

Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario

Steven B. Hill, Azim U. Mallik, and Han Y.H. Chen

Abstract: Canopy gaps play an important role in forest vegetation dynamics when fire return intervals are long. However, there is little known about the role of gaps in the development of forest stands that initially dominate following stand-replacing disturbance. We investigated gap disturbance during the breakup of trembling aspen (*Populus tremuloides* Michx.) stands at two scales: at the stand level we quantified gap fraction and gap size as stand development proceeds; at the gap level we determined causes of gap-maker mortality and evaluated resulting gap-maker structure and decay as stand development proceeds. We also evaluated the impact that gaps have on stand transition by quantifying the abundance and growth of juvenile trees in gaps of different sizes and ages. Ten stands between 60 and 120 years since fire in northeastern Ontario were sampled using line intersect transects. Gap fraction doubled (~18%–36%) and mean gap size was more than four times greater (~45–200 m²) over the time period. Standing dead gap makers in early states of decay were most frequent in young stands, whereas snapped gap makers in various states of decay were most frequent in old stands. Infection by fungal pathogens was the most frequent cause of mortality (56%) and was not related to time since fire. Balsam fir (*Abies balsamea* (L.) Mill.) was the most abundant juvenile recruit. However, transition probabilities for tree species were independent of gap type. These results indicate that gap creation is frequent during early stages of stand development in boreal forests; however, it is unlikely that successional trajectory is affected by their formation.

Résumé : Les trouées de canopée jouent un rôle important dans la dynamique de la végétation forestière lorsque les intervalles entre les feux sont longs. Cependant, il existe peu d'information sur le rôle des trouées dans le développement des peuplements forestiers qui s'établissent après une perturbation majeure. Nous avons étudié l'effet des trouées formées au cours de la sénescence de peuplements de peuplier faux-tremble (*Populus tremuloides* Michx.) selon deux échelles : à l'échelle du peuplement, nous avons quantifié la proportion du peuplement occupée par des trouées et la taille de ces trouées en fonction du stade de développement des peuplements; à l'échelle de la trouée, nous avons déterminé les causes de la mortalité à l'origine des trouées et nous avons évalué la structure et la décomposition des arbres morts en fonction du stade de développement des peuplements. Nous avons aussi évalué l'impact de ces trouées sur la succession des peuplements en quantifiant l'abondance et la croissance des jeunes arbres se développant dans des trouées de tailles et d'âges différents. Dix peuplements du nord-est de l'Ontario, établis entre 60 et 120 ans après un feu, ont été échantillonnés à l'aide de transects de lignes d'intersection. La proportion du peuplement occupée par des trouées a doublé (~18–36 %) et la taille moyenne des trouées a plus que quadruplé (~ 45–200 m²) au cours de cette chronoséquence. Les jeunes peuplements comportaient plus d'arbres morts sur pied encore peu décomposés alors que les vieux peuplements comportaient plus d'arbres morts cassés ayant atteint différents stades de décomposition. Les champignons pathogènes constituaient la cause la plus fréquente de mortalité (56 %) peu importe le nombre d'années écoulées depuis le feu. Le sapin baumier (*Abies balsamea* (L.) Mill.) dominait la régénération établie dans les trouées. Cependant, les probabilités de transition des espèces arborescentes étaient indépendantes du type de trouée. Ces résultats indiquent que la création de trouées est fréquente au cours des premiers stades de développement en forêt boréale; toutefois, il est peu probable qu'elles affectent la succession végétale.

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Introduction

A major goal of gap dynamics studies has been to infer forest stand dynamics by understanding patterns of tree establishment in canopy gaps. This has been well developed in temperate and tropical forest regions (e.g., Runkle 1981, 1982; Brokaw 1985, 1987; Brokaw and Scheiner 1989; Denslow 1987; Whitmore 1989; Schnitzer and Carson 2001). However, interest in canopy gaps has only recently been developed in boreal forest ecosystems (e.g., Kneeshaw and Bergeron 1998, 1999; Cumming et al. 2000; McCarthy 2001; Pham et al. 2004).

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In the boreal forest, compositional change in dominant tree species at the stand level is related to time since fire (Bergeron and Dubuc 1989; Frelich and Reich 1995; Bergeron 2000). Despite the evidence that compositional transitions occur, there are few studies that examine the mechanisms responsible for change, particularly in even-aged postdisturbance stands (e.g., Cumming et al. 2000). One reason for this has been the emphasis on intense stand-replacing fires, which maintain even-aged forest structures (Heinselman 1981; Johnson 1992). When this is the dominant disturbance regime, small-scale disturbances that occur during the fire-free interval are thought to play a minor role in forest stand dynamics. However, in some boreal regions fire return intervals can vary as a result of climatic factors or human intervention (e.g., fire suppression programs) (Bergeron and Archambault 1993; Carleton 2000). When forest stands do not burn for long periods of time, small-scale disturbances result in the formation of canopy gaps, which in turn are predicted to influence tree recruitment and patterns of succession.

An understanding of the impact that gaps have on tree recruitment can be used to predict long-term forest dynamics (Coates 2000, 2002). Gaps create a microenvironment that is conducive to either the establishment or the release of trees in the understory. Since trees respond differentially, based on their life history, to microenvironmental conditions in a gap, patterns of canopy replacement can be predicted based on gap characteristics (Brokaw 1985, 1987; Whitmore 1989). This is commonly known as gap partitioning (Denslow 1980). The general prediction is that along a continuum of gap size, shade-tolerant species will have an advantage in small gaps and shade-intolerant species will have an advantage in large gaps. Therefore, as forest stands develop, a prevalence of small gaps should favor dominance by shade-tolerant species, whereas a prevalence of large gaps should favor dominance by shade-intolerant species.

