Gap dynamics in aspen stands of the Clay Belt of northwestern Quebec following a forest tent caterpillar outbreak

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Abstract: Forest tent caterpillar (FTC; *Malacosoma disstria* Hübner) outbreaks represent an important natural disturbance in broadleaf-dominated stands; however, their effects on forest gap dynamics are not well understood. To describe such effects on canopy gaps and tree recruitment patterns, we investigated 20 trembling aspen (*Populus tremuloides* Michx.) dominated stands defoliated severely over 0 to 3 years during the last outbreak (1998–2003) in the northwestern Clay Belt of Quebec. Results show that canopy opening more than tripled (12.3%–43.7%) from 0 to 3 years of severe defoliation, and mean gap size was more than 12 times greater (7.2–87.5 m^2) over the same gradient. Regeneration patterns suggest that aspen recruitment is not sufficient to completely restore closed canopies in stands defoliated 0, 1, and 2 years, whereas it should be sufficient in stands defoliated 3 years, where large gaps allow trembling aspen establishment. Our results clearly indicate that FTC outbreaks represent an important factor of gap formation in trembling aspen stands. At the stand level, gaps create uneven stand structures, and at the landscape level, FTC defoliation duration creates a large range of even to uneven stand structures.

Résumé : Les épidémies de Livrée des forêts (LDF; *Malacosoma disstria* Hübner) constituent une importante perturbation naturelle dans les peuplements dominés par les feuillus. Cependant leurs effets sur la dynamique des trouées ne sont pas bien compris. Afin de décrire les effets de ces épidémies sur les trouées et les patrons de recrutement, nous avons étudié 20 peuplements dominés par le peuplier faux-tremble (*Populus tremuloides* Michx.) ayant subi entre 0 et 3 années de défoliation sévère lors de la dernière épidémie survenue dans la ceinture d'argile du nord-ouest du Québec de 1998 à 2003. Les résultats montrent que le taux d'ouverture du couvert a plus que triplé (12,3–43,7 %) en passant de 0 à 3 années de défoliation et que la surface moyenne des trouées a augmenté d'un facteur 12 (7,2–87,5 m^2). Les patrons de régénération indiquent que le recrutement de peuplier faux-tremble ne devrait pas être pour complètement refermer le couvert des peuplements sévèrement défoliés pendant 0, 1 et 2 années, alors qu'il devrait l'être suffisant dans les peuplements défoliés 3 ans où les grandes trouées permettent l'établissement du peuplier faux-tremble. Nos résultats montrent clairement que les épidémies de LDF représentent un facteur important dans la formation de trouées dans les peuplements de peuplier faux-tremble. Les trouées créent des structures inéquiennes à l'échelle du peuplement et la durée de la défoliation par la LDF crée une large gamme de peuplements de structure équienne à inéquienne à l'échelle du paysage.

Introduction

The boreal forest is recognized as a disturbance-controlled ecosystem in which fire and insect outbreaks are defined as the main disturbances that determine stand species composition and structure (McCullough et al. 1998; Bergeron 2000). Although fire has been considered as the major disturbance in this system, insect outbreaks are currently the agent of natural disturbance causing the most important losses in boreal forests (Logan et al. 2003). In Canada, only 20 million hectares were burned between 1997 and 2007, whereas more than 120 million hectares were disturbed by insect outbreaks during the same period (Natural Resources Canada 2010). This is partly explained by the increase in fire return interval

observed over the last century in several boreal regions (Bergeron and Archambault 1993) but also by human intervention via fire suppression, which has contributed to the increase in the impact of insect outbreaks on boreal forest dynamics. Moreover, the effects of global warming should tend to increase insect demographic parameters such as phenology, survival, growth, and reproduction (Ayres and Lombardero 2000; Parmesan 2006; Altermatt 2010), and therefore, insect outbreaks should continue to increase in importance.

The forest tent caterpillar (FTC; *Malacosoma disstria* Hübner) is a major disturbance-causing insect in hardwood and mixedwood forests across North America (Witter 1979). The FTC is a generalist insect and a voracious defoliator whose preferred host tree species in the boreal zone are trembling

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aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), and balsam poplar (*Populus balsamifera* L.) (Witter 1979; Peterson and Peterson 1992). In Quebec and Ontario, FTC outbreaks are recurrent events with a periodicity of 9 to 13 years (Cooke and Lorenzetti 2006) that can occur as far north as 54° of latitude (Huang et al. 2008). Outbreaks usually last only 1–2 years, but local infestations may persist for up to 5 years (Cooke et al. 2009). Moreover, within three cores areas situated in Quebec and Ontario where six outbreaks were reported since 1938, Cooke et al. (2009) have demonstrated that individual outbreaks tended to last for 2.6 ± 0.5 years. Severe defoliations have been shown to cause a reduction in radial growth (Hildahl and Reeks 1960; Hogg et al. 2002) and a consequent decrease in forest productivity (Bergeron and Charron 1994; Hogg and Schwarz 1999; Candau et al. 2002). Authors generally agree that defoliation reduces tree growth; however, defoliation-caused tree mortality appears to be a more complex, less understood, and controversial phenomenon. Indeed, tree mortality in defoliated stands is generally associated with other factors such as age (Brandt et al. 2003; Sutton and Tardif 2007), drought (Hogg et al. 2008), wood-boring insects (Hogg et al. 2002), or fungal pathogens (Brandt et al. 2003) rather than FTC defoliation (Churchill et al. 1964; Brandt et al. 2003; Man and Rice 2010). Tree mortality in stands severely defoliated over multiple years can extend for 6 to 10 years after the end of an FTC outbreak (Duncan and Hodson 1958; Churchill et al. 1964).

