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Site factors contribute to aspen decline and stand vulnerability following a forest tent caterpillar outbreak in the Canadian Clay Belt



Guillaume Perrette^{a,b}, François Lorenzetti^{b,*}, Julien Moulinier^c, Yves Bergeron^{a,c}

^a NSERC/UQAT/UQAM Industrial Chair in Sustainable Forest Management, Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succursale centre-ville, Montréal, Québec H3C 3P8, Canada

^b Institut des Sciences de la Forêt tempérée, Université du Québec en Outaouais, 58, rue Principale, Ripon, Québec JOV 1V0, Canada

^c 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

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ABSTRACT

Following the recent forest tent caterpillar (Malacosoma disstria Hbn.; FTC) outbreaks in the Canadian Clay Belt, several trembling aspen (Populus tremuloides Michx.) stands that have expressed variable mortality levels did not regenerate and were invaded by speckled alder (Alnus rugosa (DuRoi.) Sprengel.). The present study has been initiated to identify the causes of aspen dieback and of suckering inhibition, and to test silvicultural treatments to reinitiate stands having high stocking levels. A total of 84 plots were established in 2009 along a gradient of tree mortality based on the residual aspen live basal area (ALBA) in stands that had a high crown closure prior the last FTC outbreak. Treatments included winter and early summer harvest prior to the 2010 growing season, with or without alder removal in the winter of 2011. Results indicate that alder removal is not needed to regenerate the stands, that apical dominance of the residual trees played an important role in the inhibition of suckering but that ALBA was the main factor leading to higher sucker densities, suggesting that the root system was affected in the most degraded stands. A clear threshold of 11 m² ha⁻¹ ALBA has been evidenced above which stands can be regenerated. Below this threshold, suckering is too low to regenerate to productive stands. Moreover, this study is the first to show a strong and positive association between aspen mortality, humus layer thickness and water table height. Aspen was more vulnerable to FTC defoliation on sites combining a high water table and a thick humus layer. Because the basal area increment of residual trees has been lower since the 1950s on those sites, aspen dieback following the last FTC outbreak appears to be a symptom of a slower, long-term process of aspen decline. From a management viewpoint, it is suggested to convert these degraded sites to conifer stands.

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1. Introduction

Climate-induced forest decline is becoming prevalent worldwide (Allen et al., 2010). Trembling aspen (*Populus tremuloides* Michx.), the most widely distributed tree species in North America (Perala, 1990), recently exhibited evidence of widespread decline and of tree-and stand-level dieback (Frey et al., 2004; Michaelian et al., 2011; Anderegg et al., 2012; Worrall et al., 2013). The common view is that several predisposing and inciting factors initiated the decline and hastened the spread of dieback over millions of hectares (Wang et al., 2012). Drought, linked to climate change (Rehfeldt et al., 2009; Worrall et al., 2013), defoliation by insects (Cooke et al., 2009; Man and Rice, 2010; Moulinier et al., 2011),

* Corresponding author. *E-mail address:* Francois.Lorenzetti@uqo.ca (F. Lorenzetti). or both, acted in concert to cause widespread die-offs (Candau et al., 2002; Hogg et al., 2002).

Independent assessments have confirmed a strong link between aspen mortality and drought in western Canadian forests (Hogg et al., 2008; Steinkamp and Hickler, 2013). Aspen dieback in normally wetter areas of the eastern Canadian boreal biome such as the Clay Belt has also been extensive in the recent years. The Clay Belt of northeastern Ontario and northwestern Quebec, or the Northern Clay Section of the Boreal Forest Region of Canada (Rowe, 1972), is a 125,000 km² area of flat lowlands with surficial deposits resistant to drainage on which the development of organic soil is facilitated by the cold and wet climate (Lefort et al., 2002; Lavoie et al., 2005). Historically, the Clay Belt did not experience moisture limitation (Parker et al., 2012) and the increase in mean annual temperature over the last century has not led to increased summer drought severity (Girardin et al., 2004). Aspen dieback in Ontario's Clay Belt has been precisely mapped (Candau et al., 2002; Worrall et al., 2013) but not in Quebec. Candau et al. (2002) noted a significant drought event in 1998 for northeastern Ontario. However, in 1998 the concerned area was in the midst of a second wave of a Forest Tent Caterpillar (Malacosoma disstria Hbn.; FTC) outbreak, the initial wave having started in 1989 (Cooke et al., 2009). The highest levels of aspen dieback, which extended over 500,000 ha, were observed precisely where the two waves of FTC defoliation occurred with little respite between them. Hence, it is a challenge to tease apart the respective effects of climate and of defoliation on aspen dieback. Quebec's Clay Belt did not experience such a double wave of FTC attack, but defoliation reached 1.45 million ha over the period 1999-2002 with about 40% of the area experiencing more than one year of moderate to severe defoliation (Charbonneau et al., 2012). Aspen dieback was observable throughout the area following this FTC outbreak (Chouinard and Lorenzetti, 2006).

Investigations in both Ontario's and Quebec's Clay Belt indicated that aspen stands that were vulnerable following FTC defoliation have the potential to recover through gap-phase replacement dynamics, even in the presence of a shrub layer, or to accelerate the transition to coniferous dominance (Man and Rice, 2010; Moulinier et al., 2011, 2013). Although those regenerated stands expressed resilience following FTC defoliation, there is an impact on annual allowable cut. There are extensive areas in Quebec's Clay Belt, however, where forest succession halted due to a lack of aspen suckering and, presumably, to the establishment of an aggressive shrub layer (Chabot, 2009). This observation is in sharp contrast with the ability of aspen to rapidly regenerate from suckers following disturbances such as fires (Brown and Debyle, 1987; Wang, 2003) and partial- or clear-cuts (Brais et al., 2004; Gradowski et al., 2010). Aspen mortality in Quebec's Clay Belt has been shown to be a function of the number of years of moderate to severe FTC defoliation (Moulinier et al., 2011, 2013), with considerable variability when defoliation reaches three years in duration. This variability can be observed over a very small spatial scale, with aspen mortality spanning 0-100%.