A key stage of boreal forest development, following stand-replacing disturbance, is the breakup or decline of the post-disturbance cohort; this has commonly been observed in trembling aspen (*Populus tremuloides* Michx.) dominated forests (Frey et al. 2004; Pothier et al. 2004). This stage of development is analogous to the understory reinitiation stage (Oliver and Larson 1990), transition stage (Peet and Christensen 1987), canopy transition stage (Chen and Popadiouk 2002), or biomass accumulation and (or) competitive exclusion – maturation stages (Franklin et al. 2002). During this stage, synchronous or gradual senescence of mature trees results in opening of the canopy, and gaps are created (Frey et al. 2004; Senecal et al. 2004). We predict that variability in gap characteristics (in particular size) during this stage will have important implications for recruitment or release of trees in the understory. Previous work has shown that in Canada's western boreal forests, shade-intolerant *Populus* sp. are more abundant in gaps than in the adjacent, closed-canopy understory, thereby facilitating replacement by conspecifics (Cumming et al. 2000), whereas in eastern boreal forests, gaps facilitate replacement by shade-tolerant conifers such as balsam fir (*Abies balsamea* (L.) Mill.) (Kneeshaw and Bergeron 1998). There is also indirect evidence that gaps play a role in the establishment of a second cohort of trembling aspen in Canada's eastern boreal forests (Paré and Bergeron 1995; Bergeron 2000).

Evaluating the importance of gap disturbance should involve a complete description of the process, including mechanisms of formation, resulting characteristics, and ecological impact (Runkle 1992). Most gap-related studies in the boreal forest focus on the two latter criteria (see, however, Ott and Juday 2002; Bartemucci et al. 2002). In some instances, the mechanism of gap formation has been explained as "random mortality as trees senesce" during early stages of forest development (Kneeshaw and Bergeron 1998, p. 784); this may be the case if stands undergo a stage of density-dependent mortality (thinning). However, we contend that any factor, edaphic or biological, that increases the likelihood of tree mortality will provide a deterministic explanation of gap creation, regardless of developmental stage (Castello et al. 1995). Evaluating these factors is extremely valuable for a more complete understanding of stand dynamics; particularly when sustainable management silviculture systems ascribe to the emulation of natural disturbance as a best management practice.

The purpose of this study was to gain a better understanding of the frequency of small-scale disturbance resulting in canopy gap formation, and of its impact on tree recruitment in postdisturbance boreal forests. Our major assumption was that if gaps provide a suitable environment for establishment or release of trees in the understory, they will have important consequences for stand-level canopy transition. Our specific objectives were to (1) at the stand level, quantify characteristics such as gap fraction and gap size as stand development proceeds; (2) at the gap level, determine the causes of gap-maker mortality, and quantify the resulting physical structure and decay state as stand development proceeds; and (3) determine whether gap characteristics (size and age of gap) influence species transition probabilities calculated from juvenile tree abundance and growth rate. The first two objectives were accomplished by sampling a chronosequence of 10 trembling aspen stands, ranging in age from 60 to 120 years. The final objective was accomplished by sampling gaps that were found in a subset of the five older forest stands, ranging in age from 95 to 120 years.

Methods

Study area

The study was conducted in forests near the city of Timmins (48.34°N, 81.22°W, 295 m altitude), in northeastern Ontario. The study area has a moderately dry, cool climate with short summers. The average annual temperature for Timmins is 1.3 °C, and the average annual precipitation is 831 mm (Environment Canada 2005). Major topographic features are the result of deposits from the retreat of glaciers during the past ice age (approximately 10 000 years ago). The study sites were randomly located within a radius of 50 km from Timmins, on outwash plains, predominantly composed of various loamy soils, silty very fine sands, and fine sands.

Common associations of tree species in the study area include trembling aspen, white birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca* (Moench) Voss) on upland moderately well drained soils; jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP) on upland well-drained soils; and black spruce, balsam fir, and eastern white-cedar (*Thuja occidentalis* L.) on lowland poorly

Table 1. Description of study stands including Universal Transverse Mercator (UTM) location, time since fire (TSF), stand basal area, and stand composition.

Site	Geographic description	UTM easting	UTM northing	TSF (years)	Basal area (m ² /ha)	Species composition (%)									
						Po	Sw	Bf	Sb	Pj	Ce	Bw	Pw	Pr	Pb
1	Lake Papakomeka	478187	5347693	80	39.5	72	5	3	6	6	0	8	0	0	0
2	Horwood Turnoff	407012	5337681	101	35.4	62	2	14	5	7	0	9	<1	<1	0
3	Groundhog Lake	406925	5330654	115	39.2	68	5	19	1	0	1	3	0	0	3
4	Porcupine Pond	491316	5355916	80	34.7	64	6	3	10	0	0	0	0	0	17
5	Night Hawk Rd 1	501477	5343402	95	38.1	65	6	7	4	0	0	3	0	0	15
6	Night Hawk Rd 2	499958	5348129	101	28.5	74	1	<1	15	1	0	1	0	0	8
7	Horwood Lake	404452	5327992	105	35.0	64	6	16	6	1	3	4	0	0	<1
8	Kenogamissi Lake	460033	5334745	60	31.3	85	<1	2	0	0	0	13	0	0	<1
9	Horwood Tracks	404969	5335831	120	31.6	64	1	19	8	0	1	5	1	0	1
10	South Kettle Lakes	509533	5376759	95	37.0	64	10	21	<1	0	0	4	0	0	<1

Note: Species are as follows: Po, trembling aspen; Sw, white spruce; Bf, balsam fir; Sb, black spruce; Pj, jack pine; Ce, white-cedar; Bw, white birch; Pw, white pine; Pr, red pine; Pb, balsam poplar.

drained soils (Taylor et al. 2000). Successional relationships among species and their respective associations have been studied in adjacent areas of Quebec (Bergeron and Dubuc 1989; Bergeron 2000). Forests in that area typically develop from dominance of shade-intolerant hardwood species following large-scale disturbance toward dominance of shade-tolerant conifer species (Bergeron 2000).