In the absence of large-scale disturbances in the boreal forest, stands dynamics is controlled by the creation of gaps (McCarthy 2001). Such gaps commonly originate from discrete disturbance events such as localized insect outbreaks or windstorms and by the senescence of trees. Gap dynamics theory aims at inferring forest stand dynamics by understanding patterns of tree recruitment in canopy gaps (see Shugart 1998). In boreal forest ecosystems of North America, gap dynamics is a research field that has recently gained more interest (Kneeshaw and Bergeron 1998; Cumming et al. 2000; McCarthy 2001; Hill et al. 2005). In the absence of an exogenous disturbance, small gap formation in early successional deciduous stages of the boreal forest is controlled mainly by the death of individual trees or small groups of trees. During this early stage, gap-phase replacement can maintain nearly pure deciduous stands but can also favour the recruitment of shade-tolerant species when coniferous trees are present in the subcanopy (Cumming et al. 2000; Hill et al. 2005). The presence of shrubby understory species such as hazel (*Corylus cornuta*), raspberry (*Rubus idaeus*), mountain maple (*Acer spicatum*), or alder (*Alnus* spp.) can limit hardwood regeneration, as well as delay conifer establishment. In late successional coniferous-dominated stages, spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks drive the gap dynamics and allow the establishment of tolerant conifers in small gaps and the persistence of intolerant hardwood in large openings (Kneeshaw and Bergeron 1998).

Although these studies provide a good portrayal of the diverse gap dynamic patterns and trajectories of the boreal forest successional stages with the time since fire, there is still a real lack of knowledge on the impacts of FTC outbreaks on gap dynamics in deciduous stands. A more complete understanding of such outbreak effects on stand dynamics would

be valuable (see also Man and Rice 2010), particularly in the present context in which sustainable forest management systems include the emulation of natural disturbance as the best management practice (Gauthier et al. 2008).

Resilience is an emergent property of a natural system that may be estimated from the magnitude of disturbance that this system can absorb without undergoing significant transformational change of its functions, structure, identity, and feedbacks (Holling 1973; Walker and Meyers 2004). In the forest ecosystem, it refers to the capacity to recover from severe disturbance such as fire, insect outbreaks, or logging to an original state. In this study, resilience after FTC defoliation in deciduous-dominated stands is estimated by the potential replacement of lost canopy trees so as to eventually regain a closed canopy structure. In other words, here we ask: Will aspen regeneration in gaps be sufficient to replace dead canopy trees after FTC outbreak?

Contrary to previous studies using typical stand-level analyses to describe FTC outbreak effects on stand dynamics (Churchill et al. 1964; Hogg et al. 2002; Man and Rice 2010), our theoretical approach was based on gap dynamics and patterns of regeneration at gap level to infer post-outbreak forest succession at the stand level. The main objective of this study was to provide a better understanding of the effect of severe FTC defoliations on gap formation in early deciduous stages of boreal succession. The second objective was to characterize the post disturbance tree recruitment response and evaluate stand resilience. Our major hypothesis was that the duration of the FTC disturbance should modify gap and tree recruitment patterns of trembling aspen stands. Our main predictions were as follows: (*i*) increased mortality of trembling aspen with increasing defoliation duration will increase the proportion of canopy gaps; (*ii*) gap area and proportion of large gaps (aggregated mortality) should increase with defoliation duration; and (*iii*) compared with small gaps, large gaps should provide better environments for recruitment and consequently have higher regeneration density. This study took place in the mixedwood boreal forest of northwestern Quebec 5 years after the last FTC outbreak (1998–2003) in stands dominated by trembling aspen that experienced severe defoliation over 0 to 3 years during the outbreak.

Material and methods

Study area

The study area is located in Abitibi–Témiscamingue region, Quebec, Canada (48°N–48°50′N; 77°40′W–79°15′W). This area is situated within the Clay Belt, a vast physiographic region created by lacustrine deposits from the proglacial Lakes Barlow and Ojibway where clay soil dominates but organic soils and glaciofluvial deposits are also common (Veillette 1994). With less than 300 m of variation in elevation, the landscape is generally flat but punctuated by rocky outcrops and eroded morainic deposits forming hills (Bergeron et al. 1982). The climate is continental, with cold, dry winters and short, mild summers (average annual temperature, 1.2 °C; average annual precipitation, 918.4 mm; Environment Canada 2009). The region is mainly in the balsam fir – white birch bioclimatic domain (Saucier et al. 1998), which forms the southern limit of the coniferous boreal for-

est. Common tree species include balsam fir (*Abies balsamea* (L.) Mill.), trembling aspen (*Populus tremuloides* Michx), black spruce (*Picea mariana* (Mill.) BSP), white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), and jack pine (*Pinus banksiana* Lamb.).

In this region, the most recent FTC outbreak occurred from 1998 to 2003. This was the sixth such event recorded since 1938. This last outbreak was exceptional for its extent, severity, and duration, unseen since the early 1950s. During the 1999–2002 period, annual aerial surveys were conducted by the Quebec Ministry of Natural Resources and Wildlife to quantify the severity and extent of the defoliation. In every survey, the proportion of foliage lost to defoliation in each stand was estimated and classified as low (1%–25%), moderate (26%–65%), or severe (66%–100%). Survey data were then digitized to generate georeferenced maps. The cumulative area disturbed during this last outbreak was approximately 1.4 million hectares, with a larger extent in 2001 of more than 0.9 million hectares. In the study area, 30% of the territory entirely escaped FTC defoliation, 38% was defoliated for 1 year, 24% for 2 years, 7% for 3 years, and less than 1% for 4 years.

Stands selection

Defoliation data from the aerial surveys were overlaid on digitized forest cover maps (1 : 20 000 scale) from the Quebec Ministry of Natural Resources and Wildlife using Arc-View 3.3 (ESRI, Redlands, California). Twenty deciduous stands (Appendix A, Table A1) dominated by trembling aspen were selected: no defoliation or control ($n = 3$) and after 1 year ($n = 9$), 2 years ($n = 5$), and 3 years ($n = 3$) of severe defoliation. To control for stand origin, all selected stands were classified as either originating from fire (dated between 1932 and 1959; $n = 9$) or from clearcuts (dated between 1940 and 1963; $n = 11$). Stand origin was determined by using forest cover maps that included harvest years, overlayed with fire history maps from the Quebec Ministry of Natural Resources and Wildlife. Drainage was moderate to imperfect, with low to nonexistent slopes in all stands. Analyses of cores sampled at breast height from 10 dominant canopy trees in each stand were used to confirm defoliation regimes and to determine mean stand age.