This study was undertaken to specifically investigate the very low resilience observed in many aspen stands following the last FTC outbreak in Quebec's Clay Belt. Because apical dominance is considered an important factor inhibiting aspen sucker initiation (Farmer, 1962; Schier, 1975; Schier et al., 1985; Frey et al., 2003), a first objective was to determine the magnitude of this effect by cutting the trees still alive after the last FTC outbreak over a large range of aspen residual basal area. A second objective was to evaluate the benefits, or lack thereof, of speckled alder (*Alnus rugosa* (DuRoi.) Sprengel.) removal on aspen suckers generated after cutting. Our final objective was to investigate site factors that may explain the variation in stand vulnerability to FTC defoliation in the first place.

2. Material and methods

2.1. Study site

Located 95 km north of Amos, Quebec, Canada (Fig. 1), the study area is at the transition between the balsam fir-white birch and the black spruce-feather moss bioclimatic domains (Saucier et al., 1998). Mean annual temperature is -0.7 °C and mean annual precipitation is 905.5 mm, including 313.8 cm of snow (Environment Canada, 2012). The area belongs to the Canadian Clay Belt which is a vast physiographic region formed of glacio-lacustrine deposits originating from the proglacial Ojibway Lake (Vincent and Hardy, 1977). Mature aspen stands that originated from fires in the 1910s and 1920s contemporaneously dominate the area (Bergeron et al., 2004). These aspen stands extend over 10,000 ha (Chabot, 2009). Following a FTC outbreak of large amplitude in the early 2000s (Charbonneau et al., 2012), the stands started to exhibit different stages of decline and to be invaded by speckled alder (Chouinard and Lorenzetti, 2006). In 2009, georeferenced forest inventory maps produced in the late 1990s were used to delimit a large contiguous area which was homogenous for aspen dominance and for high crown closure. Poorly drained areas were avoided. Using this information, it was possible to delineate an operational-scale study site 300 ha in size. The study site lies close to the eastern edge of the Harricana interlobar moraine (Allard, 1974; Fig. 1; *inset*). An analysis of pre-disturbance aerial photos (1995) further confirmed that there were no large gaps or groups of snags at the selected site prior to the last FTC outbreak.

2.2. Experimental design and silvicultural treatments

A post-disturbance LANDSAT satellite image (2005) of the study site was calibrated to define three classes of aspen decline: 0–33, >33–66 and >66–100%. The resulting map served two purposes. First, it helped in delineating areas to apply different silvicultural treatments. Second, it served in 2009 to distribute evenly to each class of decline a total of 84 circular plots 20 m in radius (1256.6 m²). The true residual aspen live basal area (ALBA) in each plot was then measured on the ground with the aid of a prism (factor of 2 m² ha⁻¹). One measurement was taken at 10 m from the center in each of the cardinal directions and the four measurements were averaged to obtain the ALBA for the plot. The 84 plots covered a range of 0–36.5 m² ha⁻¹. ALBA was thus considered as a planned covariable in this study.

Sections of the study site were harvested during the winter (February and March of 2010) to circumvent the buildup of apical dominance through hormonal control during leaf flush (Schier et al., 1985; Weber, 1990). The remaining of the study site was harvested starting at the onset of the northern summer (June to mid-July 2010) when aspen trees were developing their leaves and apical dominance is thus the greatest. Since the stands have been determined to have no signs of dieback prior to the last FTC outbreak, it was expected that the residual basal area would have little to no effect on the density of aspen suckers. Winter- and summer-cut areas each encompassed 27 plots covering the ALBA range. No heavy machinery was allowed within the experimental plots. Trees too deep into the plots to be reached with a harvester head were cut using a chain saw, felled towards the edges of the plots and removed using a cable. The passage of the machinery at the edges of the 20 m-radius plots respects the prescription of keeping skid trails at a minimum distance of 20 m of each other so as to minimise soil compaction on the cutover area. This prescription is referred to as harvest with protection of soils (HPS). Hence, hereafter, the winter- and early summer-cut treatments will be referred to as HPS W and HPS S, respectively.

Alder was cleared in the winter of 2011 (January to March) in sections of both the winter and summer cutovers to test the hypothesis that alder impeded aspen sucker initiation and growth (Mundell et al., 2007). A bulldozer equipped with a sharp blade was run over the frozen ground without disturbing the forest floor (*protocol modified from Ministère des ressources naturelles du Québec* (MRNQ), 2010). The treatment encompassed 18 plots covering the ALBA range in both the winter and summer cutovers, leaving 9 winter-cut and 9 summer-cut plots untouched. Plots in which the alder removal treatment (AR) was performed will be referred to as HPS W+AR and HPS S+AR.

Of the 30 remaining plots, also covering the ALBA range, 18 were uncut and left as controls and 12 were used to cut down individual trees for dendrochronological analysis (*see* Section 2.3.3). It is to be noted that one HPS S+AR plot and one plot for dendrochronological



Fig. 1. Map of the study area and distribution of plots within the study site. The forest road shown on this map was established in 2009, one year before treatments began for this study.

analyses were destroyed during the alder removal operations due to a GPS malfunction. An additional plot (HPS S) was removed from analyses as it was considered an outlier due to data inconsistency with respect to many of the measured variables. Hence, 70 plots remained for statistical analyses and 11 plots for dendrochronological analyses.

2.3. Data collection

2.3.1. Aspen sucker and alder inventories

Aspen suckers were counted in late summer in each of the 70 plots in 2009 (before harvest), as well as in late summer from 2010 to 2012 (after harvest). All suckers within the same northand east-trending 1 m wide and 40 m long transects were counted. Each inventoried sucker was classified relative to the year of its establishment, i.e., 2010 or 2011, and to a height class (50 cm increments). The very few suckers established before 2009 counted after harvest were pooled with the 2010 cohort. No new suckers were established in 2012. Sucker density is hereafter reported on ha^{-1} basis. The stocking of >1.3 m suckers was also estimated in the same year. The presence/absence of healthy (no apparent damage or pathogens present on stems or leaves, and no leaf chlorosis) was determined in three microplots 1.6 m in radius and 5 m apart in each cardinal direction from plot centers i.e., twelve measurements per plot (*protocol modified from MRNQ*, 2007). To be counted as a free-to-grow, a sucker needed to be free of competition in the top third of the stem. The height and diameter at collar of healthy free-growing suckers were measured and the year of establishment was noted.

Alder inventory was undertaken using a 1×1 m quadrat. The quadrat was randomly launched one time within each quarter of the inner 10 m radius area and two times within each quarter of the outer 10 m radius area of each plot. Alder density was thus estimated on 12 m^2 in each plot and was converted to ha⁻¹ for

analyses. Alder density was determined by counting individual stems clearly arising directly out of the ground, whereas stems sprouting from one stump counted as one when they occurred. Each inventoried alder was classified relative to a height class (50 cm increments).

