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Effects of a forest tent caterpillar outbreak on the dynamics of mixedwood boreal forests of eastern Canada[1]

Julien MOULINIER[2], NSERC/UQAT/UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada, e-mail: julien.moulinier@uqat.ca
François LORENZETTI, Institut des sciences de la forêt tempérée, Université du Québec en Outaouais, 58, rue Principale, Ripon, Québec J0V 1V0, Canada.
Yves BERGERON, NSERC/UQAT/UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada.

Abstract: In boreal mixedwood stands dominated by trembling aspen (*Populus tremuloides*), forest tent caterpillar (*Malacosoma disstria*, FTC) outbreaks are recurrent events whose effects on stand dynamics are poorly documented. To describe and characterize the effects of FTC outbreaks, we assessed canopy opening, gap size, and understory tree recruitment in 12 stands dominated by trembling aspen that had experienced different levels of defoliation (in terms of severity and duration) during the last outbreak in northwestern Quebec (1999–2002). The study showed a significant increase in canopy opening and gap size with defoliation intensity. Furthermore, the proportion of large gaps and aspen mortality increased with defoliation intensity. Balsam fir (*Abies balsamea*) regeneration benefited from changes in canopy structure caused by the FTC, while aspen did not. Forest succession in mixedwood stands that had been defoliated for 1 y was not profoundly affected, while multiple years of defoliation likely caused more rapid canopy transition from aspen to fir. By creating a variety of gaps, FTC outbreaks modify stand structure in ways that differ from succession to coniferous dominance controlled by single-stem exclusion.
Keywords: boreal mixedwood succession, forest tent caterpillar, gap dynamics, insect disturbance, tree recruitment, trembling aspen.

Résumé : En forêt boréale mixte dominée par le peuplier faux-tremble (*Populus tremuloides*), les épidémies de livrée des forêts (*Malacosoma disstria*, LDF) sont des évènements récurrents dont les effets sur la dynamique des peuplements ont été peu documentés. Afin de décrire et de caractériser les effets d'une telle perturbation, nous avons évalué l'ouverture du couvert, la taille des trouées et la régénération dans 12 peuplements dominés par le peuplier faux-tremble ayant subi différents niveaux de défoliation (en termes de sévérité et de durée) durant la dernière épidémie survenue dans le nord-ouest du Québec (1999–2002). Les résultats de cette étude ont montré une augmentation significative de l'ouverture du couvert et de la taille des trouées avec l'intensité de la défoliation. La régénération en sapin baumier (*Abies balsamea*) a bénéficié des changements à la structure des peuplements entraînés par la LDF alors que ça n'a pas été le cas pour le peuplier. La trajectoire successionnelle des peuplements mixtes défoliés une seule année ne semblait pas être affectée tandis que plusieurs années de défoliation entraînaient vraisemblablement une conversion plus rapide d'un couvert mixte à dominance feuillue vers un couvert mixte à dominance résineuse. En créant une variété de trouées, les épidémies de LDF modifient la structure des peuplements d'une façon qui diffère de la succession vers une dominance par les conifères contrôlée par l'exclusion de tiges individuelles.
Mots-clés : épidémie d'insectes, livrée des forêts, peuplements mixtes, peuplier faux-tremble, succession forestière, trouées, régénération.

Nomenclature: Brouillet *et al*., 2013; Entomological Society of Canada, 2013.

Introduction

Mixedwood stands are widespread throughout North American boreal forests, where they are the most productive and diversified forest ecosystems (Chen & Popadiouk, 2002). In these forests, compositional change in dominant tree species is related to time-since-fire and depends upon species life-history traits (Bergeron, 2000). After fire, pioneer and shade-intolerant tree species such as trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) generally initiate stand succession and generate an even-aged structure. With the increase in time-since-fire, intra- and inter-specific competition increase intolerant hardwood stem exclusion and favour shade-tolerant softwood establishment and growth (Bergeron, 2000; Taylor & Chen, 2011; Bergeron *et al.*, 2013). Also, the death of dominant canopy trees, either from ageing or from non-stand-replacing disturbances such as wind or insect outbreaks, enables the recruitment of shade-tolerant coniferous trees from the understory to the main

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[2]Author for correspondence.
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canopy (Greene *et al.*, 1999; Chen & Popadiouk, 2002). Therefore, mixed stands that are dominated by intolerant hardwoods generally switch to softwood dominance, and in the absence of fire, they ultimately develop into uneven-aged coniferous stands.

During the fire-free interval, insect outbreaks play an important role in mixedwood stand dynamics. In mixedwood forests dominated by conifers, spruce budworm (*Choristoneura fumiferana*) outbreaks have been well documented (Morin, Laprise & Bergeron, 1993; Morin, 1994; Bergeron *et al.*, 1995; Bouchard, Kneeshaw & Bergeron, 2006; Bouchard, Kneeshaw & Messier, 2007). By contrast, the effects of outbreaks of insects such as the forest tent caterpillar (*Malacosoma disstria*) on mixedwood forests dominated by deciduous tree species are just beginning to be understood (Senecal, Kneeshaw & Messier, 2004; Man *et al.*, 2008; Man & Rice, 2010; Reinikainen, D'Amato & Fraver, 2012).

Forest tent caterpillar (FTC) outbreaks are important insect-driven disturbances in the southern boreal forests of North America (Witter, 1979; Fitzgerald, 1995). The FTC is a voracious defoliator of trembling aspen, white birch, and balsam poplar (*Populus balsamifera*) (Witter, 1979; Peterson & Peterson, 1992). FTC outbreaks generally last 1 to 6 y (Cooke, Lorenzetti & Roland, 2009) and occur every 9 to 13 y (Cooke & Lorenzetti, 2006) as far north as 54°N in Quebec (Huang *et al.*, 2008). Severe FTC defoliation reduces tree growth (Hildahl & Reeks, 1960; Hogg, Brandt & Kochtubajda, 2002) and decreases forest productivity (Bergeron & Charron, 1994; Hogg & Schwarz, 1999; Candau, Abt & Keatley, 2002). Tree mortality, particularly that of trembling aspen, is more frequently associated with predisposing, inciting, and contributing factors (see Frey *et al.*, 2004), such as climate (Hogg, Brandt & Michaellian, 2008), age (Brandt *et al.*, 2003; Sutton & Tardif, 2007), wildlife damage (Peterson & Peterson, 1992), wood-boring insects (Hogg, Brandt & Kochtubajda, 2002), or fungal pathogens (Brandt *et al.*, 2003), than with FTC defoliation itself (Churchill *et al.*, 1964; Candau, Abt & Keatley, 2002; Brandt *et al.*, 2003; Man *et al.*, 2010; Moulinier, Lorenzetti & Bergeron, 2011).