To represent gap characteristics during the breakup or decline of trembling aspen forest development, a chronosequence of 10 stands between 60 and 120 years since fire were chosen. All forest stands were dominated by trembling aspen (relative basal area per hectare 60% or greater) on well to moderately well drained sites with silty very fine sands as the dominant soil type (Table 1). After preliminary analysis revealed that gaps become more frequent with time since stand initiation, five of the older stands between 95 and 120 years since fire were selected to sample tree recruitment patterns in different gap types.

Field measurements

Forest stands

Start points for each transect were located at a random point at least 50 m from any large openings such as roads, wetlands, and lakes. Between five and nine transects varying in length between 50 and 300 m were established in each stand; since numerous transects were used in each stand, total transect length was between 1000 and 1300 m within a stand. Along each transect, tree species basal area was measured every 50 m using prism sweeps (Avery and Burkhart 2002). Forest areas that showed evidence of anthropogenic disturbance (e.g., mining claim lines) or that were within 50 m of prominent edges such as clearcuts or water bodies were avoided. Stand age was measured as time since fire (TSF) following Bergeron (1991); tree rings were counted from increment cores taken at breast height (1.3 m) from 10 representative canopy trees. Time to reach breast height was corrected using models provided by Vasiliauskas and Chen (2002).

Gap and gap-maker characteristics

We defined gaps as forest canopy openings that were (1) larger than the interstitial spaces between living trees and

(2) resulted from the death of an individual or group of trees (gap makers), living trees that were leaning (i.e., trees displaced enough that a gap was created), broken tree branches, or localized edaphic characteristics (sensu Bartemucci et al. 2002). Expanded gap measurements were used to determine the amount of gap disturbance (gap fraction). The expanded gap describes the area bounded by the stems of living trees adjacent to the gap created by a canopy opening (i.e., canopy gap) (Runkle 1992).

To determine gap fraction, the forest canopy was evaluated as being either open or closed at each metre along the same sample transects as those used to measure tree basal area (sensu Kneeshaw and Bergeron 1998). For time efficiency, assessments of canopy openness were determined by visual estimation (Betchtold et al. 2002). Between 20 and 24 gaps were encountered in each stand. When the sample transect was intersected by a gap, we measured the distance along the transect that its expanded gap and canopy gap occupied. To determine the encountered gap size, we then measured the longest axis and the shortest perpendicular axis in the expanded gap (or numerous axes if the gap shape was irregular). For irregular-shaped gaps, we typically used two to four minor axes to estimate the length of the minor axis.

Gap makers were characterized based on their physical structure, cause of mortality, and state of decay. Gap-maker structure was categorized as standing dead, snapped, uprooted, displaced, or crown damage. Gap-maker mortality was diagnosed based on evidence that suggested trees were killed by pathogenic wood-decay fungi, wind, insects, or mammals; in the event that we could not diagnose the reason for mortality we categorized it as unidentified. In all cases, evidence for mortality was limited to recent gap makers in early stages of decay. Evidence of infection by three groups of wood-decay fungi including root rots (i.e., *Armillaria* spp.), polypores (i.e., *Phellinus* spp.), and cankers (i.e., *Hypoxylon* spp.) was used. *Armillaria* root rot, a common cause of death among conifers and hardwoods in the boreal forest, can be easily diagnosed from thick shoestring-like rhizomorphs and white mycelial mats between the bark and the cambial layer at the base of a tree (Lundquist 2000; Thompson 2000). We removed the bark at the base of each gap maker to assess the presence of these structures. Polypore- and canker-

Table 2. Decay classes used to categorize the state of gap-maker decay.

Decay class	Branches			Wood decomposition
	Large	Fine	Bark	
1	Intact	Intact	Intact	None
2	Mostly intact	Mostly present	Mostly intact	Little
3	Some intact	Missing	Mostly missing	Moderate
4	Missing	Missing	Very little remaining	Advanced
5	Missing	Missing	Missing	Advanced

Note: Decay class 1 represents living or most recently deceased gap makers, and decay class 5 represents the most advanced stages of decay. In analyses, gap makers in decay classes 1 and 2 were grouped to form an early decay class.

related wood decay was implicated if basidiomata or stroma was found on the stems of the gap maker. In some cases gap makers showed symptoms described above, but the appearance of broken stems revealed the heartwood and sapwood had decayed prior to falling or snapping. These gap makers were categorized as being caused by pathogenic wood-decay fungi. To eliminate the possibility that wood decay was post mortem, mortality caused by pathogenic wood-decay fungi was only implicated if there was strong evidence that the tree was still alive when the stem broke (i.e., leaves and fine branches of gap maker were evident); therefore, our estimates for fungal infection are conservative.

A five-level decay class was used to describe the decay state of each gap maker (adapted from Bartemucci et al. 2002; Ott and Juday 2002; see Table 2). Decay class 1 represented gap makers either still alive or recently deceased, and decay class 5 represented gap makers that were in advanced stages of decay.

Understory recruitment

We assumed that differences in understory recruitment between gaps and underneath the closed canopy were the result of gap formation. Therefore, reference to recruitment patterns in this study is used to describe differences in tree abundance in the understory of gap and closed-canopy conditions.

