proportion of dead trees observed after the first year of defoliation were comparable to those measured after three years in CtrlPlot and CtrlBuff treatments, suggesting that mortality of small diameter trees tended to be exacerbated directly after the first year of defoliation. Conversely, the diameters in 2007 of trees dead after the second (2008) and third (2009) years of artificial defoliation confirmed that those trees were already larger at the beginning of the experiment (Fig. 4). These increases in aspen mortality rates and the larger size of dead trees with repeated defoliation were consistent with patterns of tree mortality that have been reported after consecutive years of moderate to severe FTC defoliation in mature aspen stands (Churchill et al., 1964; Man and Rice, 2010; Moulinier et al., 2011) and corroborated that repeated FTC defoliation can reduce stand density by more than 50% (Churchill et al., 1964; Man and Rice, 2010).

Contrary to expectations, mortality of CtrlTrees growing within artificial defoliation plots (ArtDefol) was negligible and did not increase with repeated defoliation. Those undefoliated trees were expected to support the large energetic costs of the common parental root system (Shepperd and Smith, 1993) that they share with defoliated trees (Baret and Desrochers, 2011; DesRochers and Lieffers, 2001b). Defoliation-induced foliage loss and mortality should have contributed to exacerbate the imbalance between leaf area and root biomass, and demands upon undefoliated trees, which should have led some to die. However, the low mortality of undefoliated trees suggested that these trees did not suffer from the effects of defoliation of neighbouring trees but likely benefited from their deaths. As for the increased growth observed in these undefoliated trees, we speculate that their high survivorship may result from the combination of several mechanisms: a new equilibrium that is established between leaf area and live root biomass (DesRochers and Lieffers, 2001b) through the death or integration of part of the common root system (DesRochers and Lieffers, 2001a;

Table 4
Summary of linear mixed-model regression analysis of dead tree root collar diameter. Treatment and year, and the interaction between the two factors were considered as explanatory factors. Treatments were defined as follow: artificial defoliation (ArtDefol), control buffer (CtrlBuff) and control plot (CtrlPlot). Reference level was Control plot and year 2007.

	Value	SE	DF	*t*-value	*p*-value
Intercept	1.042	0.047	718	21.83	**<0.01**
ArtDefol	−0.018	0.048	718	−0.38	0.70
CtrlBuff	−0.047	0.053	718	−0.89	0.37
2008	−0.021	0.055	718	−0.39	0.69
2009	0.056	0.051	718	1.11	0.26
ArtDefol × 2008	0.233	0.061	718	3.81	**<0.01**
CtrlBuff × 2008	0.090	0.073	718	1.24	0.22
ArtDefol × 2009	0.367	0.058	718	6.39	**<0.01**
CtrlBuff × 2009	0.011	0.07	718	0.15	0.87

Note: DF, degree of freedom.

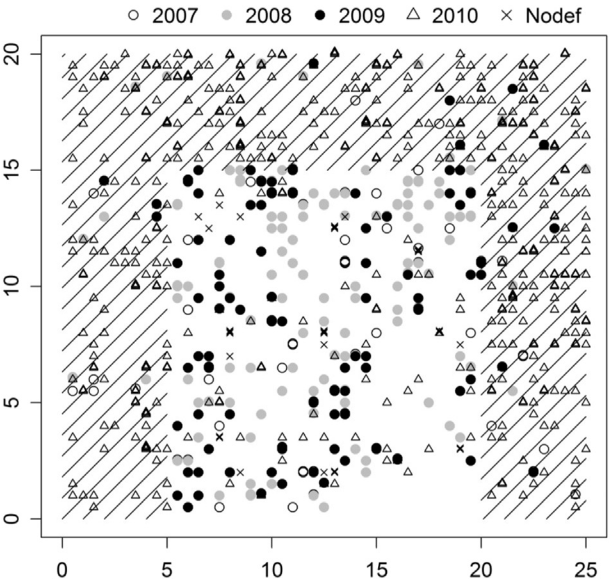

Fig. 5. Example of trembling aspen distribution in artificially defoliated plot 1 (ArtDefol 1) (20 m × 25 m). Trees were categorised as dead in 2007 (open circles), 2008 (grey circles), 2009 (black circles), or alive in 2010 (open triangles). The undefoliated trees within the defoliation plot are marked by an x. Hatched lines indicate the buffer zone.