In mixed boreal stands, canopy transition from deciduous dominance to coniferous dominance generally involves autogenic processes such as tree senescence and competition, but it is also affected by exogenous factors, such as disease, insects, or climatic events. In the absence of fire, insect outbreaks may occur frequently and create canopy gaps (Kneeshaw & Bergeron, 1998; McCarthy, 2001). Such gaps modify understory conditions, principally the availability of resources such as light and water (Canham, 1988; McCarthy, 2001). Consequently, gaps may favour different tree species depending on gap size and the life-history traits of the species present (longevity, growth rate, shade tolerance) (Bergeron, 2000). Small gaps (<200 m^2, following McCarthy, 2001) have little effect on light levels and tend to favour shade-tolerant softwoods, while large gaps (>200 m^2) generally alter light levels and improve the recruitment of intolerant hardwoods. Moreover, dominant deciduous and coniferous tree species can have different effects on the recruitment and growth of understory species. On the one hand, for example, the litter of deciduous species generally improves soil nutrient conditions (Thiffault & Jobidon, 2006), but it can present a significant barrier to conifer seed germination (Zasada, Sharik & Nygren, 1992; Simard, Bergeron & Sirois, 2003). On the other hand, litter of coniferous species usually reduces soil nutrients (Légaré, Paré & Bergeron, 2005) and increases organic soil layer thickness (Laganière, Paré & Bradley, 2009), which can prevent soil temperatures from reaching the levels required for seed germination and aspen suckering (see Frey *et al.*, 2003).

Recent studies have documented forest succession and gap dynamics following FTC outbreaks in pure poplar stands of Quebec and Ontario (Man & Rice, 2010; Moulinier, Lorenzetti & Bergeron, 2011), but the effects of such disturbances in mixedwood boreal stands have yet to be described. The last FTC outbreak (1999–2002) that occurred in the mixedwood boreal forests of northwestern Quebec exhibited great variation in defoliation intensity (in terms of severity and duration) and constituted a real opportunity for studying how such disturbances can affect the dynamics of mixed stands dominated by trembling aspen. The main objective of this study was to describe the effects of different FTC outbreak intensity regimes on overstory and understory stand structure, and on the composition of mixedwood forests. Specifically, we hypothesized that 1) the proportion of canopy openings would increase with increased FTC outbreak intensity; 2) gap characteristics, such as gap size and number of gap makers per gap (dead trees that form gaps), would increase with defoliation intensity; 3) gap size following FTC defoliation would affect understory tree recruitment, with small gaps favouring shade-tolerant conifers and large gaps favouring intolerant deciduous species; and 4) growth of pre-established conifers would be higher in defoliated than in undefoliated stands. Our study was undertaken in 2009, 6 y after the last year of FTC defoliation, by sampling 12 mixedwood stands dominated by *P. tremuloides* that had experienced different levels of FTC defoliation intensity.

Methods

Study area

The study area (48°40' to 48°59'N, 77°10' to 78°20'W) is located in Abitibi-Temiscamingue, in northwestern Quebec, Canada. This area is situated within the Quebec portion of the Quebec–Ontario Clay Belt (Vincent & Hardy, 1977) and is included in the balsam fir–white birch bioclimatic domain (Robitaille & Saucier, 1998; Saucier *et al.*, 1998). The climate is continental, with cold, dry winters and short, mild summers. Common tree species include trembling aspen, balsam fir, white birch, white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banksiana*).

In this region, the most recent FTC outbreak occurred from 1998 to 2003 and was the sixth event recorded since 1938 (Cooke & Lorenzetti, 2006). In 1998 and in 2003, defoliation was localized and was monitored at ground level by the Quebec Ministry of Natural Resources (MRNQ). During the period 1999–2002, the extent of the defoliation was great enough to warrant annual aerial surveys by the MRNQ. We will thus refer to 1999–2002 as the outbreak period. In every yearly survey, the proportion of foliage that had been lost to defoliation in each stand was estimated and classified into 1 of 4 classes (undetectable, 0%; light, 1–25%; moderate, 26–65%; severe, 66–100%) defined by the Forest Insect and Disease Survey (FIDS) program of the Canadian Forest Service. The cumulative area defoliated during this outbreak was about 1.4 million hectares, with a total defoliated extent in 2001 of nearly 1 million hectares (Bordeleau, 2011).

Data collection

We selected 12 mixedwood stands that had experienced a range of defoliation intensities over the period 1999–2002. These stands were homogeneous in terms of overstory composition (trembling aspen basal area ≥50% of total basal area) and tree density (Table I). The 12 stands were also similar in terms of understory vegetation type, particularly the shrub species component (height and density). We were careful in selecting stands where shrub competition was low so as to emphasize the effect of gaps on tree regeneration. For each stand, mean defoliation intensity was calculated as the 4-y average of the aerial defoliation survey class midpoints. Stand characteristics (composition, basal area, and stem density) were estimated using the data from two 400-m^2 inventory plots that had been established under closed canopy in each stand. Diameter at breast height (DBH, 1.3 m) and species of all living trees ≥9 cm were recorded. In addition, 2 cores were taken at breast height from 5 dominant trembling aspen and 5 dominant balsam fir or white spruce to determine maximum ages.

In each stand, 1 transect was established to evaluate the percentage of canopy openings. Transects varied in length from 500 to 800 m (for a total of 7.4 km). The starting point for each transect was randomly assigned after applying a 50-m-wide buffer to any open area. At every metre along the transects, the forest canopy was visually inspected and classified as closed if a live tree crown was present or open if 1 or more mature dead trees were present (Kneeshaw & Bergeron, 1998). The proportion of open canopy at the stand level was subsequently calculated as the relative frequency of open canopy to total length of transect (Runkle, 1992). To confirm that canopy openings were not influenced by gaps the formation of which pre-dated the most recent FTC outbreak, we used pre-disturbance aerial photos (1994–1995) to verify that pre-existing gap areas were within the range of natural variability of undisturbed stands (5–10%, following Kneeshaw & Bergeron, 1998; Moulinier, Lorenzetti & Bergeron, 2011).

Gap characterization was performed in each stand on the first third of the total transect length, resulting in a subsample of 112 (out of 378) gaps. A canopy gap is created by the death of an individual or a small cluster of trees and is defined as the vertical projection upward from the ground surface of the canopy opening (Runkle, 1982). For circular-shaped gaps, measures of the longest and shortest perpendicular axes were recorded. Multiple extra axis measurements were performed in the case of irregular-shaped gaps. Dead trees within the gaps, which were referred to as gap makers, were counted, identified, and classified as either standing dead, snapped, uprooted, or crown damaged (crown or branch dieback).