We used tree recruitment patterns in canopy gaps to predict canopy replacement by calculating Markovian transition probabilities. Transition probabilities are typically calculated by relating the relative abundance of tree species to different types of gap-maker species (Frelich and Reich 1995; Kneeshaw and Bergeron 1998; Pham et al. 2004). In our study, mortality of trembling aspen created all the gaps. Thus, we focused on the effect of gap size and age on transition probabilities. Since asynchronies in growth rate give faster growing species an advantage when filling gaps, we also included information about species-specific growth rates when calculating transition probabilities.

In each of the five stands selected for studying patterns of tree recruitment in the understory, four characteristic gaps (small young, small old, large young, and large old) and an understory control were used to measure density of tree recruitment and growth. Gaps smaller than 350 m² were chosen, since they represented 95% of the gaps sampled across all stands and were responsible for 95% of the occupied gap area along transects. Gap age was estimated using several techniques including gap-maker decay class and release of

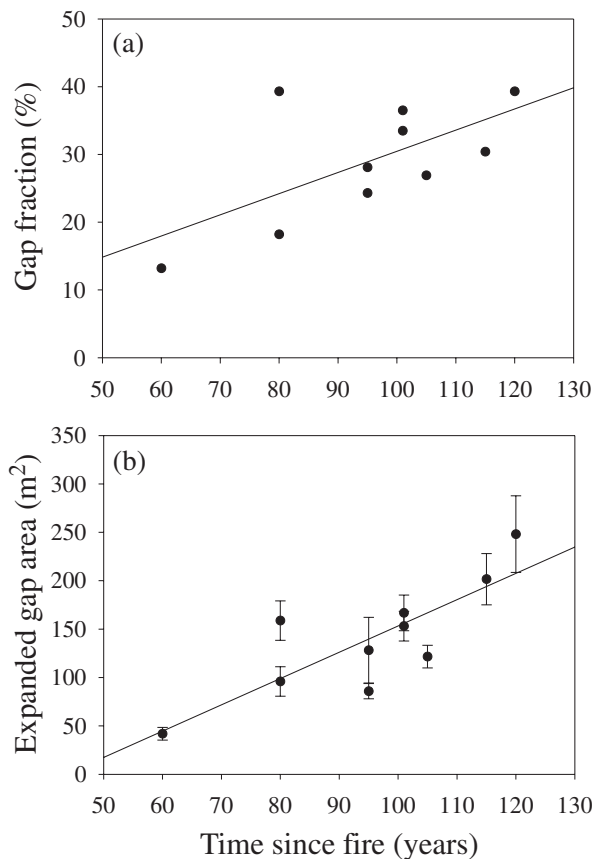
understory vegetation (Dynesius and Jonsson 1991). Gap age was classified into young (<5 years since gap-maker mortality) and old (≥5 years) for single- and multiple-tree mortality gaps. Understory controls were represented by 400-m² quadrats, placed underneath a closed canopy, away from the direct influence of canopy openings large enough to be considered a gap.

Within each gap and understory plot the abundance of all juvenile tree species was tallied and grouped into one of three height classes: 0–0.5, 0.5–2.0, and 2.0–5.0 m. Three individuals (if present) of each species from each height class were randomly chosen to estimate species height growth. Height growth during the past 1 to 5 years was measured to estimate yearly growth rate in older gaps. Only the previous-year growth was used for young gaps, since measurements of earlier growth would confound growth associated with being in a gap versus in the understory. Height growth of coniferous species such as balsam fir, black spruce, and white spruce was measured as the length between each whorl of branches. The current-year growth of coniferous stems was assessed to make sure suppression causing missing whorls was not a problem. The indeterminate growth of trembling aspen and white birch allowed only the past couple of years to be measured, as bud scale scars became inconspicuous as diameter of the stems increased. However, the majority of shade-intolerant hardwood recruitment was 2 years old or younger based on growth ring counts from a random sample of cut stems. Current-year growth was not included for any stems as a measurement, as differential growth of individuals over the sampling period may have resulted in higher estimates for those sampled later in the field season.

Data analysis

Least-square linear regression models were used to determine the effect of time since fire (TSF) on the development of gaps and gap characteristics. Expanded gap fraction, canopy gap fraction, edaphic gap fraction, and mean gap area were analyzed to determine stand-level changes in gap characteristics with time. Gap-level characteristics, including frequency of single-tree gaps and gaps created by one disturbance event, were also analyzed with respect to TSF. We assumed that gap makers that were in same state of decay originated from the same disturbance event (*sensu* Bartemucci et al. 2002). For each stand, the proportion of each gap-maker structure type, cause of mortality, and decay class were calculated based on occurrence, not gap area. Decay classes 1 and 2 of gap makers were grouped to form an early decay class (Ta-

Fig. 1. Relationships between time since fire and (a) expanded gap fraction and (b) mean expanded gap area. Expanded gap fraction corresponds to model 1 in Table 3. Expanded gap area corresponds to model 3 in Table 3.



ble 2). For all analyses, residuals were analyzed to ensure that statistical assumptions were met. When one or more outliers were identified, we inspected the results of the analysis without them to ensure that they were not a source of large bias. Final analyses included all data points. When TSF had no effect on gap or gap-maker characteristics, the mean values were reported and assumed to be consistent with time.