2.3.2. Soil and foliar measurements

Twenty-four harvested plots selected to cover the ALBA range, six in each of the four treatments (one HPS S plot was later declared an outlier) were selected to conduct soil and foliar measurements. In the early summer of the third growing season after harvest, three healthy free-growing aspen suckers in each of the four cardinal directions were selected in each plot. Investigations at the study site indicated that aspen suckers occurred consistently within a dark horizon and 5-10 cm below the surface of the forest floor. Thus, soil samples were collected at the same depth. Three bulk soil samples for chemical analyses were collected close to each selected sucker and all samples from a plot were pooled and mixed. The pooled samples were put on ice and brought to the lab to be air-dried and analyzed. A preliminary analysis of the samples based on the loss on ignition method (Heiri et al., 2001) indicated a range of 17-40% organic matter content. Based on the criterion by the Soil Classification Working Group (1998), 28% of the sampled plots had an organic horizon (\geq 30% organic matter) whereas the remaining plots had a mineral horizon enriched with organic matter. Consequently, according to Green et al. (1993), these horizons are considered a humus layer. Thereafter, the layer located between the B mineral horizon and the litter will be referred to as the humus layer (HL). The HL samples were further analyzed for total carbon (%C), total nitrogen (%N), total sulfur (%S) and pH using the protocols of Laganière et al. (2010), and for soil ammonium (N-NH₄) and soil nitrates (N-NO₃) using the protocols of Bilodeau-Gauthier et al. (2011).

Because it was observed that HL thickness varied widely among plots, this variable was measured in all remaining plots at every 5 m from plot centers in each of the cardinal directions, i.e., twelve measurements per plot. Additionally, the texture of the B mineral horizon was determined in the field using the feel method (Thien, 1979), but no samples were taken for additional analyses. Field observations indicated that the water table was close to the forest floor where HL was thick. To quantify the relationship between HL thickness and water table depth, and to estimate correlation coefficients with chemical soil variables, four piezometers 1.2 m in length were installed 10 m from plot centers, one in each of the cardinal directions, in each plot for which chemical analyses were conducted. The piezometers were made of PVC tubes (25 mm \emptyset) and inserted into the soil after a borehole was drilled using an auger. The space between the piezometers and the soil was filled with coarse sand and fine gravel. Measurements were collected at two different times: early September (when the water table is generally low) and mid-November (when the water table is generally high). At the time of each measurement, it did not rain 10-days prior. All piezometers were visited within two days during each measurement period. Measurements were then averaged for analysis.

To determine whether healthy free-growing aspen suckers differed in their nutritional status in relation to site variables (ALBA, HL thickness, HL chemical profiles and water table depth), leaf samples were collected at the same time HL was sampled. Before the leaves were sampled, their chlorophyll content was estimated using a chlorophyll meter (SPAD 502, Spectrum Technologies, Aurora, IL, USA) following the protocol of Bonneville and Fyles (2006). Three leaves from three different branches were collected at the apex of each sucker and four chlorophyll measurements were taken on each leaf. These measurements are hereafter reported as SPAD. All SPAD leaves were collected and conserved on ice, brought to the lab and dried in a forced-air drier (35 °C/48 h) prior to chemical analyses. The total carbon, nitrogen and sulfur contents of the foliar samples were determined using the same protocols for HL. Chlorophyll measurements were extended to all other treated plots to determine if the same range of values was observed at the scale of the study site. Collectively, the chlorophyll measurements made in all treated plots are thereafter referred to as SPADTOT.

2.3.3. Tree-ring data and analyses

Circular cross-sections were collected in 2012 at 30 cm above ground on the four largest live aspen trees found within the inner 10 m radius area of the 11 uncut plots left aside for dendrochronological analyses. Those plots covered most of the ALBA range, but to sample more of the lower ALBA range, cross-sections were also collected in four control plots. We note that when no live trees were present within plots in the low ALBA range, circular cross-sections were collected on snags from the largest trees that died during or after the last FTC outbreak. However, average growth over periods with low disturbance did not differ between live and dead trees (*results not shown*).

Cross-sections were air-dried and progressively polished with up to 600-grit sandpaper. Annual ring widths were measured on three radii per cross-section using a stereomicroscope (Leica MZ125) coupled to a Velmex numeric table with a precision of 10 µm. Individual ring-width series were cross-dated based on pointer years, i.e. years in which 75% or more of the cross-dated trees had $\ge 10\%$ narrower or wider rings than the previous year (Becker, 1989; Mérian and Lebourgeois, 2011). Absolute dating was checked using the COFECHA software (Grissino-Mayer, 2001). Ring width data were then used to calculate annual basal area increments. White rings indicative of severe caterpillar defoliations (Hogg et al., 2002) were dated. When one white ring was observed within at least one tree, the plot was determined as defoliated. Thus, the defoliation history of the study site is reported as the proportion of affected plots.

2.4. Statistical analyses

Unless otherwise indicated, statistical analyses were performed using the JMP software, version 10.0.0 (SAS Institute, Cary, NC, USA). Analysis of covariance (ANCOVA) was used with ALBA as a covariate on aspen sucker density data. Wilks and Brown-Forsythe tests were used to test normality and homoscedasticity assumptions, respectively. Data were transformed using the Box-Cox model (Box and Cox, 1964) when model residuals did not meet the assumptions of normality and homoscedasticity. Because zero values in aspen sucker counts occurred at the sub-plot level, a value of 1 was added to all counts. Interactions between treatments and ALBA in all ANCOVA models were first tested, and as they were found not significant, models were rerun without the interaction term. When the presented results are back-transformed values from Box-Cox transformations applied prior to analyses, it is stated explicitly. To examine treatment effects over time on the density of the 2010 and 2011 aspen sucker cohorts and on alder density, a multivariate analysis of variance (MANOVA) was performed. After it was determined by ANCOVA that water table and HL thickness data were not different among treatments, including the control plots, linear regressions were performed to model the relationships between those variables and the covariate ALBA. Concentrations of HL and foliar contents were analyzed using a correlation matrix. Prior to correlation matrix analysis, ANCOVA were also performed with ALBA, water table depth, and HL thickness as covariates in order to confirm that there was no interaction between treatments and covariates. Difference in height, diameter and H/D ratio of healthy free-to-grow aspen suckers, and height of all aspen suckers and alder among treatment were determined using ANOVA analyses as no interaction between treatments, and no ALBA effect, occurred. Finally, differences in height between cohorts of outcompeted and free-to-grow aspen suckers within treatment were assessed by paired *t*-tests.