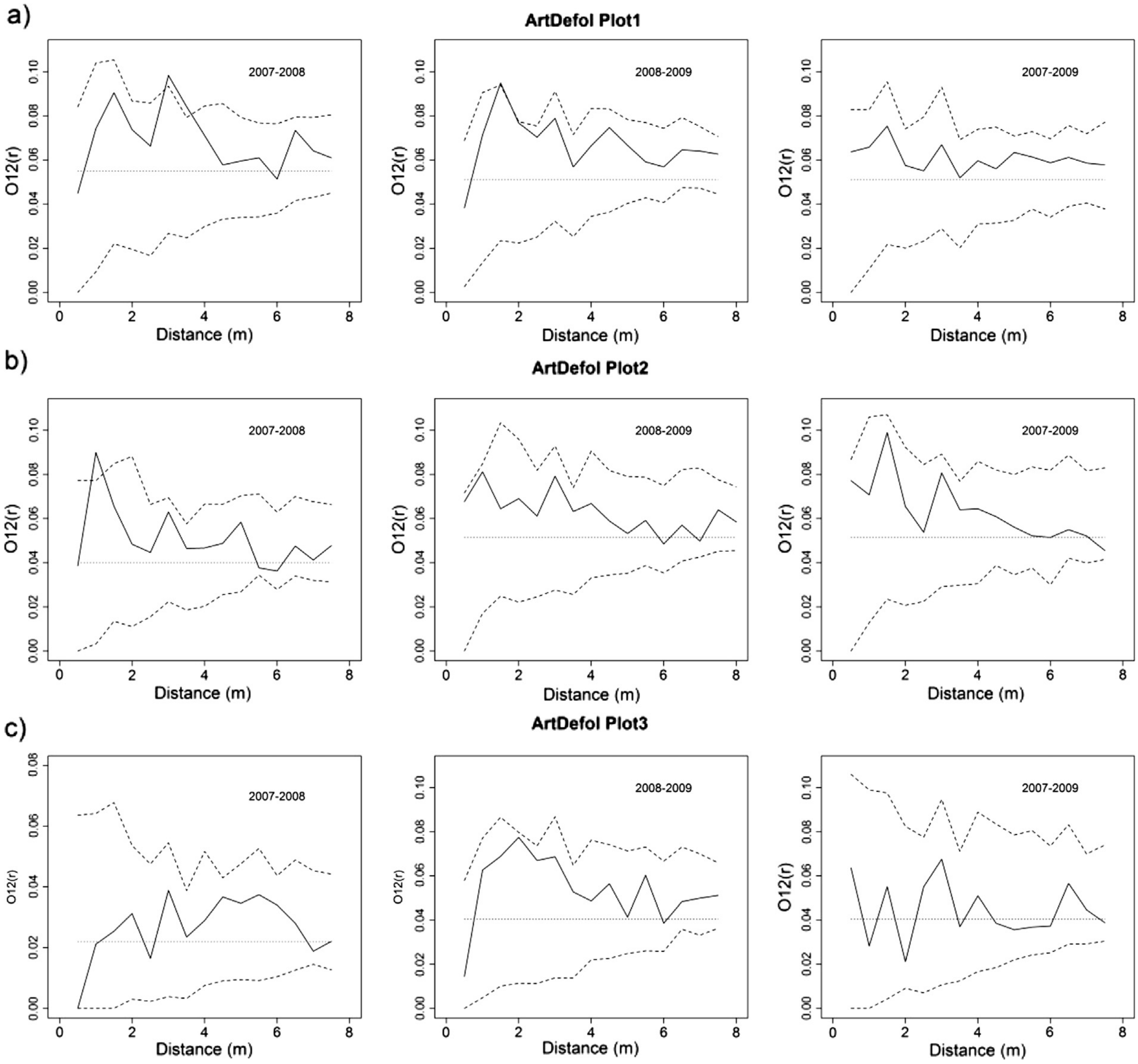

Fig. 6. O ring function ($O_{12}(r)$, solid lines) illustrating the relationship between the spatial distribution of dead trees observed in the 'artificial defoliation' plot (ArtDefol) 1 (a), 2 (b), and 3 (c) between 2007 and 2008, 2008–2009, and 2007–2009. Dashed lines are the upper and lower 99% confidence intervals (CI) based on Monte Carlo simulation (1000 runs). $O_{12}(r)$ values above the CI suggest a clumped distribution whereas values below the CI a dispersed distribution. Values within the CI suggest randomness or no spatial pattern.

Jelínková et al., 2009), compensatory photosynthesis induced through root connections (Baret and Desrochers, 2011), and increases in photosynthetic activity in response to canopy opening and increased light availability (Pritchard and Comeau, 2004).

The positive spatial association observed between years for trembling aspen mortality was weaker than expected, but spatial patterns observed in ArtDefol 1 and ArtDefol 2 suggested that tree mortality tended to be aggregated at a small scale (<5 m). The absence of a clear spatial pattern in ArtDefol 3 may be related to the initially lower stem density in that plot (Table 1), or more specifically to the death just prior to the experiment (through self-thinning) of smaller diameter stems sharing the same root at close distance with larger diameter stems. Indeed, only nine stems died in 2007 in ArtDefol 3, whereas 18 and 36 stems were found dead that year in ArtDefol 1 and 2, respectively. As mortality increased in the second year in ArtDefol 3 to close to the equivalent of 2000 stems/ha, the aggregated pattern at a small scale became almost significant (Fig. 6c). The mechanism of mortality after artificial defoliation was likely enhanced by the imbalance between above- and below-ground biomass of interconnected trees (DesRochers and Lieffers, 2001b). Interconnected trees that originated from root suckering are closely situated on the same parental root system, which *a priori* contributed to the production of aggregated patterns. Our results are consistent with aggregative mortality patterns that have been described in mature stands (Kneeshaw and Bergeron, 1998) and detected in young stands (Reinikainen et al., 2012) from which gaps emerge following FTC outbreaks (Kneeshaw and Bergeron, 1998; Moulinier et al., 2011