We used species-specific transition probabilities to infer canopy transition. For each sampled gap or understory plot, species-specific transition probability, defined to account for both its abundance and growth potential, was calculated as the summed proportion of being the first stem or group of stems to grow to 5 m (eq. 1). We assumed stems that reach 5 m have the best chance of becoming gap fillers. We weighted the stem density by time to reach 5 m, since differential height growth among species can result in smaller stems of some species having a higher probability of becoming a gap filler. To estimate the time to reach 5 m, we modelled species-specific height growth rate from the species height using a regression fitting procedure, after determining that height growth rate was not influenced by gap type (data not presented). The time for a given height class of each species to reach 5 m was then calculated by integrating the inverse of the growth function and solving for the difference in time between mean initial height for each height class (equal to 0.25, 1.25, and 3.5 m, respectively) and 5 m. This value was

then ranked as a proportion relative to the fastest growing species group within each gap or understory.

$$[1] \quad P_t = \frac{\sum_{i=1}^3 (RA_i / \Delta T_i)}{\sum_{t=1}^n \sum_{i=1}^3 (RA_i / \Delta T_i)_n}$$

where P_t is the transition probability for a given species t ($t = 1, 2, \dots, n$), RA_i is the relative abundance expressed as a proportion for height classes $i = 1$ (0–0.5 m), 2 (0.5–2 m), and 3 (2–5 m), and ΔT_i is the relative time to reach 5 m for species t with initial height of 0.25, 1.25, and 3.5 m. The sum of P_t within each gap or understory is 1, except for small young gaps, where one of the samples for this gap type had no juvenile trees present, resulting in a sum of 0.8 (see Table 4).

Since transition probabilities were non-normal (Kolmogorov–Smirnov normality test of residuals, $P < 0.001$), species differences were based on rank, and differences among understory environment (gap or closed canopy) were compared using a Kruskal–Wallis test.

Results

Gap characteristics

Expanded gap fraction increased significantly from 17.8% to 36.4% between 60 and 120 years since fire (Fig. 1a). Canopy gap fraction was approximately 1.4 to 1.9 times lower than expanded gap fraction and increased marginally with TSF ($P = 0.071$; Table 3). Expanded gap fraction resulting from edaphic gaps averaged 5.7% and showed no significant relationship with TSF (data not shown). Mean expanded gap area increased significantly from 44.7 to 207.9 m² with TSF (Fig. 1b). The proportion of gaps formed by mortality of a single tree was highest in younger stands and decreased significantly with TSF (Fig. 2a). Gaps resulting from one disturbance event were more likely to occur in the younger stands (Fig. 2b).

The most common structural characteristics of gap makers were snapped, standing dead, and uprooted gap makers, accounting for 51%, 27%, and 18% of all gap makers, respectively. The proportion of snapped gap makers more than doubled between 60 (33%) and 120 (69%) years since fire (Table 3). This increase was mirrored by a decrease in standing dead gap makers between the two time periods (Table 3). The proportion of uprooted gap makers averaged 17% and was not significantly related with TSF (Table 3). Other types of gap-maker structure, including trees that were displaced or had broken branches, only accounted for 4% of all gap makers and showed no trend with TSF ($P > 0.05$).

The proportions of gap makers killed by wood-decay fungi, insects, mammals, wind, and unidentified factors were not significantly related to TSF ($P > 0.05$ in all cases). Infection by wood-decay fungi was the most predominant factor responsible for gap-maker mortality (56%) and was significantly greater than the other causes of mortality ($F_{[2,27]} = 387.76$, $P < 0.001$). Wind was responsible for killing 16% of all gap makers. Other factors (including mammals, insects, and those unidentified) accounted for 28% of all gap-maker mortality.

The proportion of gap makers in early stages of decay (decay classes 1 and 2 combined) decreased significantly with TSF (Fig. 2c). At 60 years since fire, the proportion of

Table 3. Linear models for gap and gap-maker characteristics in relation to time since fire.

	Model	<i>N</i>	<i>b</i> ₀	<i>b</i> ₁	<i>R</i> ²	<i>F</i>	<i>P</i> (<i>b</i> ₁)
Gap characteristic							
Expanded gap fraction	1	10	-0.77	0.31	0.34	5.55	0.046
Canopy gap fraction	2	10	-5.67	0.23	0.31	4.54	0.071
Gap area	3	9	-118.47	2.72	0.63	16.16	0.004
Single gap maker proportion	4	10	1.03	-0.01	0.51	10.51	0.012
Single decay class proportion	5	10	1.1	-0.01	0.41	7.16	0.028
Gap-maker characteristic							
Snapped proportion	6	10	-0.03	0.01	0.29	4.81	0.060
Standing dead proportion	7	10	0.91	-0.01	0.31	4.95	0.057
Uprooted proportion	8	10	ns	ns	ns	ns	ns
Fungal infection proportion	9	10	ns	ns	ns	ns	ns
Wind proportion	10	10	ns	ns	ns	ns	ns
Other mortality proportions	11	10	ns	ns	ns	ns	ns
Decay class (1 + 2) proportion	12	10	1.25	-0.01	0.32	5.225	0.052

Note: Probability values are only presented for the linear coefficient (*b*₁) in each model. ns means there was no significant relationship with time since fire (*P* ≥ 0.1).

Table 4. Transition probabilities (mean ± 1 SE) for tree recruitment based on proportion in different gap types (*N* = 5) weighted by time to reach 5 m.

Gap type	Balsam fir	Trembling aspen	Black spruce	White spruce	White birch
sy	0.60 (0.16)	0.11 (0.05)	0.04 (0.03)	0.03 (0.02)	0.02 (0.01)
so	0.60 (0.20)	0.38 (0.19)	<0.01 (<0.01)	0.02 (0.02)	<0.01 (<0.01)
ly	0.67 (0.11)	0.15 (0.04)	0.08 (0.05)	0.02 (0.01)	0.09 (0.04)
lo	0.83 (0.04)	0.04 (0.02)	0.04 (0.02)	0.07 (0.03)	0.02 (0.01)
us	0.58 (0.16)	0.39 (0.17)	0.02 (0.02)	0.01 (<0.01)	0.01 (0.01)
Overall mean	0.66 (0.07)	0.21 (0.06)	0.04 (0.01)	0.03 (0.01)	0.03 (0.01)
χ^2	2.308	6.713	4.818	5.733	11.542
<i>P</i>	0.679	0.152	0.307	0.22	0.021

Note: See Figs. 3 and 4 for stem density and growth measurements used for transition probability calculations. Gap types are as follows: sy, small young; so, small old; ly, large young; lo, large old; us, understory.

early decay stage gap makers was 89%, which decreased to 54% at 120 years (Fig. 2c). This decrease mirrors the increased occurrence of gap makers in mid to late stages of decay in the older stands.