3. Results

In 2009, prior to harvest, aspen sucker density was positively and significantly related to ALBA (Table 1) although their mean number throughout the ALBA range was low (146 stems ha⁻¹;

Table 1

Results of ANCOVA analyses comparing aspen sucker densities between (a) plots allocated to silvicultural treatments and to control prior harvest, between (b) HPS W, HPS S and control plots in the first growing season after harvest, and between (c, d) HPS W, HPS S, HPS W+AR, HPS S+AR and control plots in the second and third growing seasons, with aspen live basal area (ALBA) as a covariate. Data were transformed using Box–Cox transformations prior to analyses. Significant effects (p < 0.05) are indicated in bold.

| | Source | df | MS | F | Р |
|-----|--|----|------------|--------|---------|
| (a) | 2009 – Before harvest | | | | |
| | Model | 3 | 250858 | 2.56 | 0.0622 |
| | Treatment + control | 2 | 470 | 0.01 | 0.9928 |
| | ALBA | 1 | 249718 | 7.65 | 0.0073 |
| | Error | 66 | 2153480 | | |
| | Corrected total | 69 | 2404338 | | |
| (b) | 2010 – After harvest | | | | |
| | Model | 3 | 3276161355 | 70.32 | <0.0001 |
| | Treatment + control | 2 | 567433936 | 18.27 | <0.0001 |
| | ALBA | 1 | 2571494322 | 165.59 | <0.0001 |
| | Error | 66 | 1024915466 | | |
| | Corrected total | 69 | 4301076821 | | |
| (c) | 2011 – After harvest and alder removal | | | | |
| | Model | 5 | 1.27E+10 | 27.88 | <0.0001 |
| | Treatment + control | 4 | 4043483366 | 11.09 | <0.0001 |
| | ALBA | 1 | 7341054099 | 80.53 | <0.0001 |
| | Error | 64 | 5834096422 | | |
| | Corrected total | 69 | 1.85E+10 | | |
| (d) | (d) 2012 – After harvest and alder removal | | | | |
| | Model | 5 | 3972611574 | 32.19 | <0.0001 |
| | Treatment + control | 4 | 1137787126 | 11.53 | <0.0001 |
| | ALBA | 1 | 2121868777 | 85.98 | <0.0001 |
| | Error | 64 | 1579481645 | | |
| | Corrected total | 69 | 5552093219 | | |

| Table 2). Suckers were present in 73% of the 70 experimental plots. |
|--|
| However, 50% of the plots with no sucker present were below an |
| ALBA of 11 m ² ha ⁻¹ . Using piecewise regression (NCSS, version |
| 2004, Kaysville, Utah, USA), this threshold of 11 m ² ha ⁻¹ was also |
| found to be significant ($F_{4,66}$ = 206.5, $p < 0.0001$) in distinguishing |
| two different relationships between alder densities and ALBA be- |
| fore harvest: below 11 m ² ha ⁻¹ alder density increased when ALBA |
| decreased ($F_{1,13}$ = 23.94, p = 0.0003, R^2 = 0.65), and above |
| $11 \text{ m}^2 \text{ ha}^{-1}$ alder density was not related to ALBA ($F_{1,53}$ = 1.61, |
| $p = 0.2096$, $R^2 = 0.03$). The threshold of 11 m ² ha ⁻¹ has also proved |
| to be important in relation to site factors as it will be presented |
| later. |

3.1. Aspen regeneration after silvicultural treatments

In all years following harvest, ALBA had a significant positive effect on sucker density and treated plots had significantly higher sucker densities than control plots (Tables 1 and 2; Fig. 2). In 2010, one year after harvest, aspen sucker density was two times higher for winter-cut (HPS W) than for summer-cut (HPS S). In 2011, two years after harvest, HPS W had the same sucker density as HPS S. Alder removal in the winter before the 2011 growing season had no effect on aspen sucker density at the end of the season compared to leaving alder untreated. Aspen sucker density increased in all treatments in 2011 compared to 2010, but there were no significant differences among them. In 2012, aspen sucker densities started to decline in all treatments but with no significant differences among them.

3.2. Aspen sucker cohort establishment and survivorship dynamics

To analyse the establishment and survivorship dynamics of aspen sucker cohorts, plots with ALBA > 11 m² ha⁻¹ were used due to the lack of, or very low, suckering observed in plots below 11 m² ha⁻¹ (Fig. 2). Between 2010 and 2012, total aspen sucker densities varied over time, peaking in 2011, i.e., two years after harvest (Fig. 3; MANOVA, $F_{2,37} = 34.35$, p < 0.0001). The 2010 sucker cohort was influenced by treatments (MANOVA, $F_{3,38} = 5.19$, p = 0.0042), by years (MANOVA, $F_{2,37} = 21.63$, p < 0.0001), and by the interaction between treatments and years (MANOVA, Pillai's trace = 0.43, $F_{6,76} = 3.51$, p = 0.0041). Subsequent univariate ANO-VAs and Tukey HSD post hoc tests indicated that in 2011, two years

Table 2

ALBA adjusted aspen sucker mean densities (stems ha^{-1}) calculated from ANCOVA. Results were backtransformed from Box–Cox transformations. Values within each year with similar letters are not significantly different based on Tukey HSD post hoc tests (p < 0.05).

| Year | Treatment | Mean - SD | Mean | Mean + SD |
|------|-----------------------|-----------|----------|-----------|
| 2009 | All plots | 13 | 146 | 745 |
| 2010 | HPS W ^a | 5215 | 15,432 a | 37,619 |
| | HPS S ^b | 2019 | 7315 b | 20,346 |
| | Control | 288 | 1669 c | 6111 |
| 2011 | HPS W ^a | 12,836 | 27,416 a | 49,030 |
| | HPS S ^b | 9957 | 23,061 a | 43,193 |
| | HPS W+AR ^c | 13,144 | 27,784 a | 49,389 |
| | HPS S+AR ^d | 17,421 | 34,202 a | 58,149 |
| | Control | 1441 | 6601 b | 16,883 |
| 2012 | HPS W ^a | 10,843 | 20,378 a | 33,710 |
| | HPS S ^b | 7188 | 15,057 a | 26,623 |
| | HPS W+AR ^c | 6163 | 13,234 a | 23,742 |
| | HPS S+AR ^d | 8703 | 17,074 a | 29,016 |
| | Control | 933 | 3805 b | 9304 |

^a Harvest with protection of soils in winter.