Regeneration was inventoried in the 112 subsampled gaps. An exhaustive count of regeneration by species was achieved in the smaller gaps (area <100 m^2), whereas two 2-m-wide transects (north, south) perpendicular to the north–south axis were used for larger gaps. Regeneration was categorized into 1 of 3 height classes for each species: suckers (<1 m), saplings (1–2 m), and large saplings (2–4 m) for trembling aspen and seedlings (<0.5 m), saplings (0.5–2 m), and large saplings (2–4 m) for conifers. Regeneration density was calculated by species for the entire gap (total density) and for each of the 3 height classes. Because trembling aspen and balsam fir represented 99% and 85% of deciduous and coniferous regeneration, respectively, we only considered the abundance of these 2 species. The remaining 1% of deciduous and 15% of conifer regeneration were white birch and white spruce, respectively. Regeneration density under forest cover was quantified in two 10-m^2 subplots, which were sampled in each 400-m^2 plot that had been used to describe stand characteristics.

Table I. Description of the 12 mixedwood stands from plots measured under closed canopies in 2009, including defoliation regime during the last outbreak (1999, 2000, 2001, 2002), mean defoliation intensity (mean percent removal of foliage per year), maximum tree age at breast height, basal area (mean ± SE, $m^2 \cdot ha^{-1}$), tree density (mean ± SE, stems·ha^{-1}, ≥9 cm), and proportion of trembling aspen basal area (%).

Stand	Defoliation regime [a]	Mean defoliation intensity [b]	Trembling aspen			Conifers [c]			% basal area aspen
			Age	Basal area	Density	Age	Basal area	Density	
1	0,1,1,0	6.5	47	11.2 ± 2.5	300 ± 62	70	8.4 ± 1.8	450 ± 112	57.1
2	0,0,2,0	11	57	17.2 ± 3.7	337 ± 63	54	8.6 ± 1.0	325 ± 25	66.7
3	0,0,2,0	11	79	13.5 ± 0.5	263 ± 13	92	12.3 ± 1.0	550 ± 25	52.3
4	0,0,3,0	21	104	24.0 ± 2.0	338 ± 69	79	8.7 ± 1.8	400 ± 100	73.4
5	0,0,3,0	21	102	15.3 ± 6.5	213 ± 63	80	14.7 ± 4.6	450 ± 100	51.0
6	0,0,3,0	21	58	20.3 ± 0.8	338 ± 63	54	8.6 ± 3.6	363 ± 63	70.2
7	2,2,3,0	43	60	14.4 ± 3.4	288 ± 63	50	10.7 ± 3.4	450 ± 100	57.4
8	2,2,3,0	43	54	17.7 ± 4.0	713 ± 187	69	11.9 ± 1.0	600 ± 75	59.8
9	2,3,3,0	53	59	10.2 ± 1.7	388 ± 38	48	7.2 ± 0.8	338 ± 38	58.6
10	2,3,3,0	53	53	10.9 ± 2.8	313 ± 88	54	8.0 ± 3.4	363 ± 153	57.7
11	2,3,3,0	53	59	11.6 ± 6.5	238 ± 110	60	8.2 ± 4.7	425 ± 200	58.6
12	3,3,3,1	65	78	14.4 ± 0.8	263 ± 63	67	10.1 ± 2.4	400 ± 75	58.8

[a] Defoliation regime: 0 = no defoliation, 1 = light, 2 = moderate, 3 = severe.

[b] Mean defoliation intensity: mean % removal of foliage over 4 y during the last forest tent caterpillar outbreak (1999–2002).

[c] Conifers refers to balsam fir (95%) and white spruce (5%).

Apical growth of balsam fir was quantified along the gradient of mean defoliation intensity in gaps of different sizes and under forest cover. In each of the 12 investigated stands, from 5 to 42 balsam fir trees were sampled among 3 height classes, for a total of 247 stems (75 seedlings, 80 saplings, and 92 large saplings). To determine apical growth before, during, and after the outbreak, we measured internode lengths for each fir stem from its apex to the base until those internodes could no longer be identified. We subsequently were able to measure apical growth from 1994 to 2009. Apical growth measurements were not attempted for aspen since internodes are less conspicuous and frequent apical stem mortality can lead to errors.

Data analysis

Canopy opening, mean gap area, number of gap makers per gap, and proportion of gap maker types were each analyzed by linear regression to determine stand-level changes in relation to defoliation intensity. Log-transformation was performed on gap area prior to analysis, and the residuals from all 4 regressions were examined to ensure that statistical assumptions of normality and homoscedasticity had been met.

Gaps were grouped into classes based on 25-m^2 increments of surface area, with upper class limits ranging from 0 (under forest cover) to 475 m^2. Comparisons of gap size-class distributions between defoliation regimes were performed using Kolmogorov–Smirnov tests. As we applied multiple comparisons, Bonferroni corrections were performed to adjust the significance level from α (0.05) to α/n (0.004), with n (12) being the number of comparisons.

A linear mixed-effects model (Pinheiro & Bates, 2000; Pinheiro *et al.*, 2008) was used to analyze regeneration density of trembling aspen and balsam fir. Stand was considered as a random effect in this analysis. We used model selection methods to assess which factors significantly affected gap regeneration density. We formed a set of plausible models to identify which of the predictor variables and their interactions might explain patterns of regeneration density. The fit of the global model was assessed for this analysis, and models were compared using the second-order Akaike Information Criterion (AIC_c) and the information-theoretic approach presented by Burnham and Anderson (1998; 2002). We considered models with ΔAIC_c values ≤ 2 to have strong support; we also calculated model weights from the AIC_c values to indicate the level of support for each of the models that were considered (Burnham & Anderson, 2002).

Regeneration density was categorized into 2 classes (<0.1 stems·m^{-2} *versus* >0.1 stems·m^{-2}). The threshold of 0.1 stems·m^{-2} was used to discriminate between minimally and poorly regenerated gaps, following MRNQ regeneration survey guidelines. Density data from minimally regenerated gaps were analyzed with mixed logistic regression to test effects of defoliation intensity, gap area, species, height class, and 3 interactions, *viz*: [defoliation intensity × height class], [gap area × height class], and [species × height class]. Stand and gap were considered as random effects in the model. Model selection analysis was also performed, and only 1 model with a ΔAIC_c value ≤ 2 was used to predict height class regeneration density.

Apical growth of balsam fir was analyzed with a linear mixed-effect model. We defined 4 periods of growth: prior to the outbreak (1994–1998), during the outbreak (1999–2002), immediately following the outbreak (2003–2006), and 5–7 y after the outbreak (2007–2009). We also determined the height class of the stems in 1998 to test how the different height classes at the inception of the FTC outbreak responded to different defoliation intensities. The same height classes as previously described were used: seedlings (0 < 0.5 m), saplings (0.5–2 m), and large saplings (2–4 m). Apical growth was analyzed as a function of defoliation intensity, gap area, height class in 1998, growth period, and 2 interactions: [defoliation intensity × period] and [height class × period].

All statistical analyses were performed in R (version 2.10.1, R Development Core Team, Vienna).

Results

Canopy and gap characteristics

The proportion of canopy opening increased significantly from 11.3% to 46.8% with the increase in mean defoliation intensity, the index that combines defoliation severity and duration over the 4-y period of the forest tent caterpillar outbreak (Figure 1a). Mean gap area also showed a significant positive relationship ($R^2 = 0.65$, $P < 0.01$) with mean defoliation intensity and increased at a rate of about 1 m^2 per percent of mean defoliation intensity across the gradient of defoliation (Figure 1b).