Tree recruitment

Based on rank, balsam fir and trembling aspen were the most abundant juvenile species found in the study forests, and consequently they had the highest transition probabilities among the five dominant species (Fig. 3, Table 4). Trembling aspen was the fastest growing species, followed by white birch, balsam fir, black spruce, and white spruce (Fig. 4). Transition probabilities calculated for all species among different gap types and the understory showed no difference, except for white birch (Table 4). The overall replacement pattern is that balsam fir and trembling aspen will be the dominant succeeding species, followed by black spruce, white spruce, and white birch, respectively (Table 4).

Discussion

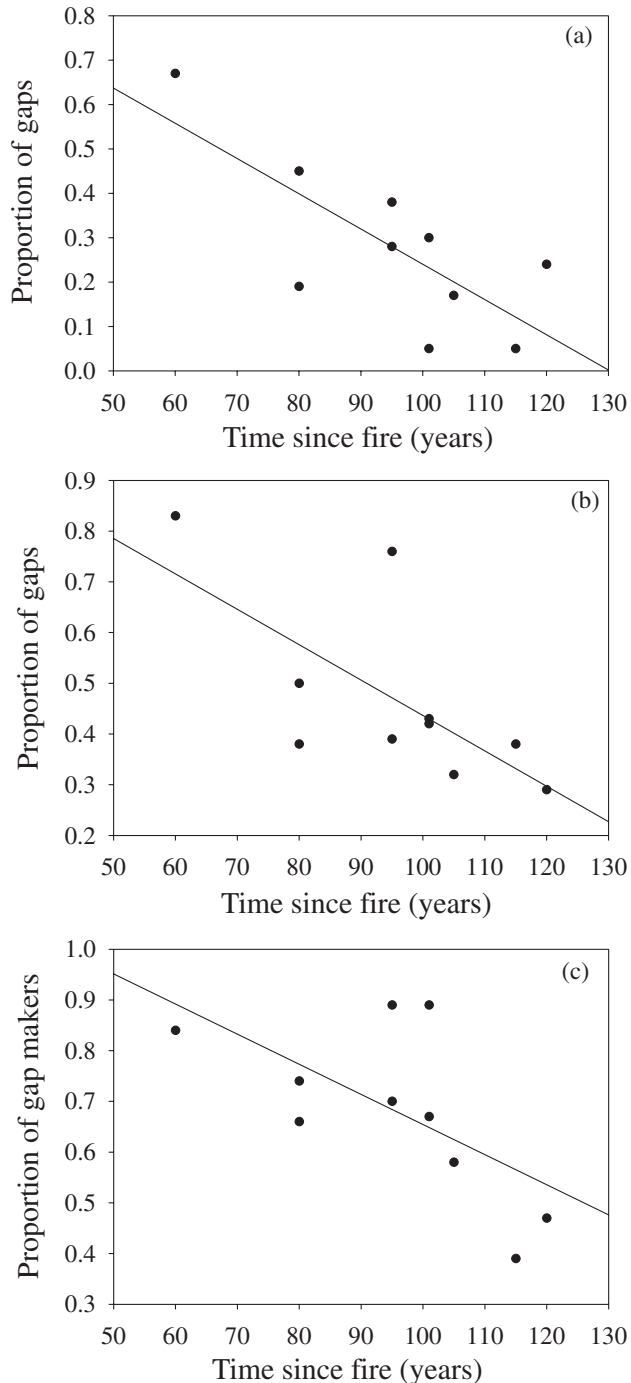
Gap characteristics

Our study reveals that gap creation and associated characteristics are dynamic during the development of trembling aspen stands. Young stands are characterized by (1) low gap fraction and gaps of small area (Fig. 1); (2) gaps with single

gap makers in early and similar decay stages (Fig. 2); and (3) gaps with predominantly standing dead gap makers (Table 3). Our results are consistent with results from gap studies in trembling aspen stands in other regions. Cumming et al. (2000) found that gaps are created as early as 40 years following a stand-replacing disturbance, with a range of gap fraction from 5.9% to 16.6% and mean gap area of 52.3 m². Similarly, Kneeshaw and Bergeron (1998) found that trembling aspen stands of age 50, 78, and 124 years ranged in gap fraction from 19% to 32%, with a range of gap area from 11.6 to 1450 m². This regional consistency is indicative of a gradual decline associated with even-aged forests that develop following stand-replacing disturbance; not a sudden decline, which can also occur in trembling aspen forests across North America (Frey et al. 2004).

As was the case for gap characteristics, gap-maker characteristics varied with time since fire. Gaps in young stands had gap makers in early and similar states of decay, whereas gaps in older stands had gap makers in more advanced and various states of decay. This suggests that gap expansion is an important process of gap formation; gaps increase in size and structural complexity with time. In general, forest stands in earlier stages of development have had less time to be exposed to factors responsible for gap creation than stands in later stages of development. This was commonly observed in older stands, where individual gaps had numerous gap mak-

Fig. 2. Relationships between time since fire and (a) proportion of gaps resulting from a single gap maker (see model 4 in Table 3), (b) proportion of gaps with gap makers in a single decay class (see model 5 in Table 3), and (c) proportion of gap makers in early stages of decay (decay classes 1 and 2) (see model 12 in Table 3).



ers that resulted from independent disturbance events. The transition from gaps having predominantly standing dead gap makers to gaps having predominantly snapped gap makers reflects two distinct resource-release processes: gap makers with dead crowns remaining in the forest canopy (standing dead) provide a gradual release of resources, whereas dead

crowns removed from the canopy (snapped or uprooted) provide a punctuated release of resources (Krasny and Whitmore 1992). Beyond the impact that gap-maker structure has on resource release, the production of coarse woody debris by snapped or uprooted gap makers may create favorable microsites for tree establishment (e.g., eastern white-cedar; Simard et al. 1998) and habitat for animals (Fan et al. 2003; Payer and Harrison 2003).