Stand measurements

Data acquisition in the field was carried out in July and August 2008. In each stand, one transect varying from 500 to 1100 m was established to evaluate the percentage of canopy opening. The start point of each transect was randomly assigned after applying a 50 m buffer to any open area such as a road, lake, wetland, or clearcut. At each metre along the transect, the overhead canopy cover directly above the stop point was visually inspected. The canopy was classified as closed if a virtual vertical line perpendicular to the transect intersected a live tree crown or as open if the line extended to the open sky because of the presence of one or more dead trees (following Kneeshaw and Bergeron 1998). Canopy opening at the stand level was subsequently calculated as the relative frequency of open canopy to total transect length (Runkle 1992). Natural large interstices between trees were also noted but not integrated in the calculation of canopy opening as they do not result from tree mortality. A total of

14.4 km of stand transects were surveyed: 6.2 and 8.2 km in fire- and clearcut-initiated stands, respectively, and 2.1, 6.5, 3.6, and 2.2 km in control stands and stands severely defoliated for 1, 2, and 3 years, respectively.

To understand predisturbance stand characteristics, three to five 400 m^2 plots were also sampled in each stand under closed canopy at fixed intervals along the transect. Tree species composition basal area and stem density were measured in each plot (Appendix A, Table A1). In each plot, diameter at breast height (DBH) of all living trees > 9.9 cm was recorded, as well as species and status (suppressed, codominant, dominant). Mean height of stand was also approximated by randomly measuring 10 trees within each plot using a clinometer.

Gap characterization

A canopy gap is created by the death of an individual or a group of trees and is defined as the projection on the ground of the canopy opening. The expanded gap is the area circumscribed by the stems of the trees surrounding the gap and is usually larger than the gap itself (Runkle 1982). In each stand, gap characterization was performed on gaps encountered along the first one-third of the total transect length (232 gaps sampled out of 728). For circular-shaped gaps, measures of the longest and shortest perpendicular axes of canopy and expanded gaps were recorded. Multiple extra axis measurements were performed in the case of irregular-shaped gaps. Dead trees within the gaps, referred to as gap makers, were counted, identified, measured (DBH), and classified as either standing dead, snapped, uprooted, or crown-damaged.

To measure the potential impact of gap size on the direct light reaching the forest floor, the gap diameter to canopy height ratio or sky view factor (Lieffers et al. 1999) was calculated for each gap. Because the maximum sun elevation decreases with increased latitude (Canham 1988), shadow length also varies with latitude and is 1.1224 times the canopy height on the summer solstice at the latitude of this study. This means that a gap must have a larger diameter than the height of the trees at its perimeter for direct sunlight to reach the forest floor.

Gap regeneration

Regeneration was inventoried in the 232 characterized gaps. An exhaustive count of regeneration by species was achieved in the smaller gaps (area < 100m^2), whereas three 2 m wide transects perpendicular to the north–south axis (north, center, south) were used for larger gaps. Regeneration was categorized in three height classes: suckers (<1 m), saplings (1–2 m), and poles (2–5 m). The poles class was also referred to as gap fillers because they are likely to reach the canopy and to partially or completely close the gap. Because trembling aspen represented more than 80% of the total sampled regeneration (other species were balsam fir, black spruce, and white birch), results are only presented for this species. Aspen regeneration density was calculated for each gap in total and by height class. Finally, tree replacement probability was estimated per height classes as the ratio of the number of stems to the number of gap makers for each gap to estimate stand resilience capacity.

Statistical analysis

Stand origin

Analysis of covariance (ANCOVA) was conducted to determine the effect of stand origin on gap characteristics using the number of years of severe defoliation as covariate. There was no significant effect of stand origin alone or in interaction with defoliation. This permitted simplification of statistical analysis from covariance models to linear regressions. Only the results of the latter are presented.

Canopy opening and gaps

Canopy opening, mean canopy gap size, mean expanded gap size, proportion of gaps with a single gap maker, number of gap makers per gap, and proportion of gap maker types were analyzed to determine stand-level changes in gap characteristics in relation to defoliation duration. Log transformations were performed on mean gap area and expanded gap area, and residuals were examined to ensure that statistical assumptions of normality and homoscedasticity were met. When extreme values were identified, analyses were tested without them to ensure that they did not represent a source of bias; however, no datum had to be removed.

Gaps were grouped in classes of 25 m² increments of surface area, with upper class limits ranging from 25 to 950 m². Comparisons of gap size class distributions between defoliation regimes were done using Kolmogorov–Smirnov tests. As we applied multiple comparisons, Bonferroni corrections were performed to adjust the significance level α (0.05) to α/n (0.008), with n (= 6) being the number of comparisons. The same analyses of distribution were performed with the sky view factor and DBH of gap makers. DBH were grouped into classes of 5 cm increments for gap makers and into classes of 0.1 increments for the sky view factor (the last class, 1.2, including all values > 1.1224).

Regeneration

Linear mixed-effect models (Pinheiro et al. 2008) were used to analyze log-transformed regeneration density of trembling aspen as a function of defoliation duration, origin, gap area, and height class. We used model selection analyses to assess which factors significantly affected total gap regeneration density and regeneration density in each height class. We considered defoliation, origin, gap area, and the defoliation × gap area interaction in all models, and we added defoliation × origin for the first model and height class, gap area × height class, and defoliation × height class for the second model. Stand was considered as a random effect in both analyses and gap was added as random effect in the second. For each analysis, we formed sets 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 each analysis, and models were compared using the second-order Akaike information criterion (AIC_c) and the information theoretic approach presented by Burnham and Anderson (2002). We considered models with ΔAIC_c values ≤ 2 to have strong support, and we also calculated model weights from the AIC_c values to indicate the level of support for each of the models considered (Burnham and Anderson 2002). Model averaging was performed to discriminate if a variable had a significant effect on regeneration

density using all models in which the corresponding variable was present (Burnham and Anderson 2002). This enabled the computation of unconditional 95% confidence intervals for the variables of interest. Variables with confidence intervals excluding 0 were deemed good predictors of log-transformed regeneration density. Estimates obtained with this method have better precision and less bias than when based on a single model (Anderson et al. 2000).

The tree replacement probability was categorized in two classes (<0.5 or >0.5) and analyzed with mixed logistic regression to test the effects of defoliation, origin, gap area, and height class and of the interactions gap area × height class and defoliation × height class using stand and gap as random effects. Log transformation of regeneration density and gap area were done for all analyses. All statistical analyses were performed using R software (version 2.10.1; R Development Core Team 2010).