5. Conclusion

This experimental study is the first which showed increased mortality and decreased stem growth in young trembling aspen stands following artificial defoliation, and in the absence of abiotic or biotic co-factors. The reported patterns were observable as soon as after the first year of the experiment. Root collar diameter growth reductions and increased mortality of trembling aspen observed after artificial defoliation were consistent with patterns reported after natural FTC defoliation. The larger size of dead trees with repeated defoliation confirmed natural patterns of dead tree diameters that have been reported after FTC outbreaks. Our results also showed that undefoliated trees in defoliated areas could have benefitted directly or indirectly from the loss of foliage of their neighbours. It is known, however, that in extreme situations where all trees are defoliated, defoliation-induced mortality can affect all trees (Man and Rice, 2010), thereby causing stand-wide collapse (DesRochers and Lieffers, 2001a). Aggregative mortality of trembling aspen observed following artificial defoliation corroborated gap formation that have been recently confirmed in natural stands after FTC outbreaks. Rather than merely reporting trembling aspen mortality following artificial defoliation, this study allowed us to infer that short-duration outbreaks (1 year) tended to accelerate natural exclusion (self-thinning) of suppressed and small diameter trees, while long-duration outbreaks (2 + years) should more profoundly alter stand structure by removing both small and large diameter trees (Moulinier et al., 2011). Finally, further research is required to increase our understanding of FTC defoliation effects, particularly in the role of root connections in young and mature stands and how they could affect patterns of growth and mortality of trembling aspen in a context of an outbreak.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2013.12.007.

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