^b Harvest with protection of soils in early summer.

^c HPS W, followed by alder removal.

^d HPS S, followed by alder removal.



Fig. 2. Aspen sucker densities (a) after winter (HPS W) and early summer (HPS S) harvests in 2010, (b) after harvest (HPS W and HPS S) and alder removal (HPS W+AR and HPS S+AR) in 2011 and (c) in 2012, in relation to the aspen live basal area (ALBA) measured in 2009. Variations in ALBA are due to aspen mortality following a forest tent caterpillar outbreak during the years 2000–2002 at the study site. In 2010, ANCOVA analysis yielded significantly different predicted curves for HPS W (full grey line), HPS S (dashed grey line) and control (dotted black line) plots. In 2011 and 2012, ANCOVA analyses indicated that aspen sucker densities were similar in all treatments (full black line) but different from controls. Prior to ANCOVAs, data were transformed using Box–Cox transformations with the following parameter values: (a) $\lambda = 0.2$, $\alpha = 3.406E-4$, (b) $\lambda = 0.4$, $\alpha = 1.605E-3$, and (c) $\lambda = 0.4$, $\alpha = 2.335E-3$. Legend for (c) same as in (b).

after harvest and one year after alder removal, the 2010 cohort was significantly more dense in winter-cuts (HPS W) compared to all other treatments, except HPS W+AR, the sucker density of which was not different from other treatments. In 2012, the 2010 sucker cohort in the winter-cut was more dense than in all other treatments, whereas in the summer-cut, the 2010 cohort had a density intermediate between the winter-cut and both the HPS W+AR and HPS S+AR treatments, the latter having the lowest 2010 cohort density. The 2011 sucker cohort was also influenced by treatments (MANOVA, $F_{3,38} = 11.28$, p < 0.0001), by years (MANOVA, $F_{1,38}$ = 50.47, p < 0.0001), and by the interaction between treatments and years (MANOVA, $F_{3,38} = 6.62$, p = 0.001). The contribution of the 2011 cohort to the total density of aspen suckers in the winter-cuts was minimal both in 2011 and 2012 and its absolute density was always lower than in any other treatment, except for HPS W+AR in 2012 (univariate ANOVAs and Tukey HSD post hoc tests). The 2011 cohort densities did not differ between HPS S, HPS S+AR, and HPS W+AR in 2011 and were only transitively different in 2012 (HPS S+AR \ge HPS S > HPS W+AR). In all treatments, the 2011 cohort compensated for the decline in the densities of the 2010 cohorts, and total densities reached similar levels from 2011 onwards (Fig. 3).

3.3. Alder density and height before and after silvicultural treatments

The temporal dynamics of alder were similar among treatments and followed the same significant pattern observed with aspen suckers, i.e. peaking in 2011 and declining in 2012 (Fig. 4; MANO-VA, $F_{3,47}$ = 28.51, p < 0.0001). The removal treatment of alder during the winter of 2010, one growing season after cutting remaining aspen trees, did not decrease alder density (Fig. 4). In 2009 and 2010, before alder removal, and in 2011 and 2012, after alder removal, alder density was similar for treatments with ALBA > 11 m² ha⁻¹, whereas it was greater for treatments with ALBA < 11 m² ha⁻¹, as expected from Fig. 4 (MANOVA, $F_{2,49}$ = 25.44, p < 0.0001). If using a bulldozer blade had no effect on alder density, on the other hand it did significantly reduce their height by half (Fig. 5, *horizontal dashed lines*; ANOVA, $F_{1,39}$ = 48.60, p < 0.0001).

3.4. Aspen sucker stocking and vigor

ALBA positively influenced the stocking of healthy free-to-grow (>1.3 m) aspen suckers, as measured in 2012 in treated plots with an ALBA > 11 m² ha⁻¹ (ANCOVA, $F_{1,37}$ = 13.66, p = 0.0007). However, ALBA did not influence the height (ANCOVA, $F_{1,37}$ = 0.75, p = 0.3927), nor the diameter (ANCOVA, $F_{1,37}$ = 2.86, p = 0.0993), or the H/D ratio (ANCOVA, $F_{1,37}$ = 0.48, p = 0.4933) of those suckers. The influence of ALBA on stocking is major considering that the slope of the relationship is 1.74. Over an ALBA range of 11–40 m² ha⁻¹, this effect reduces stocking by 51 percentage points.

In plots with an ALBA < $11 \text{ m}^2 \text{ ha}^{-1}$, stocking was low with a mean of 12% (SD ± 14). In plots with an ALBA > 11 m² ha⁻¹, stocking was significantly higher, and greater than 70%, for HPS plots than for HPS+AR plots (Table 3; ANCOVA, $F_{4,37} = 17.82$, p < 0.0001). Cutting season had no effect on stocking. Free-growing suckers were taller in the HPS W treatment than in the HPS S treatment, but in both treatments suckers were taller than when alder removal was applied (ANOVA, $F_{3,38}$ = 46.08, p < 0.0001). Differences in stocking do not appear to be related to differences in height between 2010 and 2011 suckers as no height difference was observed between free-growing suckers of the two cohorts (Fig. 5b). Hence, even if stems from the 2010 sucker cohort varied in proportion between the HPS W (98%), HPS S (72%), HPS W+AR (71%) and the HPS S+AR (39%) plots, the differences in stocking are attributable to a treatment effect rather than to a cohort effect. Most often, within treatments, free-growing suckers were double in height compared to outcompeted aspen suckers, but differences among treatments were similar between free-growing and outcompeted suckers within cohorts (Fig. 5a and b). As for stocking, diameter at collar was significantly higher for HPS than for HPS+AR, regardless of harvest season (Table 3; ANOVA, *F*_{3,38} = 34.62, *p* < 0.0001). However, height-diameter (H/D) ratios were similar among treatments (Table 3; ANOVA, *F*_{3,38} = 1.71, *p* = 0.1813).