The number of gap makers increased significantly with defoliation intensity for trembling aspen ($R^2 = 0.86$, $P < 0.01$) but not for balsam fir (Figure 1c). Among the 521 dead trembling aspen that were sampled in the gaps, 72.1% were classified as snapped, 22.5% as standing dead, 3.5% as uprooted, and 1.9% as crown-damaged. Among the 172 coniferous gap makers, 47.7% were snapped, 39.5% were uprooted, 12.2% were standing dead, and 0.6% were crown-damaged. In contrast to coniferous gap makers, which did not exhibit any relationship with mean defoliation intensity (data not shown), the proportion of snapped trembling aspen increased significantly with mean defoliation intensity, while the proportion of trees standing dead decreased marginally (Figure 1d). The proportions of crown-damaged and uprooted aspen trees were not significantly related to defoliation intensity (Figure 1d).

Patterns of gap size distribution showed that gap size frequency did not differ between mean defoliation intensities (Bonferroni-corrected $P > 0.004$). However, this result revealed an increase in the proportion of 100-m^2 gaps in stands that had been defoliated during 3 or 4 y (mean defoliation intensities $\geq 43\%$, Figure 2).

Regeneration

Analysis of regeneration density by height class showed that only 1 of the 9 mixed logistic regression models considered had strong support, with an AIC_c weight of 0.78 (Table II). This model showed that the density of balsam fir was higher than that of trembling aspen ($\beta = 0.64$, $P < 0.01$). Density of small-sized regeneration (seedlings for balsam fir, suckers for trembling aspen) was higher than that of saplings ($\beta = -1.11$, $P < 0.01$) and large saplings (β = –2.06, $P < 0.01$). The density of fir seedlings and aspen suckers decreased more strongly with increasing gap area than did the density of saplings in both species (β = 0.24, $P = 0.06$; Figure 3a,b), while large sapling density was not affected by gap area in either species (β = –0.01, $P = 0.97$; Figure 3a,b). There was a significant and positive effect of defoliation intensity on regeneration density (β = 0.01, $P = 0.01$), principally for fir seedlings and saplings (Figure 3c), which increased more than did aspen suckers and saplings (Figure 3d). Overall, our analysis showed a significant effect of defoliation intensity on small and intermediate regeneration for both species and a less important effect of gap size on regeneration patterns.

In stands containing white spruce in the understory, the mean density of white spruce regeneration (data not shown) was similar between gaps and under forest cover along the gradient of defoliation intensity (about 200 ± 40 stem·ha^{-1}), except in the stand that had been defoliated for 4 consecutive years and in which mean density reached 400 ± 200 stem·ha^{-1}. The seedling class represented 52% of total white spruce regeneration, while sapling and large sapling classes represented 43% and 5%, respectively.

Balsam fir apical growth

Mixed-effects regression analysis (Table III) showed that mean apical growth of balsam fir increased significantly with gap area (β = 0.07, $P < 0.01$). Apical growth was greater in gaps ≥100 m^2 (13.2 ± 0.8 cm·y^{-1}) than in gaps <100 m^2 (11.1 ± 0.4 cm·y^{-1}) and under forest cover (9.4 ± 0.4 cm·y^{-1}). The interaction [defoliation intensity × period] had a significant and positive effect on mean apical growth ($P < 0.01$). This result means that mean apical growth increased more with defoliation intensity directly after the outbreak (2003–2006, β = 0.43) and during the most recent period (2007–2009, β = 0.48) than during the actual outbreak (1999–2002, β = 0.26). Mean apical growth of balsam fir observed between 1994 and 1998 was consistent between stands before the outbreak (Figure 4a). Mean apical growth by height class in 1998 (Figure 4b) showed that, before the outbreak, large saplings grew more