Results

Gap characteristics

The mean percentage of canopy opening showed a significant positive relationship with defoliation duration ($P < 0.01$; Fig. 1a) with an increase from 12.3% to 43.7% across the defoliation gradient (Table 1). Mean gap area and expanded gap area responded to defoliation by increasing 11.9 times and 3.7 times, respectively, and regression analysis showed a positive and significant effect of duration of defoliation on these two variables (Table 1; Figs. 1b and 1c).
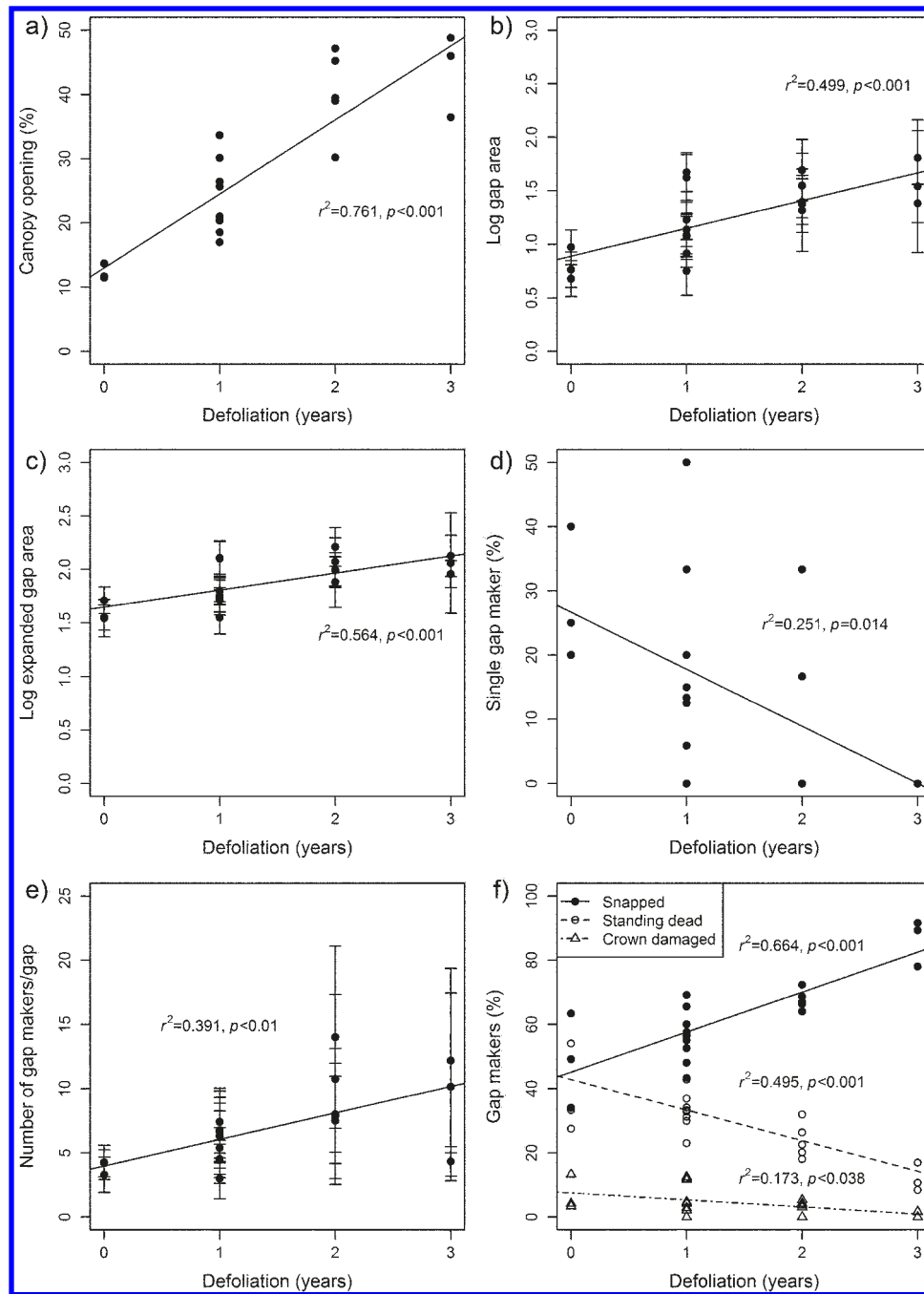
The mean proportion of gaps with a single gap maker was highest in control stands (28.3%) and decreased significantly with defoliation duration ($P < 0.014$; Fig. 1d) to zero in stands defoliated for 3 years. The mean number of gap makers per gap increased significantly with defoliation duration (Fig. 1e), doubling from 0 to 3 years of severe defoliation (3.9 to 8.2 trees/gap). Gap makers were classified as snapped (69.4%), standing dead (22.9%), uprooted (4%), or crown-damaged (3.7%). Snapped trees significantly increased from control (47.9%) to stands with 3 years of defoliation (84.9%), whereas the proportion of standing dead and crown-damaged trees decreased with defoliation (Fig. 1f). Uprooted trees were not significantly related to defoliation duration ($P = 0.344$; Table 1).

Analysis of gap patterns indicated that gap size distributions differed with duration of defoliation ($P < 0.008$) except for stands defoliated for 2 or 3 years ($P = 0.806$). Small gaps dominated the undefoliated stands, but the proportion of small gaps decreased with defoliation duration (Fig. 2a). On the other hand, the proportion of large gaps increased with defoliation duration, revealing that FTC disturbance changed gap size distribution patterns.

Distributions of the sky view factor also differed with defoliation duration ($P < 0.008$), except for stands defoliated for 2 or 3 years ($P = 0.725$). The frequency of gaps in the 1.2 ratio class increased with defoliation from 0% to 16% with increasing defoliation duration (Fig. 2b), demonstrating an increase in the proportion of gaps receiving direct sunlight at the forest floor with defoliation duration.

Analysis of the distribution of gap maker DBH classes showed no difference between control and stands defoliated 1 year ($P = 0.243$) and between stands defoliated 2 and

Fig. 1. Relationship between defoliation duration and (*a*) canopy opening (%), (*b*) mean gap area (log-transformed), (*c*) mean expanded gap area (log-transformed), (*d*) gap with a single gap maker (%), (*e*) mean number of gap makers per gap, and (*f*) proportion of gap makers per status.

3 years ($P = 0.168$), whereas all other comparisons were significantly different ($P < 0.008$). This result indicates a shift in the size distribution of gap makers (Fig. 2*c*), with dead tree diameters increasing with defoliation duration.