3.5. Relationships between aspen foliar and HL chemistries

The chlorophyll contents of leaves collected on healthy freegrowing aspen suckers were similar throughout the experimental plots (SPADTOT range = 29.4–40.8 *vs* SPAD range = 30.0–40.8). SPAD was positively correlated to total foliar nitrogen (N) content (range = 2.36–3.41%; r = 0.51, p = 0.0119; Table S1). However, SPAD values and total foliar N content were not significantly correlated to the total HL N content (range = 1.39–2.16%; r = -0.36, p = 0.0917 and r = -0.11, p = 0.6285, respectively), nor with the



Fig. 3. Temporal dynamics of aspen sucker densities by cohort and by year, for plots with an ALBA > 11 m² ha⁻¹, in each of the silvicultural treatments. The dark vertical lines in the bottom panel indicate when the alder removal treatment was applied.



Fig. 4. Temporal dynamics of mean alder density (stems ha^{-1}) for harvested plots, with or without alder removal (HPS, HPS+AR respectively), and below or above an ALBA of 11 m² ha⁻¹. Note that there were no plots below an ALBA of 11 m² ha⁻¹ in the HPS treatment. Error bars are ± SD.

N–NH₄ (range = 129.2–339.0 mg kg⁻¹; r = -0.16, p = 0.4674 and r = -0.24, p = 0.2673, respectively) or the N–NO₃ (range = 4.0–43.0 mg kg⁻¹; r = -0.34, p = 0.1079 and r = 0.04, p = 0.8722, respectively) contents of HL.

Despite the small observed ranges in SPADTOT, SPAD and total foliar N, values significantly increased with ALBA (r = 0.79,

p < 0.0001, r = 0.89, p < 0.0001 and r = 0.56, p = 0.0051, respectively). Inversely, the N and N–NH₄ (range = 129.2–339.0 mg kg⁻¹) contents of HL significantly decreased with ALBA (r = -0.53, p = 0.0097 and r = -0.44, p = 0.0377). The N–NO₃ content of HL (range = 4.0–43.0 mg kg⁻¹) also decreased with ALBA, but not significantly so (r = -0.37, p = 0.0796). The sulfur (S) contents of the aspen foliage (range = 0.12–0.29%) and of the HL (range = 0.21–0.32%) significantly increased and decreased, respectively, with ALBA (r = 0.55, p = 0.0061 and r = -0.77, p < 0.0001, respectively). The pH of HL (range = 4.24–5.86) was highly and positively correlated with ALBA (r = 0.79, p < 0.0001).

3.6. Relationships between water table depth, HL thickness and ALBA

HL thickness and water table depth were strongly and inversely related (r = -0.91, p < 0.0001; Table S1). HL thickness decreased with ALBA (r = -0.78, p < 0.0001) while water table depth increased (r = 0.68, p < 0.0004). When HL depth interfaced with water table depth at around 20 cm below the surface of the forest floor, it coincided closely with the break point identified in the relationship between alder density before harvest and ALBA, i.e. $11 \text{ m}^2 \text{ ha}^{-1}$ (Fig. 6). The texture of the mineral layer below HL (B horizon) was determined to be that of clay in plots below the ALBA



Fig. 5. Mean (\pm SD) height (cm) after three growing seasons of (a) all aspen suckers and (b) free-growing suckers, by cohort and by treatment, in plots with an ALBA > 11 m² ha⁻¹. Differences between cohorts within treatments, based on paired *t*-tests with Bonferroni-correction criteria applied for significance level: ^{*} and ns above bar pairs indicate significant and no significant differences, respectively. Differences between treatments within cohorts: different letters above bars indicate significant differences based on Tukey HSD post hoc tests (*p* > 0.05). The black dashed lines in (a) and (b) are mean height (cm) of alder in the same year in plots with or without alder removal (HPS, HPS+AR respectively). Note that there is no bar for the free-growing 2011 cohort in HPS W plots since only one stem was counted.

Table 3

Mean stocking, height, diameter at collar, and H/D ratio of free-growing aspen suckers in treated plots with an ALBA > $11 \text{ m}^2 \text{ ha}^{-1}$ in the third growing season. Standard errors of means are presented in parentheses. Values with similar letters in the same column are not significantly different based on Tukey's HSD post hoc tests (p < 0.05).

| Treatment | No. of plots | Stocking (%) ^a | Height (cm) | Diameter (cm) | H/D |
|-----------|--------------|---------------------------|---------------|---------------|--------------|
| HPS W | 9 | 86.7 (6.5) a | 230.3 (5.3) a | 2.50 (0.06) a | 93.8 (2.7) a |
| HPS S | 8 | 77.1 (7.0) a | 200.9 (5.9) b | 2.33 (0.07) a | 87.8 (2.9) a |
| HPS W+AR | 12 | 33.4 (5.6) b | 160.6 (4.6) c | 1.89 (0.06) b | 86.7 (2.4) a |
| HPS S+AR | 13 | 51.4 (5.5) b | 158.5 (4.5) c | 1.75 (0.05) b | 92.0 (2.3) a |

^a Means and standards errors for stocking values were adjusted using the ALBA covariate.



Fig. 6. Predicted curves of the relationships for humus layer (HL) thickness ($F_{1,68} = 116.24$, p < 0.0001, $R^2 = 0.63$) and water table depth ($F_{1,39} = 53.70$, p < 0.0001, $R^2 = 0.58$), measured in the third growing season, with ALBA in pooled treated and control plots. Plot-level alder densities prior to harvest are overlaid (filled and open circles: clay and clay loam, respectively; mineral soil texture determined by the feel method). A piecewise regression indicated a breaking point at 11.1 m² ha⁻¹ in the relationship between alder density and ALBA ($F_{4,66} = 5.20$, p = 0.001, $R^2 = 0.58$; grey shaded areas: 95% confidence intervals).

threshold of 11 m² ha⁻¹. Above this threshold, the number of plots with a clay loam texture increased with ALBA.

3.7. Divergence in growth of aspen trees in relation to ALBA

Dendrochronology plots were distinct from treatment plots, but their HL thickness also decreased significantly with ALBA ($F_{1,13} = 32.22$, p < 0.0001, $R^2 = 0.71$). Parameter estimates for this relationship for dendrochronology plots (y = -0.8147x + 29.997) were consistent with estimates found for treated plots (y = -0.7668x + 28.129).