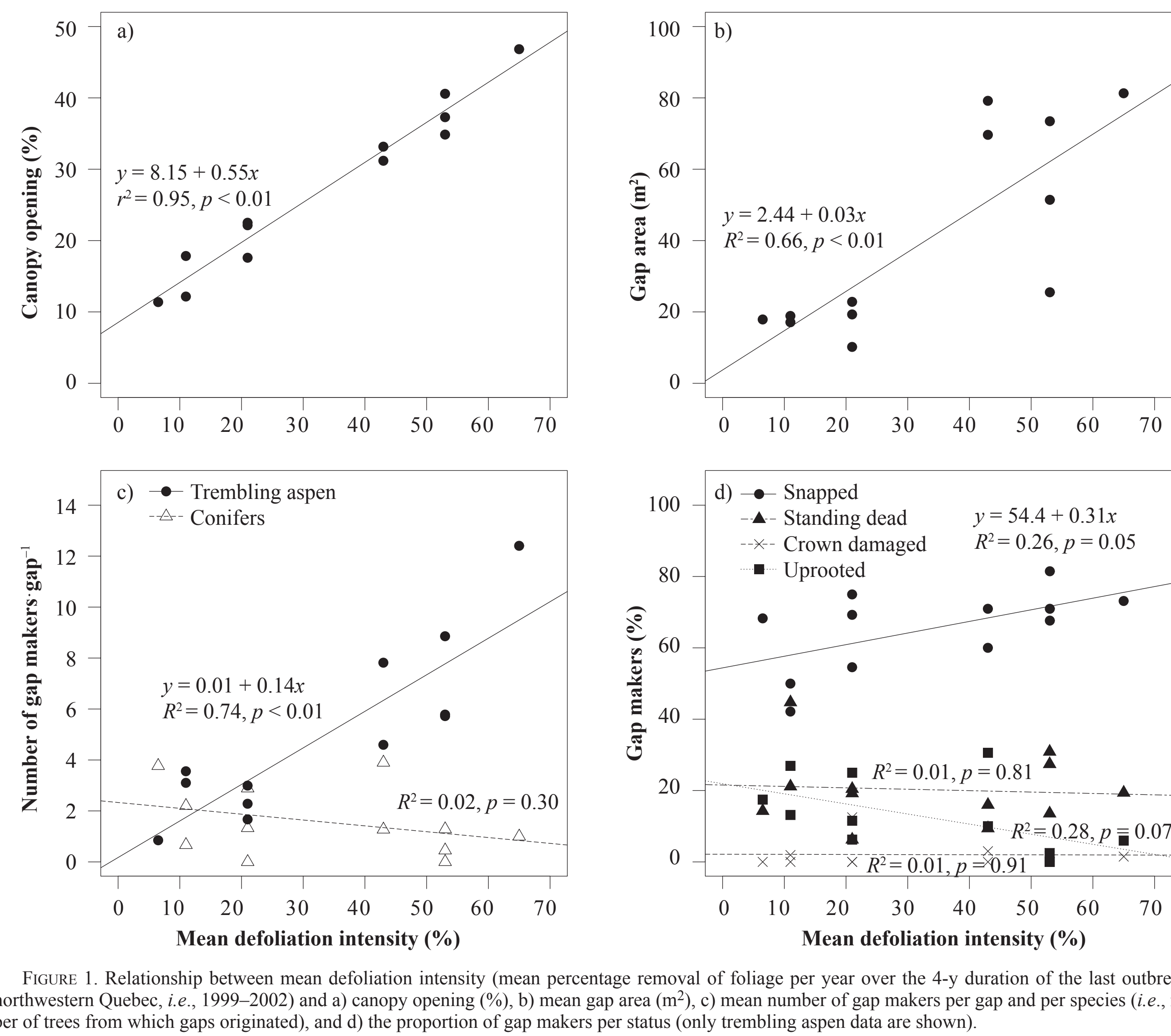

Figure 1. Relationship between mean defoliation intensity (mean percentage removal of foliage per year over the 4-y duration of the last outbreak in northwestern Quebec, *i.e.*, 1999–2002) and a) canopy opening (%), b) mean gap area (m^2), c) mean number of gap makers per gap and per species (*i.e.*, number of trees from which gaps originated), and d) the proportion of gap makers per status (only trembling aspen data are shown).

than did saplings and seedlings. After the outbreak, apical growth of saplings and seedlings was greater than that of large saplings. Apical growth of seedlings increased by 180% between 1998 and 2009, and during the same period, growth of saplings and large saplings increased by 60% and decreased by 22%, respectively. Increases in apical growth during the outbreak period did not statistically differ among seedlings, saplings, and large saplings ($P = 0.901$ for saplings; $P = 0.662$ for large saplings; Table III). However, apical growth during both of the periods after the outbreak increased more for seedlings than for either saplings ($P \leq 0.01$) or large saplings ($P \leq 0.05$, Table III), compared to apical growth during the outbreak. Thus, patterns of apical growth clearly showed that seedlings were more positively affected by the outbreak than were saplings and large saplings, although saplings exhibited the highest apical growth (Figure 4b).

Discussion

Canopy gaps and gap makers

This study showed a close relationship between canopy opening (due to tree mortality) and FTC defoliation intensity in the mixedwood boreal forest of the northwestern Quebec Clay Belt (Figure 1a). The observed range in canopy opening (from 11.3% to 46.8% across the disturbance gradient) is wider than the 24.4 to 35.3% range reported by Kneeshaw and Bergeron (1998) for similar mixedwood stands of Quebec. In the latter case, canopy openings resulted from the mortality of fir trees following a spruce budworm outbreak. The wider range observed for mixedwoods in our study may be due to the generally larger size of aspen compared to fir trees (Kneeshaw & Bergeron, 1998). The increase in canopy opening following defoliation that we observed was comparable to the results that

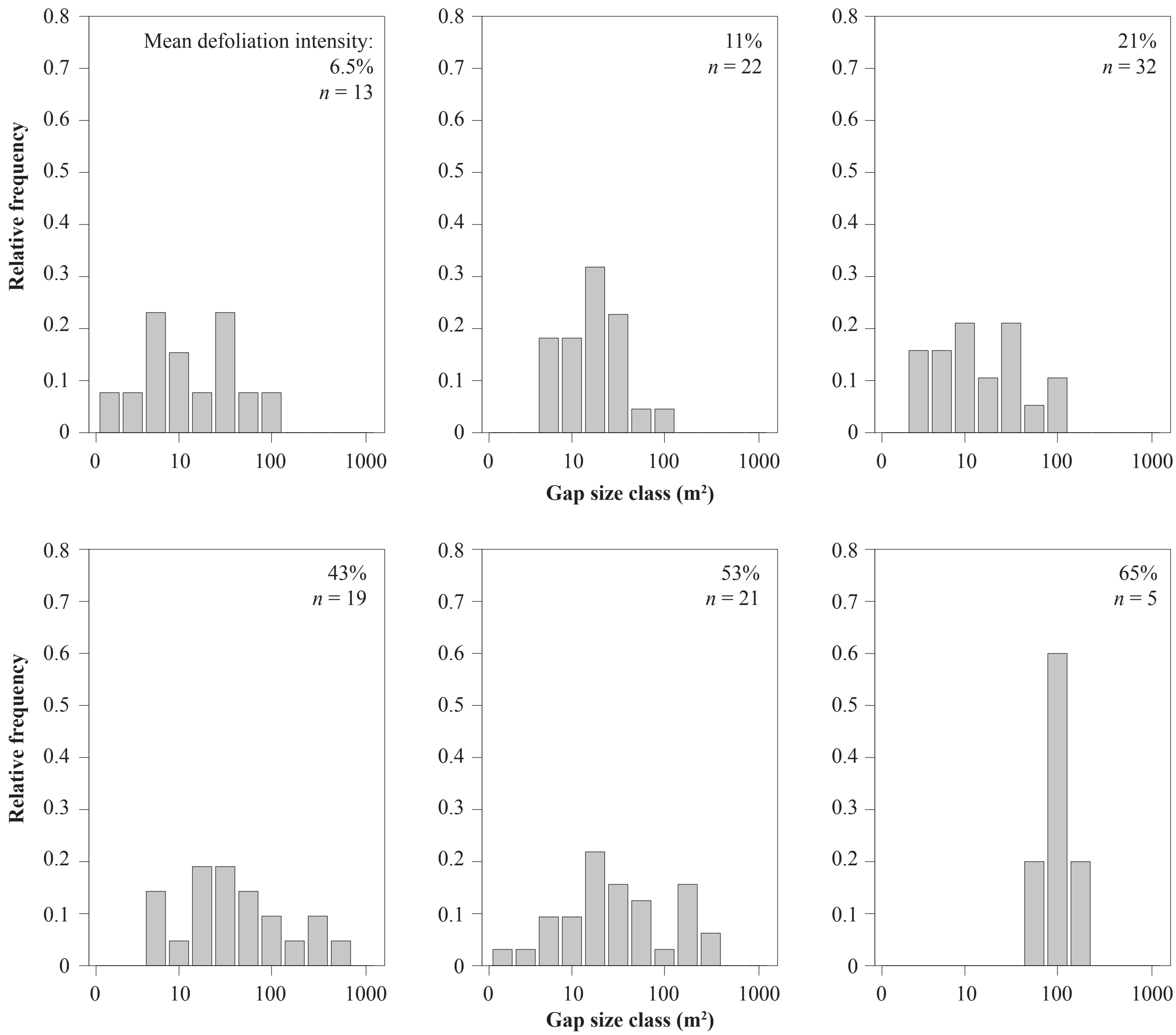

Figure 2. Relative frequency distributions of gap sizes in mixedwood stands that experienced increasing defoliation intensities during the last outbreak of forest tent caterpillar in northwestern Quebec (1999–2002).