Regeneration

Among the nine candidate models considered for total regeneration density, the one that provided the best fit to the data (AIC$_c$ weight (w_i) = 0.37) was based on defoliation duration and gap area (Table 2). There were three other models with strong support (ΔAIC$_c \leq 2$), including all variables

tested, alone or combined, and one interaction. These four first models accounted for 97% of the cumulative AIC$_c$ weight (i.e., sum of the w_i). Model averaging showed that total density of regeneration increased significantly with gap area (0.49 $\pm$ 0.09), whereas none of the other variables was significant (Table 3).
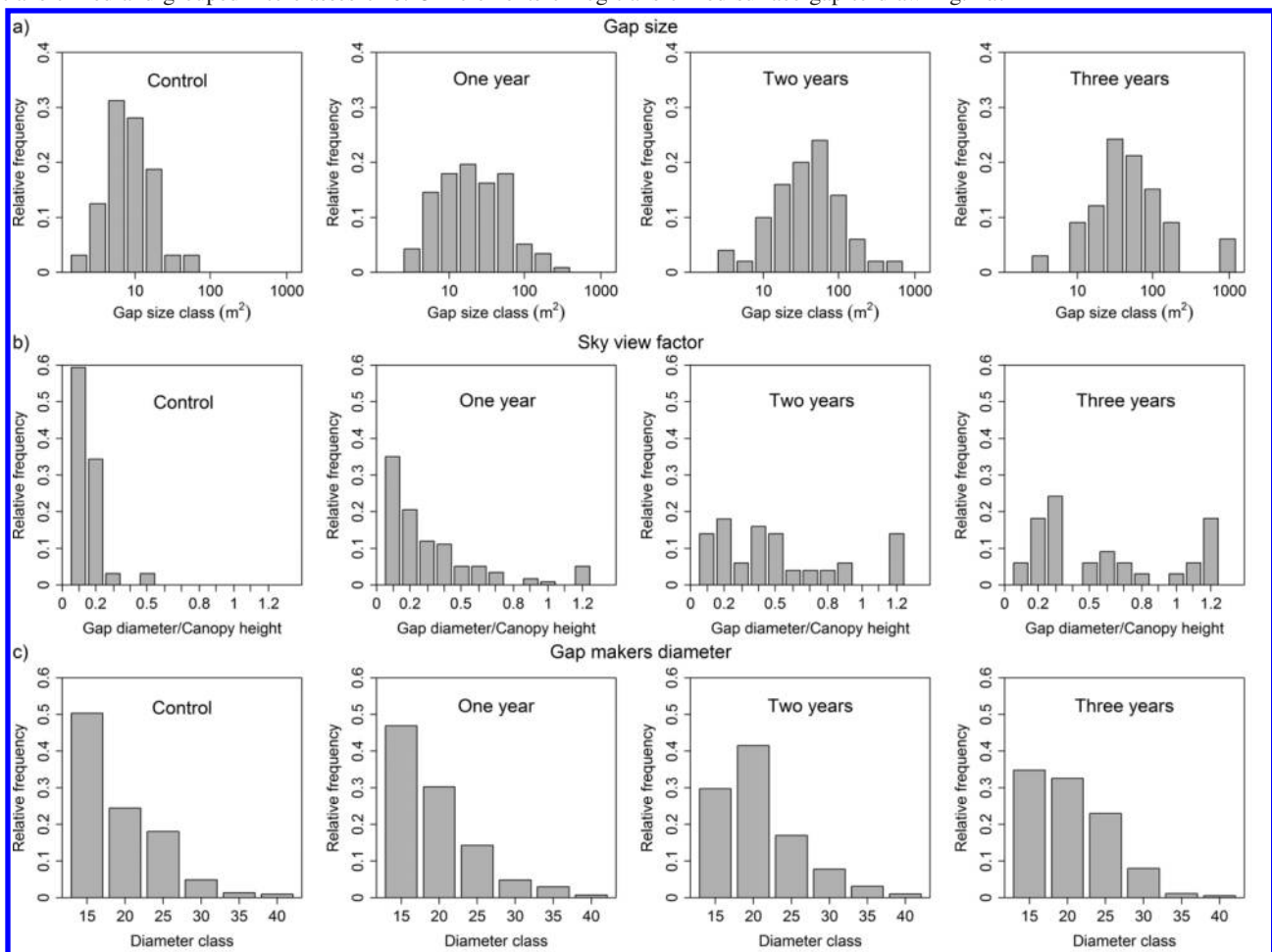
The analysis of regeneration density by height class showed that only one of the 13 models considered had strong support, with a w_i of 0.92 (Table 2). Model averaging revealed significant effects of gap area × height class and defoliation × height class interactions on the density of aspen

Table 1. Summary of linear regression analyses testing the effect of defoliation duration (number of years of severe defoliation) on gap and gap maker characteristics at the stand level ($n = 20$).

	b_0	b_1	R^2	$F_{(1,18)}$	$P\ (b_1)$
Gaps					
Co	12.97	11.53	0.761	**61.51**	**<0.01**
Gap	0.88	0.26	0.499	**19.90**	**<0.01**
EGap	1.66	0.21	0.564	**25.64**	**<0.01**
Sgm	26.67	–8.87	0.251	**1.36**	**0.01**
Gap makers					
Gm	3.97	2.07	0.391	**13.19**	**<0.01**
Snp	45.14	12.44	0.664	**38.49**	**<0.01**
Upr	4.50	–0.73	0.049	0.94	0.34
Crd	7.49	–2.19	0.173	**4.97**	**0.04**
Std	42.85	–9.52	0.495	**19.61**	**<0.01**

Note: Co, canopy opening (%); Gap, gap area (log-transformed); EGap, expanded gap area (log-transformed); Sgm, single gap maker (%); Gm, mean number of gap makers per gap; Snp, snapped (%); Upr, uprooted (%); Crd, crown-damaged (%); Std, standing dead (%). Significant effects are shown in bold ($P < 0.05$).