The basal area increment (BAI) of aspen trees at the study site was found to have large interannual variations over the span of ~90 years (Fig. 7b). Large growth reductions occurred every decade and coincided with the presence of white rings (Fig. 7c). Based on the non-overlap of 95% confidence intervals, plots with an ALBA < 11 m² ha⁻¹ after the last FTC outbreak started to exhibit reduced BAI in the 1950s compared to plots with an ALBA > 11 m² ha⁻¹. This lower growth was maintained much of the time up to 2012.

4. Discussion

4.1. Reinitiating aspen stands after disturbances by the forest tent caterpillar

Results from our 300 ha study site show that aspen can be vigorously regenerated in the first growing season immediately following the removal of stems that were still alive after an FTC outbreak (Table 2, Fig. 2a). The fact that winter-cuts resulted in more suckering than early summer-cuts during the first growing season indirectly confirmed the hypothesis that apical dominance exerted by residual stems largely control the suckering response



Fig. 7. Growth of residual aspen trees: (a) number of plots, (b) tree-level annual basal area increment and (c) the proportion of plots with white rings indicative of severe forest tent caterpillar defoliation. The dark lines in (a) and (b) are for plots with ALBA > 11 m² ha⁻¹, whereas grey lines are for plots with ALBA < 11 m² ha⁻¹. The shaded areas in (b) are the 95% confidence intervals.

(Schier, 1975; Schier et al., 1985). However, apical dominance is not absolute and is not the sole factor controlling suckering since suckers were present before and after harvest in control plots and density increased with ALBA. Schier et al. (1985) previously made this observation that some suckering can occur in aspen stands. Still, the doubling of sucker density in winter cuts compared to summer cuts observed in our study is indicative that apical dominance is a major driver of the suckering response (Table 2). Our results corroborate previous findings by Weber (1990) that cutting aspen just prior to leaf flush resulted in more suckering than cutting just after leaf flush. It should be stressed though that there is also a phenological gradient in roots carbohydrate reserves (Bates et al., 1993). Those reserves are low in winter and during leaf flush because of root growth during the previous fall (Landhäusser and Lieffers, 2003). Hence, root reserves are also suspected to contribute to poor suckering, presumably in direct relation to how much has been diverted for root growth. However, since root reserves are low just before and after leaf flush, this factor does not explain the larger suckering response observed following winter cuts.

Several authors have reported that retaining aspen during harvest decreases suckering (David et al., 2001, and references therein). Brais et al. (2004) and Gradowski et al. (2010) showed a strongly significant inverse correlation between residual aspen basal area and aspen sucker density after different levels of partial cuts. In our study, the opposite pattern was observed, with aspen sucker density increasing with ALBA, even before harvest (Table 1). It was expected that the complete removal of aspen would stimulate the same level of suckering throughout much of the ALBA range. Given that the stands at our study site had similar basal area before the FTC outbreak, our results suggest that much of the root system, and not only the stems, died in plots with a lower ALBA following the outbreak.

The initial difference in sucker densities between winter and summer cuts diminishes quickly in the following growing seasons, a result similar to what Weber (1990) and Bates et al. (1993) found in eastern Ontario and in northern Minnesota, respectively. This convergence in aspen sucker densities among treatments may be related to a process, from an energy balance perspective, in which the above and below ground systems are progressing towards equilibrium. By examining individual sucker cohorts generated after applying cut-treatments to the residual stems, our study was able to show their contrasting dynamics through time (Fig. 3). The initiation of a new cohort in the second growing season in early summer-cuts that is denser than that of winter-cuts. coupled with an absence of establishment of a third cohort in both treatments, indicates that the entire system was equilibrated as soon as at the end of the second year by reaching similar sucker densities, but with different ratios of first- and second-year cohorts (Fig. 3a and b). Similarly, by attempting to remove alder after the first growing season, the first aspen sucker cohort was artificially reduced, forcing the system to generate abundant second season sucker cohorts for which densities were inversely related to the previous season densities (Fig. 3c and d). Again, sucker densities reached similar densities at the end of the second growing season, but with different ratios of first- and second-year cohorts. From a management point of view, at least for stands with a sufficient residual basal area, i.e., >11 m² ha⁻¹, it does seem that prescriptions should be based on other criteria (e.g. soil susceptibility to compaction and rutting) to determine whether to conduct winter or summer cuts. From our results, and from the literature (Baker, 1925; Bates et al., 1993; Mundell et al., 2008), it appears safe to presume that summer, or late summer, cuts, should result in aspen sucker densities much closer, if not similar, to that obtained with winter cuts, since auxin synthesis decreases as the growing season progresses (Schier, 1973), and hence apical dominance relaxes progressively (Perala, 1990).

Cutting season did not influence the stocking of healthy free-togrow (>1.3 m) aspen suckers, as measured at the end of the third growing season in our study. Stocking values are sufficient in both winter and early summer-cuts (Table 3). However, removing the aggressive alder layer established before cutting by using a blade in the winter following the first growing season significantly decreased stocking below acceptable levels. The treatment applied between the 2010 and the 2011 growing season reduced the average height of the 2010 aspen sucker cohort, but it also reduced the average height of alder (Fig. 5a). The alder removal treatment should have favored stocking. However, because our criteria in our stocking evaluation specified that the stem had to be free of damage, the alder removal treatment actually decreased stocking below acceptable levels (Table 3). If the alder removal treatment had been applied right after the cutting treatments, stocking levels likely would have been higher, but we do not see what benefit may have resulted from this, especially with respect to the cost of the treatment and the high stocking levels obtained when alder was left in place. In the context of reinitiating highly productive stands affected by FTC defoliation, the observed strong decrease in stocking with decreasing live aspen basal area is more critical.