Table II. Top-ranking models for mixed-effects analysis of total density and density by height class of trembling aspen and balsam fir regeneration sampled in 2009 from mixedwood stands having experienced 1–4 y defoliation during the last forest tent caterpillar outbreak in northwestern Quebec (1999–2002). For brevity, only the first 5 models are shown.

Model	K [a]	AIC_c †	ΔAIC_c ‡	w_i §
Total density				
Gap + Species + [Gap × Species]	6	455.1	0.00	0.46
Def + Gap + Species + [Gap × Species]	7	455.7	0.61	0.34
Species	4	458.1	2.99	0.10
Def + Gap + Species + [Def × Species]	7	458.8	3.72	0.07
Def + Species + [Def × Species]	6	460.4	5.28	0.03
Height class density				
Def + Gap + Hc + Species + [Gap × Hc]	9	814.79	0.00	0.78
Def + Gap + Hc + Species + [Species × Hc]	9	818.45	3.65	0.12
Def + Gap + Hc + Species + [Def × Hc] + [Species × Hc]	10	818.98	4.19	0.10
Hc + Species + [Species×Hc]	7	825.46	10.66	0.00
Def + Hc + [Def × Hc]	7	829.16	14.36	0.00

[a] K = no. of parameters.

† AIC_c = Akaike's Information Criterion corrected for small sample sizes.

‡ ΔAIC_c = AICc relative to the most parsimonious model.

§ w_i = AIC_c model weight.

Def = mean defoliation intensity calculated as the mean % removal of foliage per year over the 4 y of the last forest tent caterpillar outbreak (1999–2002); Gap = Gap area; Hc = Regeneration height classes (seedling for fir and sucker for aspen; sapling, and large sapling for both species).

were reported in 20 stands dominated by trembling aspen, where canopy openness increased from 12.3% in undefoliated stands to 43.7% after 3 y of severe FTC defoliation (Moulinier, Lorenzetti & Bergeron, 2011). Compared to these deciduous stands (Moulinier, Lorenzetti & Bergeron, 2011), canopy opening rates in mixedwood stands have appeared to be slightly lower for equivalent defoliation intensities (20.8 and 37.5% in mixedwood stands and 23.7 and 43.7% in deciduous stands after 1 and 3 y of severe FTC defoliation, respectively). These differences can be attributed to residual trees, principally the dominant and intermediate conifers such as balsam fir, that are exposed to increased light when dominant trembling aspen trees die, thereby reducing gap size and limiting connections between neighbouring gaps.

Patterns of gap size are also consistent with the effects of FTC defoliation on canopy openings reported in pure poplar stands (Moulinier, Lorenzetti & Bergeron, 2011). Gap size increased significantly with defoliation intensity (Figure 1b) and gaps >100 m^2 were only present in stands that had been defoliated over 3 consecutive years (Figure 2). These results reveal that the structure of mixedwood stands was not significantly affected by 1 y of severe FTC defoliation, while 3 consecutive years of moderate to severe FTC defoliation tended to alter gap size frequency distribution and significantly increase the level of canopy opening.

Gap size distribution was directly related to the increase in the number of trembling aspen gap makers per gap, which was twice as high after 3 y of FTC defoliation as it was after 1 y (Figure 1c). Snapped gap makers increased with defoliation intensity and dominated in all stands (Figure 1d). The proportions of snapped trembling aspens corroborated the observation that high densities of such gap makers constitute one of the most conspicuous footprints of severe FTC defoliations (Moulinier, Lorenzetti & Bergeron, 2011). The decreasing proportion of uprooted trembling aspen showed that windstorm events were not associated with trembling aspen mortality. However, uprooted balsam fir represented a large proportion of the coniferous gap makers (40%, data not shown), which could be attributed to the greater wind vulnerability of this species (Ruel, 2000).

Response of understory trees

Contrary to our expectation, recruitment of trembling aspen in the 12 sampled stands was not improved by FTC defoliation intensity (Figure 3b), while recruitment of balsam fir was favoured and appeared more dependent upon defoliation intensity than upon gap size. The low density of trembling aspen suckers and saplings that was observed in stands defoliated for 3 y (Figure 3d) was consistent with the response of trembling aspen regeneration observed after an FTC outbreak in mixed stands of northeastern Ontario (Man & Rice, 2010). However, our results did not compare well with patterns reported after FTC outbreaks in pure trembling aspen stands, in which trembling aspen recruitment increased with the number of years of severe FTC defoliation (Man & Rice, 2010) and with gap size (Moulinier, Lorenzetti & Bergeron, 2011). This difference may have resulted from competition from residual coniferous trees (Peterson & Peterson, 1992), which contribute to reduced understory light penetration (Messier, Parent & Bergeron, 1998), to increased organic soil layer thickness (Laganière, Paré & Bradley, 2009), and to reduced soil temperature (Bonan & Shugart, 1989). These conditions are not favourable for trembling aspen root suckering and sucker survival (see Frey *et al.*, 2003).

The density of fir seedlings significantly increased with mean defoliation intensity and significantly decreased with gap size (Figure 3a,c). Balsam fir mast years have been reported to occur every other year in the study area (Messaoud, Bergeron & Asselin, 2007), and 2006, 3 y before our sampling, was an exceptional mast year (Robert *et al.*, 2012), suggesting that the observed patterns in fir seedlings are largely associated with the last FTC disturbance in those mixed stands. These patterns suggest that FTC defoliation created conditions that favoured the establishment of balsam fir seedlings at the stand, but not at the gap, level: 1) the increase in gap size and canopy opening with mean defoliation intensity enhanced light conditions sufficiently to improve balsam fir seed production (Greene *et al.*, 2002); 2) the dispersion over short distances of the large seeds of balsam fir (Asselin, Fortin & Bergeron, 2001) restricted colonization in large gaps and thus limited seedling establishment to the understory and close to seed trees; and 3) the combination of the effects of FTC defoliation on canopy opening and balsam fir seed production resulted in an increase in seedling density with mean defoliation intensity and not with gap size. Decreasing abundance of balsam fir regeneration with increasing gap size (Figure 3a) was also reported in mixedwood stands by Kneeshaw and Bergeron (1998).