Fig. 2. Distribution of the relative frequency of (*a*) gap size, (*b*) sky view factor, and (*c*) gap makers diameter (DBH) for stands defoliated 0, 1, 2, and 3 years ($n = 3, 9, 5, 3$) during the last outbreak of forest tent caterpillar in the Abitibi region (1998–2003). Note that gap size was log-transformed and grouped into classes of 0.25 increments of log-transformed surface gap to draw Fig. 2*a*.

suckers (Table 3). The density of saplings (1–2 m) increased with gap area (0.42 ± 0.09; Fig. 3*a*) and defoliation duration (0.30 ± 0.12; Fig. 3*b*). The density of suckers (<1m) and poles (2–4 m) did not show any trend with gap size and defoliation duration, and the overlapping of their confidence intervals demonstrated that the density of suckers did not

Table 2. Top-ranking models for analyses of total density and height class density of aspen regeneration. Only the five first models are shown for brevity.

Model	K	AIC$_c$	ΔAIC$_c$	w_i
Total density model				
Def + Gap	5	810.2	0.00	0.37
Gap	4	810.6	0.41	0.30
Def + Gap + [Def × Gap]	6	811.9	1.67	0.16
Def + Origin + Gap	6	812.2	1.99	0.14
Def + Origin + Gap + [Def × Gap] + [Def × Origin]	8	815.8	5.65	0.02
Height class density model				
Def + Origin + Gap + Hc + [Gap × Hc] + [Def × Hc]	12	1013.8	0.00	0.92
Gap + Hc + [Gap × Hc]	8	1026.3	4.94	0.08
Def + Origin + Gap + Hc + [Def × Gap] + [Gap × Hc]	11	1039.5	25.74	0.00
Def + Gap + Hc	7	1055.5	39.94	0.00
Def + Origin + Gap + Hc	8	1073.4	57.83	0.00

Note: Def, defoliation duration; Gap, gap area; Hc, height regeneration class; ×, interaction; K, number of parameters; AIC$_c$, Akaike's information criterion corrected for small sample sizes; ΔAIC$_c$, AIC$_c$ relative to the most parsimonious model; w_i, AIC$_c$ model weight.

Table 3. Model-averaged parameter estimates, number of models used for model averaging (K), standard errors (SE), and 95% confidence intervals for the two analyses of aspen regeneration density: total density and height class density. Tested levels are shown in parentheses for qualitative covariates; reference level is poles (class 3).

				Confidence interval	
	K	Estimate	SE	Lower	Upper
Total density model					
Def	5	0.31	0.17	–0.07	0.68
Origin (Fire)	3	0.07	0.39	–0.70	0.84
Gap	5	**0.49**	**0.09**	**0.31**	**0.67**
Def × Origin (Fire)	1	0.09	0.38	–0.65	0.84
Def × Gap	2	0.06	0.10	–0.13	0.45
Height class density model					
Def	5	0.14	0.13	–0.12	0.39
Origin (Fire)	4	0.16	0.20	–0.23	0.56
Gap	5	**0.30**	**0.05**	**0.19**	**0.40**
Hc (2)	4	**1.43**	**0.10**	**1.23**	**1.64**
Hc (1)	4	**0.29**	**0.10**	**0.09**	**0.49**
Def × Gap	2	0.03	0.06	–0.08	0.14
Gap × Hc (2)	2	**0.42**	**0.09**	**0.24**	**0.61**
Gap × Hc (1)	2	**0.22**	**0.09**	**0.04**	**0.41**
Def × Hc (2)	2	**0.30**	**0.12**	**0.06**	**0.53**
Def × Hc (1)	2	**0.13**	**0.12**	**0.01**	**0.14**

Note: Parameter estimates in bold correspond to terms with statistically significant effect. Def, defoliation duration; Gap, gap area; Hc, height regeneration class; Hc (1), suckers; Hc (2), saplings; Hc (3), poles (reference level); ×, interaction.

significantly differ from that of poles (Figs. 3a, 3b). Total density and height class density analyses indicated that stand origin did not have a significant effect on aspen regeneration following FTC disturbance.

Replacement probability

The mixed logistic regression analysis (Table 4) reports a significant and positive effect of defoliation duration ($P = 0.05$) and gap area ($P = 0.04$) on the replacement probability of gap makers. Results also showed that the replacement probability of saplings and suckers differed from that of poles ($P < 0.01$; Table 4) and more than half of the tree replace-

ment potential was represented by saplings (Figs. 4a, 4b). Finally, there was a contrasting pattern of replacement probability that was a function of defoliation duration. In stands that were not defoliated or in small gaps, less than 50% of gap makers would potentially be replaced, whereas this potential rises to more than 80% in most defoliated stands or in large gaps (Figs. 4a, 4b).

Discussion

Canopy, gaps, and tree mortality

Our study shows that FTC disturbance represents an im-

Fig. 3. Effect of (*a*) gap area and (*b*) defoliation duration on the density of the different height classes of trembling aspen regeneration (with 95% confidence intervals).
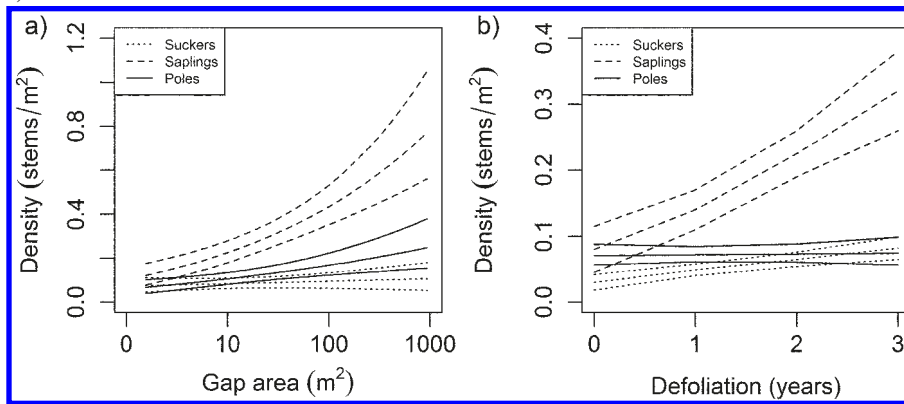