Our results also indicate that free-growing aspen suckers were unable to take advantage of the increased nitrogen pool, especially in the form of ammonium, with decreasing live aspen basal area (Table S1). Nitrogen was indeed higher in HL where ALBA was low and alder density was high. The nitrogen pool with lower ALBA values may also have benefitted from the contribution of decomposition of the dead aerial biomass. Although the height, diameter and H/D ratio of free-growing aspen suckers were not influenced by ALBA, foliar nitrogen content decreased with ALBA despite the increased availability of nitrogen in the HL. The foliar nitrogen content measured for free-growing suckers in the lower range of ALBA was rather low compared to other published results (Lorenzetti et al., 1999; Osier et al., 2000). Low foliar nitrogen is indicative that site conditions in the most degraded stands following the last FTC outbreak are no longer optimal for maintaining productive aspen stands. The lower pH measured in the lower ALBA range could explain the observed lower foliar nitrogen content. Nitrogen uptake has been shown to be positively associated with pH in aspen seedlings, which is particularly true for ammonium (DesRochers et al., 2003). Another indication of nutrient uptake being affected is that foliar sulfur content decreased in the lower ALBA range. Sulfur was more abundant in the lower ALBA range, but likely the lower pH reduced sulfur uptake. Sulfur is important in the synthesis of chlorophyll and the lower sulfur content may explain the lower chlorophyll content (Imsande, 1998), measured as SPAD, in the lower ALBA range.

The inverse relationship between HL thickness and water table depth reported in our study (Fig. 6) suggests that conditions which increased vulnerability of aspen stands in the lower ALBA range were already in place before the last outbreak occurred. Defoliation by insects can raise the water table because of reduced evapotranspiration (Hélie et al., 2005), which can lead to root asphyxia (Kamaluddin and Zwiazek, 2002). However, analyses of radial growth indicate that plots with high aspen mortality, and with low aspen regeneration density, were plots in which basal area increment was the lowest several years before the last FTC outbreak (Fig. 7b). Hogg and Schwarz (1999) reported a similar long term decrease in growth of aspen trees before symptoms of decline became apparent in the mid-90s in Saskatchewan.

4.2. A wider perspective on the forest tent caterpillar-aspen system in the Clay Belt

Prior to the last FTC outbreak, the aspen stands at the study site were classified with a high crown closure rating. Forest inventory maps also indicated that these stands were not growing on sites with poor drainage. After the last FTC outbreak, some of these stands were categorized as degraded and dendrochronology analyses revealed reduced tree growth compared to trees in more resilient stands (Fig. 7b). Aspen with lower basal area increment since the 1950s, which were growing on sites with a thick HL (>20 cm) and a high water table, were particularly affected following the 2000-2002 defoliations by the FTC. Since the 1950s, aspen periodically underwent FTC defoliation in northwestern Quebec's and northeastern Ontario's Clay Belt (Cooke et al., 2012). The presence of white rings indicated several episodes of severe growth reductions since 1950 at our study site, but some episodes were also evident before that decade (Fig. 7b and c). Since these growth reductions were simultaneously present in plots with an ALBA lower or greater than 11 m² ha⁻¹, we cannot ascertain if repeated FTC defoliations were a cofactor in the change in growth trajectories of aspen stands observed at our study site, especially given that low and high ALBA plots were spatially well dispersed. Repeated defoliations by the FTC can kill otherwise vigorous aspen trees (Moulinier et al., 2014). Though, the demise of aspen stands appears to have been hastened following the last FTC outbreak. The advanced age of the stands in our study site could be invoked for such timing. However, the annual basal area increment of trees in plots with ALBA > 11 m² ha⁻¹ returned after the outbreak to the high values observed in previous decades. An alternative hypothesis for the change in the growth trajectory of the most degraded

stands would have to be based on the evolution of site conditions over time.

At the onset of the last century, climatic conditions were probably not the same in the Clay Belt. The stands in the study area were established a few decades following the end of the Little Ice Age. Conditions were initially dryer and evolved over the course of the last century and into the current one under an increasing precipitation regime (Zhang et al., 2000; Genries et al., 2012; Parker et al., 2012). We speculate that under dryer conditions, sites which are now hydric had a lower water table and favoured vigorous aspen growth but that site conditions deteriorated over time. Under that scenario, it would become a matter of time before conditions deteriorate and lead to the decline of aspen stands. FTC outbreaks may hasten this decline and ultimately bring stands to their demise.

The precipitation regime is predicted to further increase for the northeastern boreal forests of North America (IPCC, 2013). Under this scenario, the rise of the water table may continue. Though, a more regionally detailed assessment of the future climate suggests that higher precipitation will occur mostly outside the growing season and that summer drought events will be more likely (Bergeron et al., 2010). Water table levels may thus vary more widely in the future. However, given that more precipitation in the winter months is predicted (Bergeron et al., 2010; McKenney et al., 2010) and that FTC defoliation events occur in the spring (Sterh and Cook, 1968), circumventing evapotranspiration, aspen roots may still experience asphyxia. In any case, sites which combine a high water table and an already thickening HL should not be regenerated to aspen. Given that site factors can change at a small scale, as evidenced by the present study, the current forest inventory information is too imprecise to be used for management planning. Remote sensing (Simard et al., 2009) or other techniques (e.g. ground penetrating radar, Laamrani et al., 2013) would be needed to map problematic areas more precisely.

The decline of aspen is observed throughout the boreal biome of North-America (Worrall et al., 2013). However, it appears the phenomenon has different predisposing causes in the West and the East, but the FTC is a common stressor in both regions. FTC exacerbates the effect of drought stress in the West, where the precipitation regime is decreasing, while it exacerbates the effect of a high water table in the East where precipitation is increasing.

5. Conclusion

Our study has shown that a simple cut of the residual live aspen, preferably but not necessarily in winter, was sufficient to regenerate moderately degraded stands following a FTC outbreak to fully stocked stands. In stands where degradation is too severe $(ALBA < 11 \text{ m}^2 \text{ ha}^{-1})$ and excessive moisture conditions occurred, aspen regeneration appears compromised, likely due the mortality of much of the root system. If management objectives are to regenerate aspen to high-yield stands on those sites, it will be at great expense, such as heavily disturbing the thick organic layer during or after harvesting (Lavertu et al., 1994; Belleau et al., 2011), and prior to planting, as HL thickness is detrimental for aspen (Laquerre et al., 2011; Gewehr et al., 2014). Moreover, excessive moisture conditions which contributed over time to a thick HL will persist. Under these conditions, those reinitiated stands will remain vulnerable to FTC outbreaks which are recurrent in the area. Alternatively, these sites could be converted to conifer stands in order to increase ecosystem resilience at the landscape scale. More generally, we suggest that at the strategic level the management of aspen in the Canadian Clay Belt integrates the hazard associated with sites factors and the recurrence of severe defoliation by the forest tent caterpillar.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.03. 013.

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