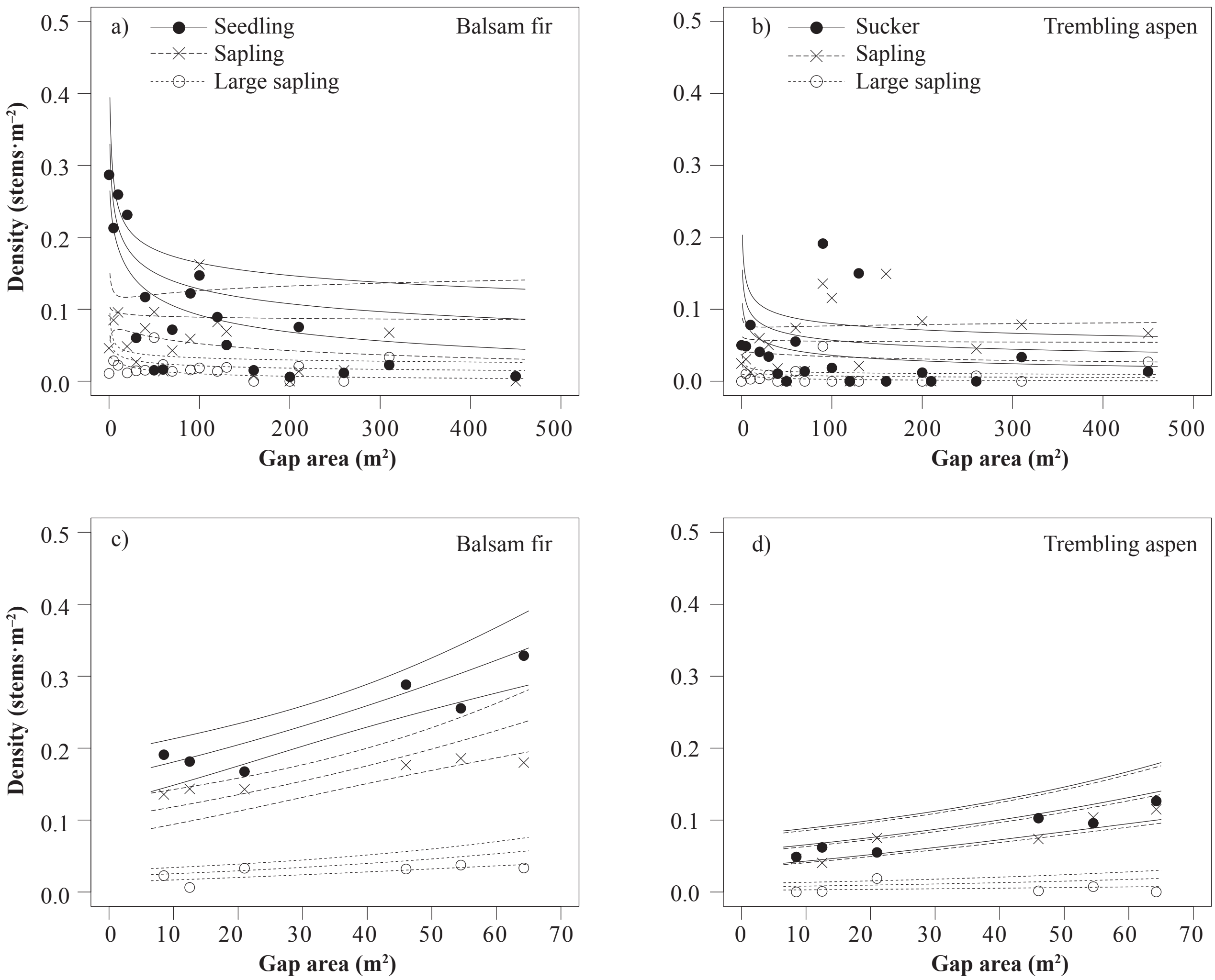

FIGURE 3. Effect of gap area and mean defoliation intensity on the density of balsam fir (a,c) and trembling aspen (b,d) regeneration in each of 3 height classes. Observed values are shown fitted with mixed logistic regression model (model-averaged estimates with 95% confidence intervals). Regeneration height classes for balsam fir: seedling (0 < 0.5 m), sapling (0.5–2 m), and large sapling (2–4 m). Regeneration height classes for trembling aspen: sucker (0 < 1 m), sapling (1–2 m), and large sapling (2–4 m).

Given that balsam fir can take 62 y to reach a height of 1.3 m (McCarthy & Weetman, 2006), most fir saplings (0.5–2 m), and most likely all large saplings (2–4 m), sampled in this study were advanced regeneration, present prior to the last FTC outbreak. The density of large fir saplings was low and not affected by gap size or by mean defoliation intensity, while the density of saplings tended to increase with defoliation intensity (Figure 3c). This increase in balsam fir sapling density may have resulted from the apical growth response of seedlings established prior to the outbreak.

In fact, apical growth of balsam fir seedlings and saplings (Figure 4b) increased during and after the last FTC outbreak, corroborating the reported effects of increased understory light availability (Parent & Messier, 1995) and patterns of balsam fir growth and survival (Arbour & Bergeron, 2011). The absence of a growth response among large saplings may have been the result of variation in resource allocation, mainly because taller balsam fir regeneration generally assigns higher priority to root diameter than to apical and radial growth after partial canopy removal (Claveau *et al.*, 2006).

GAP DYNAMICS AND FOREST STAND SUCCESSION

In stands that had been defoliated for 1 y, only a few co-dominant trees died following the FTC outbreak. In other studies, those trees were usually the smallest (Moulinier, Lorenzetti & Bergeron, 2011) and least vigorous ones (Man & Rice, 2010). Canopy opening rates revealed that gaps were more frequent after 1 y of severe defoliation than following light to moderate defoliation, but the gaps produced during severe defoliation were not larger or more aggregated than the others. Small changes in the canopy generated by low mortality rates could enable overtopped and intermediate trees (mainly conifers) to more rapidly access the canopy and thus modify stand composition and forest succession, but only slightly. In stands disturbed by 3 consecutive years of moderate or severe FTC defoliation, the presence of small and medium gaps, together with the forest matrix surrounding gaps, would favour balsam fir recruitment and alter succession

TABLE III. Linear mixed-effects model analysis describing balsam fir apical growth before, during, and after the last forest tent caterpillar outbreak in northwestern Quebec, which occurred between 1999 and 2002, and considering [height classes × period] and [defoliation intensity × period] interactions. Tested levels are shown in parentheses for categorical covariates.

Variables	Estimate	SE	*t*	*P* [a]
Def	–0.15	0.133	–1.174	0.260
Gap	0.07	0.015	4.379	**<0.010**
Hc (2)	0.78	0.093	8.423	**<0.010**
Hc (3)	1.06	0.189	5.617	**<0.010**
1999–2002	–0.53	0.184	–2.899	**<0.010**
2003–2006	–0.89	0.183	–4.883	**<0.010**
2007–2009	–0.85	0.183	–4.631	**<0.010**
Hc (2) × 1999–2002	–0.01	0.085	–0.125	0.901
Hc (2) × 2003–2006	–0.21	0.085	–2.447	**0.010**
Hc (2) × 2007–2009	–0.51	0.085	–6.002	**<0.010**
Hc (3) × 1999–2002	–0.07	0.174	–0.437	0.662
Hc (3) × 2003–2006	–0.34	0.174	–1.973	**0.050**
Hc (3) × 2007–2009	–0.56	0.174	–3.203	**<0.010**
Def × 1999–2002	0.26	0.052	5.029	**<0.010**
Def × 2003–2006	0.43	0.052	8.455	**<0.010**
Def × 2007–2009	0.48	0.052	9.277	**<0.010**

[a] Parameter estimates in bold type correspond to terms with significant effect ($P \leq 0.05$).