Fig. 4. Effect of (*a*) gap area and (*b*) defoliation duration on the replacement probability of dead trembling aspen by sucker roots of different height classes.
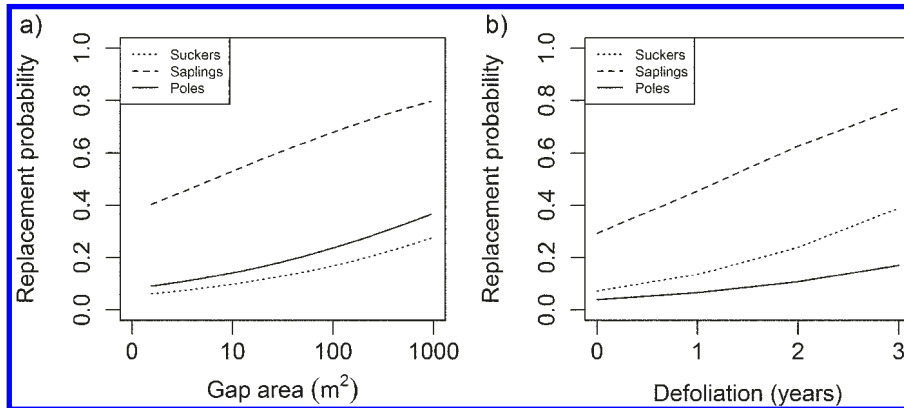

Table 4. Parameter estimates and standard errors (SE) with *z* values and *P* values from mixed logistic regression analysis describing replacement probability of trembling aspen considering defoliation × height and gap area × height interactions. Tested levels are shown in parentheses for qualitative covariates; reference level is poles (3).

Parameter	Estimate	SE	*z* value	*P* value
Intercept	–4.42	0.78	–5.60	<0.01
Def	0.73	0.36	1.94	**0.05**
Origin (Fire)	0.47	0.51	0.93	0.35
Gap	0.84	0.41	2.03	**0.04**
Hc (2)	2.27	0.57	3.84	**<0.01**
Hc (1)	2.18	0.58	3.76	**<0.01**
Def × Hc (2)	0.11	0.34	0.34	0.73
Def × Hc (1)	–1.53	0.40	–3.70	0.30
Gap × Hc (2)	0.02	0.01	1.09	0.27
Gap × Hc (1)	0.01	0.01	1.63	0.11

Note: Parameter estimates in bold correspond to terms with significant effect ($P < 0.05$). Def, defoliation duration; Gap, gap area; Hc, height regeneration class; Hc (1), suckers; Hc (2), saplings; Hc (3), poles (reference level); ×, interaction.

portant factor structuring trembling aspen stands. The proportion of canopy openings observed in control stands compared well with those reported for young aspen stands (44–78 years) in Quebec (11.3%; Kneeshaw and Bergeron 1998), Ontario (14%; Hill et al. 2005), and Alberta (4%–19%; Cumming et al. 2000), although the proportion of canopy openings in stands severely defoliated for 2 or 3 successive years were more comparable with rates reported for 120-year-old (35%; Hill et al. 2005) and 124-year-old (32%; Kneeshaw and Bergeron 1998) aspen stands. Thus, our results indicate that FTC

defoliations play a significant role in canopy deterioration in deciduous stands, conferring canopy structural attributes of older stands to younger stands. These results also show that FTC outbreaks may explain an important part of the phenomenon of aspen dieback reported for the province of Quebec (Pothier et al. 2004).

The increase in gap size and in the number of gap makers per gap, as well as the decrease of the proportion of gaps with a single gap maker correlated with defoliation duration, are consistent results regarding the effects of FTC defoliations on gap dynamics. The small gaps observed in control stands, which originate from the mortality of isolated trees or of a small group of trees, are in accordance with the post-fire gap dynamic reported in boreal young aspen stands (Kneeshaw and Bergeron 1998; Cumming et al. 2000; Hill et al. 2005). Inversely, the increase in the proportion of large gaps with defoliation duration confirms that exogenous factors such as insect outbreaks represent one of the main factors creating large canopy openings (Kuuluvainen 1994). Although our experimental design did not account for the spatial distribution of tree mortality, our observations confirm the aggregative patterns of aspen mortality described in post-fire boreal mixedwood succession (Kneeshaw and Bergeron 1998). The decreasing proportion of gaps with a single gap maker with the increase in defoliation duration revealed that aggregative mortality of canopy trees was significantly amplified after repeated defoliations. Such aggregative mortality patterns have been proposed to be linked to the clonal establishment of aspen (Kneeshaw and Bergeron 1998), and several recent studies in aspen genetics and root grafting (Namroud et al. 2005, 2006; Jelínková et al. 2009) suggest that root connections represent an important factor in aggregated tree mortality and gap creation.

As reported in northeastern Ontario poplar stands (Man and Rice 2010), our results confirm that the increase in aspen mortality is closely related to defoliation duration (Fig. 1e). The response of gap maker diameter to defoliation duration (Fig. 2c) also confirms the results of Churchill et al. (1964), who associated an increase in mortality with dominant, codominant, and intermediate canopy trees rather than with suppressed ones. Our observations also corroborate Churchill et al.'s (1964) findings of no apparent and identifiable cause of mortality (e.g., fungal pathogens, wind, or insect borers) for the majority of dead trees for which mortality was regarded as resulting from FTC defoliation. The large number of snapped trees constitutes one of the most outstanding footprints of repeated severe FTC defoliations (Fig. 1f). Snapped trees generally result from wind breakage, but the low proportion of up-rooted trees (less than 4% of total gap makers) revealed that windstorm events were not associated with tree mortality, and contrary to our expectations, the increase in canopy opening did not affect the proportion of up-rooted trees. In aspen-dominated stands, fungal pathogens such as cankers and polypores are common cause of mortality and represent a contributing factor long after FTC outbreaks capable of increasing aspen mortality at a later time (Churchill et al. 1964; Hogg et al. 2002). Given the low evidence for such pathogens on gap makers (our personal observations), we think that fungal pathogens did not represent an important cause of mortality in our study and attribute the main part of tree death to FTC defoliation.

Regeneration and resilience

The picture that emerges from the study of aspen regeneration, 5 years after the collapse of the outbreak, is that saplings (1–2 m height class) dominate in all defoliated stands and in gaps larger than 10 m^2 (Figs. 3a, 3b). Given height growth rates reported for aspen in the study area (close to 0.4 m/year during the first 10 years following establishment; Grondin et al. 2000), saplings in our study were likely recruited precisely at the time of the outbreak collapse. Poles (>2 m) established sometime during the outbreak itself, or even before. Their low density is typical of undisturbed stands (Bergeron and Charron 1994). Suckers (<1 m) thus appear to be the tail end of a single bout of recruitment induced by the FTC outbreak. As expected, aspen recruitment improved with gap size (Fig. 3a). Larger gaps with a sky view factor allowing for uninterrupted transmission of direct-beam light at ground level increased in frequency with outbreak duration (Fig. 2b). Greater light incidence and ground temperature, which stimulates aspen root suckering (Peterson and Peterson 1992; Prévost and Pothier 2003; Frey et al. 2004), likely played a key role in the establishment of the observed sapling cohort. Thus, our results clearly show that FTC defoliation affects significantly aspen root suckering by creating large canopy openings and providing a better understory environment.