Despite the dynamic nature of gap characteristics during the development of trembling aspen forests, the processes responsible for gap formation were consistent through time. None of the factors responsible for gap-maker mortality were statistically related to time since fire (Table 3). Infection by wood-decay fungi was the most frequent factor responsible for tree death regardless of time since fire (56% of all gap makers). The high incidence of infection by fungi suggests that fungal pathogens play an important role in gap formation throughout stand development. Also, we expect that wood-decay fungi have significantly contributed to the formation of standing dead and snapped gap makers, as fungi can kill or weaken trees. Furthermore, fungal infection may have a distinct impact on tree mortality at different times during stand development: during the earlier stages of development, wood-decay pathogens can augment asynchronies in competitive interactions among stems and influence thinning (Cherubini et al. 2002), whereas in the later stages of development, older stems that are infected by wood-decay pathogens presumably become more susceptible to windthrow (Whitney et al. 2002). Other factors that caused mortality, such as wind, were also independent of time since fire (Table 3). We suspect that this is related to the stochastic nature of meteorological events that are powerful enough to snap or uproot mature trees and is probably not a deterministic factor resulting in gap formation.

Stand transition

Results from our study indicate that gaps that occur during the decline of trembling aspen forests do not significantly affect tree recruitment patterns. Transition probabilities for species such as balsam fir, trembling aspen, black spruce, and white spruce did not differ statistically among gap types and between gaps and the understory (Table 4). The high transition probability to balsam fir is driven by its high abundance (Fig. 3) and is consistent with studies conducted in older, conifer-dominated eastern boreal forests (Kneeshaw and Bergeron 1998, 1999; Pham et al. 2004). Similar transition probabilities for species such as balsam fir can be explained by their shade tolerance, which enables them to have high establishment and survival under canopy cover (Osawa 1994; McLaren and Janke 1996). However, the lack of a significant gap effect for shade-intolerant species such as trembling aspen was contrary to our expectation. In conifer and mixed aspen-conifer stands, large gaps encourage intolerant hardwood regeneration (Kneeshaw and Bergeron 1998, 1999; Prevost and Pothier 2003). Presumably in these studies, the occurrence of trembling aspen regeneration was associated with increases in incident light and ground temperatures caused by canopy gaps (Frey et al. 2003; Prevost and Pothier 2003). In our study, the gaps were relatively small (<350 m²); therefore changes in the microclimate were probably minimal (compared with the closed-canopy understory environment). In most cases,

Fig. 3. Stem density (mean \pm 1 SE) of the most abundant tree species found in canopy gaps and understory: sy, small young gap; so, small old gap; ly, large young gap; lo, large old gap; us, understory. Note the different scale on the ordinate axis for balsam fir.