Def = defoliation intensity; Gap = Gap area; Hc = Regeneration height class; (2): sapling; (3): large sapling. Reference levels for the seedling height class (1) and for the period before the outbreak (1994–1998) are not shown.

from trembling aspen–balsam fir to balsam fir–trembling aspen. By contrast, the presence of large gaps, which generally favour the regeneration and survival of trembling aspen (Kneeshaw & Bergeron, 1998; Coates, 2002), could potentially contribute to the maintenance of a younger and mixed structure at the gap and stand levels (Bergeron, 2000; Cumming, Schmiegelow & Burton, 2000; Namroud *et al.*, 2005). However, our results indicate that the recruitment of aspen in large gaps is likely insufficient to completely close the canopy in years ahead.

Competition from shrub species such as mountain maple (*Acer spicatum*), speckled alder (*Alnus incana* subsp. *rugosa*), black alder (*Alnus glutinosa*), beaked hazel (*Corylus cornuta*), and raspberry (*Rubus idaeus*) was low in our study. However, shrub competition, when present, should be considered in assessing large gap trajectories, mainly because growth of such species generally increases after an FTC outbreak and where overstory mortality is high (Batzer & Popp, 1985; Kneeshaw & Bergeron, 1998; Man & Rice, 2010).

In the mixed matrix surrounding gaps, trembling aspen will likely continue to share dominance in canopy composition after an FTC outbreak until a new disturbance or natural tree senescence modifies canopy dominance. At the stand level, stand structure will evolve from an even-aged

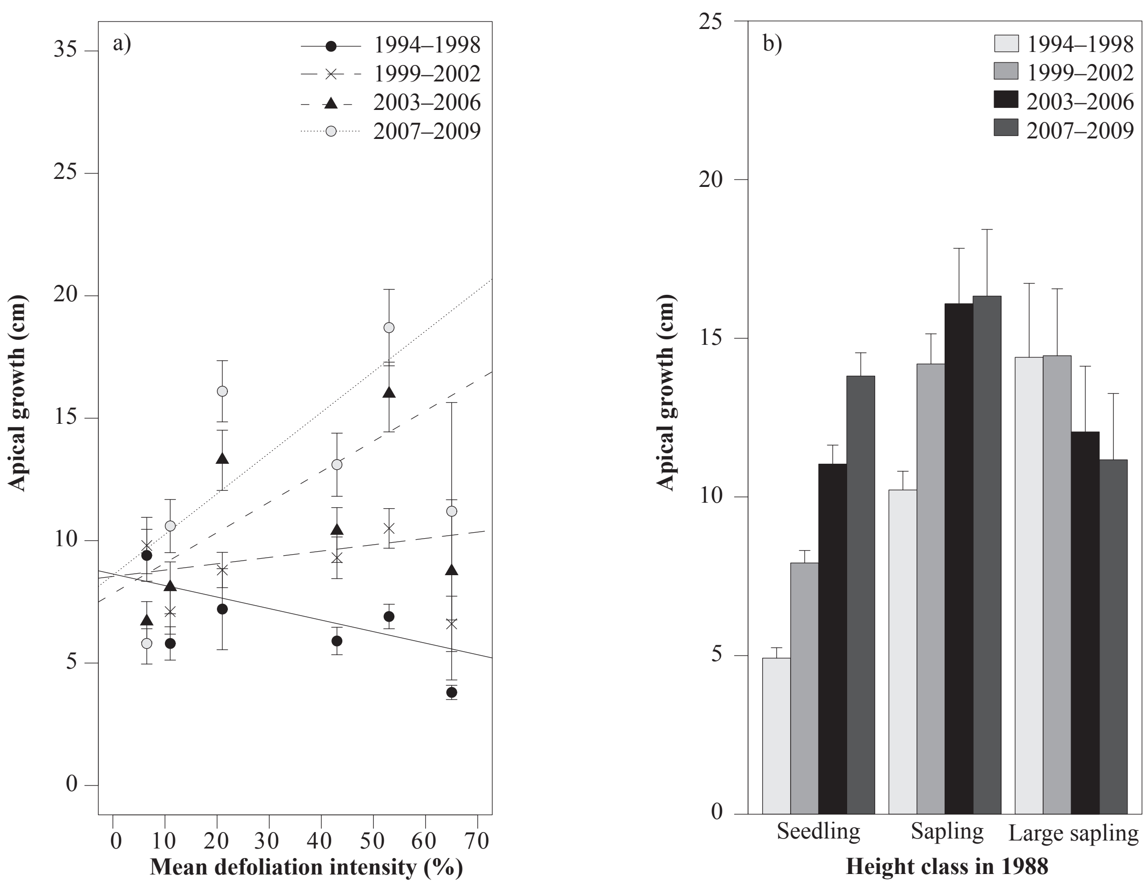

FIGURE 4. a) Effect of defoliation intensity on apical growth of balsam fir regeneration (mean ± SE) for different periods, *i.e.*, prior to (1994–1998), during (1999–2002), and following (2003–2006, 2007–2009) the last forest tent caterpillar outbreak that occurred in northwestern Quebec. b) Apical growth of balsam fir (mean + SE) for different height classes (based on height in 1998), *i.e.*, seedling (<0.5 m), sapling (0.5–2 m), and large sapling (2–4 m), during the 4 time periods.

to uneven-aged distribution because of the dynamics within gaps. In the case of repeated FTC outbreak events, exclusion of trembling aspen is expected to be exacerbated, with faster transition of stands to coniferous dominance.

Interestingly, the result of the FTC outbreak in these mixed trembling aspen–balsam fir stands was the opposite of that found following a spruce budworm outbreak in mixedwood stands, where repeated defoliations contributed to increased balsam fir mortality, thus reducing the fir component to the benefit of trembling aspen (Kneeshaw & Bergeron, 1998; Néalis & Régnière, 2004; Bouchard, Kneeshaw & Messier, 2007).

Conclusion

This study is complementary to previous work that sought to describe the effects of natural disturbances such as fire and spruce budworm outbreaks on boreal mixedwood forest succession. Our results clearly show that FTC outbreaks leave a unique signature in mixedwood stands dominated by trembling aspen. Variability in FTC outbreak severity and duration creates a range of canopy structures and modifies patterns of understory regeneration. The main difference between the responses of mixed *versus* deciduous stands to FTC defoliation lies in tree recruitment, which depends more upon defoliation intensity and canopy opening in mixedwood stands and on gap size in deciduous stands (Moulinier, Lorenzetti & Bergeron, 2011). From a successional viewpoint, less-disturbed stands will conserve their trajectories, while the transition from trembling aspen– to balsam fir–dominated mixedwoods will likely be accelerated after repeated FTC defoliation, which increases trembling aspen mortality. However, further monitoring of such disturbed mixedwood stands is required to evaluate the response of residual canopy trees and to assess the consistency of regeneration patterns and forest succession pathways over the long term.

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