Driven by the density of aspen regeneration, the replacement probability indicates that canopy stand resilience increased significantly with gap size (Fig. 4a) and defoliation duration (Fig. 4b). It clearly appears that saplings will replace the main part of gap makers and will assume mainly canopy stand resilience. In large gaps, almost all of the gap makers will be replaced (quasi total resilience), whereas less than half of dead trees would potentially be replaced in small gaps (partial resilience). Also, the limited survival of stems in shaded environments should tend to decrease the predicted replacement probabilities, particularly in small gaps (Prévost and Pothier 2003). Because of the low regeneration density in control stands, replacement probability is also low. This indicates that in small gaps, regeneration would not compensate tree loss, and in the absence of large-scale disturbance and consequently gap formation, the canopy would tend to open over time (Hill et al. 2005). After 1 and 2 years of defoliation, more regeneration was present than in control stands, but the replacement probabilities appeared insufficient to provide complete resilience. Besides, if all suckers reached the canopy layer (and assuming the trees that survived defoliation persist), such disturbed stands would recover to a more open canopy than existed prior to disturbance. Inversely, the density of aspen regeneration in stands defoliated for 3 years showed that large gaps improved aspen recruitment enough to promote the replacement of all gap makers and a reestablishment of the stand canopy over time. The density of aspen regeneration in such stands is comparable with that reported after FTC defoliation in the understory of trembling aspen stands in northeastern Ontario (Man and Rice 2010).

Finally, although our study focused on aspen regeneration, we observed that independent of defoliation duration and gap size, shade-tolerant regeneration would in some cases contribute to canopy stand resilience (in the sense of maintaining a closed canopy) and canopy conversion (Man and Rice 2010). Our observations are consistent with the actual gap

dynamics knowledge of the balsam fir – white birch forest succession of eastern Canadian boreal forest where, in absence of coniferous regeneration, trembling aspen regenerate in gaps and create multicohort aspen stands (Cumming et al. 2000). Thus, our results and observations confirm that factors creating gaps such as FTC disturbance favour the establishment of new cohorts of trembling aspen during trembling aspen – balsam fir transition (Bergeron 2000; Namroud et al. 2005). In absence of coniferous regeneration, it leads to pure trembling aspen stands with uneven structure (Cumming et al. 2000).

Conclusion

This study is the first to describe gap and regeneration patterns in pure and nearly pure aspen stands following an FTC outbreak. Our results clearly show that FTC disturbance constitutes an important agent of gap formation in trembling aspen stands. The effect of defoliation duration results in profound changes in gap patterns and gap makers. The increase of canopy opening size in response to defoliation duration contributes to increases in aspen recruitment and stand resilience. Patterns of regeneration suggest that stands maintain a pure aspen composition even after multiple defoliations, but also that duration of FTC defoliation tends to generate a large range of uneven stand structures. In other words, gaps create uneven stand structure at the stand level and FTC defoliation duration creates both even-aged stands (short duration) and uneven-aged stands with multicohorts of trembling aspen (long duration). The expected persistence of pure aspen stands may delay the expected succession to dominance by tolerant coniferous species. Man and Rice (2010) estimated that 40 to 50 years were necessary for the regenerating aspen to mature in declined stands following FTC outbreaks. In other cases, such as old trembling aspen stands or mixed stands where shrub species and shade-tolerant regeneration are more represented in the understory, the post-outbreak gap dynamics and forest succession pathways may be different.

Finally, given that aspen stands in Abitibi exhibit a large range of age at which the onset of stand decline is observed (Pothier et al. 2004) and given that the FTC historical records for the region show patchiness in defoliation recurrence (Cooke and Lorenzetti 2006), the results presented here suggest that aspen stands as observed today follow, to different degrees, the footprints of past FTC outbreaks.

Acknowledgements

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Appendix A

Table A1 follows.

Table A1. Description of the 20 investigated stands, including defoliation regime, origin, age, basal area, and stand density and composition.

Site	Defoliation duration (years)	Origin	Age (years)	Basal area (m²/ha)	Density (stem/ha)	Composition (%)						
						as	bf	bs	wb	bp	jp	tk
1	0	cc	45	27.8	1037	99	0	1	0	0	0	0
2	0	cc	55	35.8	858	85	0	4	1	5	4	1
3	0	fire	50	36.8	1450	100	0	0	0	0	0	0
4	1	cc	68	27.7	787	86	0	14	0	0	0	0
5	1	cc	62	29.5	766	86	9	5	0	0	0	0
6	1	cc	61	25.2	833	100	0	0	0	0	0	0
7	1	cc	53	25.3	800	95	0	2	0	3	0	0
8	1	fire	68	22.1	650	73	13	0	4	0	0	10
9	1	fire	50	17.6	575	100	0	0	0	0	0	0
10	1	fire	61	32.6	783	90	1	3	6	0	0	0
11	1	fire	76	42.7	1050	92	0	5	3	0	0	0
12	1	fire	57	24.3	900	74	0	0	26	0	0	0
13	2	cc	62	30.0	725	93	4	3	0	0	0	0
14	2	cc	52	25.7	637	73	20	5	2	0	0	0
15	2	cc	53	25.6	900	88	10	0	2	0	0	0
16	2	cc	48	21.3	500	81	3	15	0	1	0	0
17	2	fire	49	29.4	875	82	10	4	1	0	3	0
18	3	cc	61	27.7	716	94	3	3	0	0	0	0
19	3	fire	54	23.4	541	100	0	0	0	0	0	0
20	3	fire	54	34.3	1062	100	0	0	0	0	0	0

Note: cc, clearcut; as, trembling aspen; bf, balsam fir; bs, black spruce; wb, white birch; bp, balsam poplar; jp, jack pine; tk, tamarack.

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