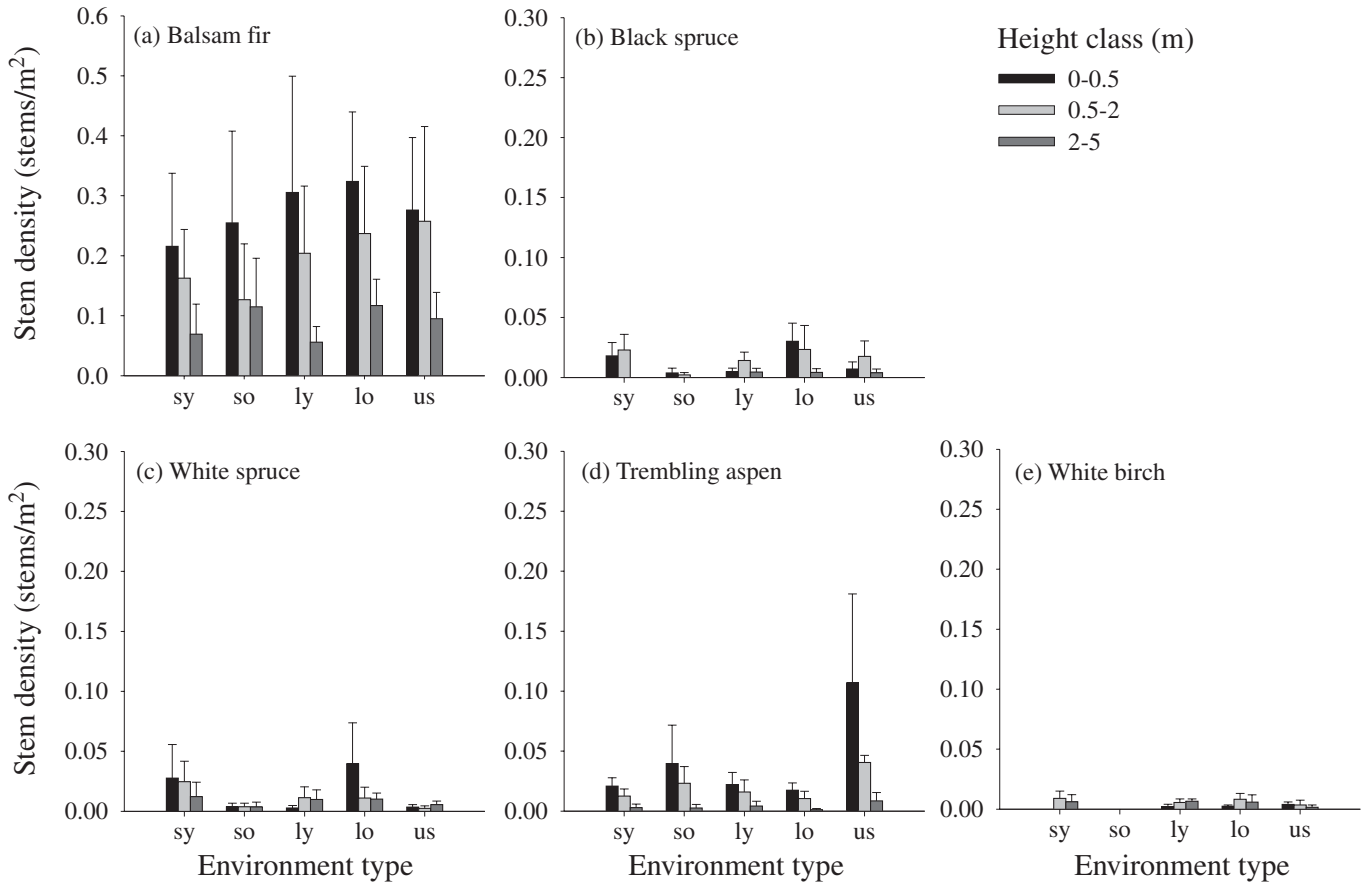
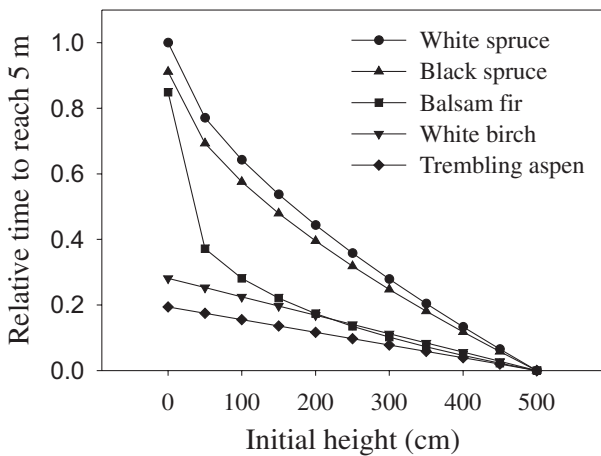


Fig. 4. Relative time to reach 5 m for common juvenile tree species found in trembling aspen stands in our study area. Relative times for each species are weighted by white spruce and show that with the same initial height, trembling aspen would reach 5 m first, followed by white birch, balsam fir, black spruce, and white spruce.



the transition probabilities for trembling aspen were based on a high abundance of relatively small (<1.5 m) root suckers (Fig. 3). Since continued survival of trembling aspen root suckers is limited in shaded environments, transition proba-

bilities for small gaps and understory environments may not be realistic and should be lower than reported values (Prevost and Pothier 2003). Alternatively, low variability in the light environment below trembling aspen canopies in high latitude forests can potentially explain the similar recruitment and growth patterns, regardless of the range of overhead crown closure (Messier et al. 1998). Similar transition probabilities among gap environments and between gaps and the understory observed in this study suggest that changes in the understory environmental conditions have a minimal impact on patterns of juvenile tree abundance and growth (for gaps smaller than 350 m²; the maximum gap size considered for inclusion of transition probability calculations in this study). The exception is for environmental changes that are associated with an increased probability of white birch in large young gaps (Table 4).

Since gap type based on size and age did not significantly influence transition probability, other factors must be responsible for influencing the observed patterns of recruitment. The well-developed population structure of shade-tolerant conifer species (in particular balsam fir) in the closed-canopy understory suggests that processes prior to the onset of gap formation are important for establishment. Establishment of an initial cohort of balsam fir following stand-replacing disturbance is related to favorable germination beds and proximity to unburned areas with parent trees (Galipeau et al. 1997). Therefore, well-developed balsam fir population struc-

tures may be limited in trembling aspen stands that undergo an intense thinning stage, since high deciduous canopy cover and leaf litter limit the survivorship and suitability of germination sites for balsam fir seedlings (Simard et al. 1998; McLaren and Janke 1996).

Processes associated with tree mortality that result in gap formation have received little attention in the boreal forest. Results from our study suggest that infection by pathogenic wood-decay fungi is an important contributing factor in gap-maker mortality, regardless of time since fire. Since an in-depth characterization of the fungal communities that influence stand dynamics was not within the scope of our study, we suggest that this should be a major emphasis of future boreal gap dynamics studies. Also, we only focused on trembling aspen dominated forests in this study. The lack of research into the patterns and impacts of small-scale disturbance in other common postfire boreal forest types seriously hinders our true understanding of the system. With this in mind, we suggest that other postfire forest types in the eastern boreal forest should receive attention, including those dominated by white birch, jack pine, or black spruce (Bergeron 2000; Chen and Popadiouk 2002).

Conclusion

The results of this study clearly show that gaps are a frequent and conspicuous phenomenon during the development of trembling aspen forests in our study region. Gaps were present as early as 60 years following stand-replacing disturbance and increased in frequency and size with time. Despite the observed patterns of gap formation, mechanism of gap-maker mortality showed no pattern with time, and gap size and age did not influence transition probabilities. Overall, we conclude that gaps that form during the breakup or decline of trembling aspen stands will have little impact on successional direction. However, we must emphasize that this result is for canopy gaps that are less than 350 m². In cases where small-scale disturbances create larger gaps or patches, patterns of abundance and growth of trees in the understory may be different.

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