Gap dynamics in Balsam Fir, *Abies balsamea* – Yellow Birch, *Betula alleghaniensis,* forests of Québec

Rémi Hébert[1] and Jean Huot

Département de biologie and Centre d'Études Nordiques, pavillon Alexandre-Vachon, Université Laval, Québec, Québec G1K 7P4, Canada
[1]Corresponding author: remi_herbert@hotmail.com

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To determine if gap dynamics can play an important role in the natural regeneration process of Balsam Fir (*Abies balsamea*)-Yellow Birch (*Betula alleghaniensis*) forests and to determine the effects of gap characteristics on regenerating woody species, we sampled 119 gaps from 64 forest stands in La Mauricie National Park. Gaps averaged 184.5 m² in size. The mean gap age was 7.8 years. Gaps were usually created by broken or uprooted trees and only rarely resulted from Spruce Budworm (*Choristoneura fumiferana*) outbreaks. We found 25 species that regenerated in the gaps or under the forest cover. When considering all species, significantly more stems/ha were in gaps than under the forest cover. Gap characteristics generally did not influence regenerating woody species. We present a comprehensive model of gap dynamics in Balsam Fir-Yellow Birch forests, starting from a dense canopy, continuing with the creation and colonization of gaps, and ending to the closure of the canopy. Gap dynamics play an important role in the natural regeneration process of Balsam Fir-Yellow Birch forests.

Key Words: Balsam Fir, *Abies balsamea,* Yellow Birch, *Betula alleghaniensis,* gap size, gap age, gap origin, mixed forest, natural regeneration model, La Mauricie National Park, Quebec.

Afin de déterminer si la dynamique par trouée peut jouer un rôle important comme processus naturel de régénération de la sapinière à Bouleau Jaune et aussi afin de déterminer les effets des caractéristiques des trouées sur la régénération, nous avons échantillonné 119 trouées dans 64 peuplements forestiers au parc national de la Mauricie. Ces ouvertures avaient une superficie moyenne de 184,5 m². L'âge moyen des ouvertures était de 7,8 ans. Elles étaient généralement créées par un arbre cassé ou déraciné. Peu d'ouvertures étaient créées par des épidémies de la Tordeuse des Bourgeons de l'Épinette. Au total, 25 espèces en régénération ont été rencontrées dans les ouvertures ou sous le couvert forestier. En considérant toutes les espèces, il y avait significativement plus de tiges/ha dans les ouvertures que sous le couvert forestier. Les caractéristiques des trouées n'influençaient généralement pas la régénération. Nous présentons un modèle complet sur la dynamique par trouée dans la sapinière à Bouleau jaune, commençant avec une canopée dense, continuant avec la création et la colonisation des trouées, et se terminant avec la fermeture de la canopée. La dynamique par trouée joue un rôle important dans le régime de perturbations de la sapinière à Bouleau jaune.

Mots-clés : Dynamique par trouée, forêt mixte, modèle de régénération naturelle, parc national de la Mauricie, sapinière à Bouleau Jaune.

In forest ecology, gap dynamics is a natural regeneration process driven by small-scale spatial disturbances (Runkle 1985). It may involve the fall of a single canopy tree, part of a canopy tree, of a very few individuals. When a canopy tree (or a part) falls, it creates a gap. A greater proportion of the light then reaches the soil surface, stimulating the regeneration of woody species. One or two trees growing in a gap will be able to reach the canopy, replacing the tree that created the gap.

Gap dynamics are found in forests around the world (Lawton and Putz 1988; Payette et al. 1990; Kohyama 1993; Abe et al. 1995). In this paper, we focus on one particular forest type, the Balsam Fir, *Abies balsamea* – Yellow Birch, *Betula alleghaniensis,* forests. The natural regeneration process of the Balsam Fir-Yellow Birch forests is very poorly understood, but the Québec forestry manual reports that gap dynamics might be the main regeneration process of this forest type (Grondin 1996). Our first objective was to describe the characteristics of gaps in this ecosystem. We hypothesized that in mature stands, gaps are abundant. For example, based on the work of Kneeshaw and Bergeron (1998) in Quebec Balsam Fir-White Birch (*Betula papyrifera*) forests, we expected 26-32% of the forest to consist of gaps.

Our second objective was to determine the effects of gaps on the regeneration of woody species. We hypothesized that canopy species, such as Balsam Fir and Yellow Birch would have more abundant regeneration in gaps than under the forest cover. Several studies showed that these species react positively to an increased light availability (Beaudet and Messier 1998; Coates 2000; McCarthy and Weetman 2006; Webster and Jensen 2007). We also hypothesized that the age or size of gaps could influence regenerating woody species. Knowing how long gaps last could be very useful in providing insight into the turnover rate of the mature Balsam Fir-Yellow Birch forests.

Study Area

Balsam Fir-Yellow Birch forests cover 6% of Québec's territory, that is about 95000 km^2 (Grondin 1996). Along with the Balsam Fir-White Birch forests, they form the mixed forest ecosystem. The mixed forest ecosystem is characterized by the simultaneous presence of deciduous and coniferous species in the same forest stand. The mixed forest ecosystem is located between the southern deciduous forest ecosystem and the northern boreal forest ecosystem.

We conducted our study in La Mauricie National Park. The park covers an area of 536 km^2 and is located about 20 km northwest of Shawinigan and Grand-Mère (46°38' / 46°56' north latitude, 72°45' / 73°11' west longitude). The Saint-Maurice River forms the park's eastern border and the Mattawin River its northern border. Annual mean temperature varies from 2.8°C to 4.4°C (Service de la conservation des ressources naturelles 1981) and annual mean precipitation from 900 to 1100 mm (Robitaille and Saucier 1998). Topography within the park is characterized by hills with rounded summits with a mean altitude of 431 m.

La Mauricie National Park is found within the transition zone between the southern deciduous forest ecosystem and the northern boreal forest ecosystem (Lalumière and Thibault 1988). Forests cover 93% of the park's surface area and these can be divided into four main groups: forested peat bogs (5%), coniferous forests (21%), deciduous forests (25%) and mixed forests (49%) (Pelletier 1998). Twenty-nine tree species have been identified within the park. Balsam Fir, Red Spruce (*Picea rubens*), Sugar Maple (*Acer saccharum*), Yellow Birch, Red Maple (*Acer rubrum*) and White Birch are the most common (Service de la conservation des ressources naturelles 1981). The park was created in 1970 in order to ensure the ecological integrity of a representative piece of the Canadian Shield (Pelletier 1998). Since the park's creation, no timber harvesting has been carried out within its borders. However, the park's forests were partially harvested in the past (Pelletier 1998).

Methods

Field work was carried out during the summer of 1999. We sampled a total of 119 gaps from 64 forest stands. We selected forest stands from a forest map (1: 20000) based on their composition and age (mature). Most mature stands had an uneven structure, so age determination was not available. It is usually assumed that these stands are >90 years old. Balsam Fir-Yellow Birch was the most common stand type selected. Usually, it was pure, but accompanying species such as Spruces, Sugar Maple and White Birch were often observed.

Gap characteristics

We adopted three criteria in order to define gaps. First, an opening in the canopy was necessary. Second, the presence of a dead tree was required. Thirdly, regenerating woody stems had to be less than half the canopy height. We sampled only the fifth, tenth and fifteenth (if applicable) gaps, viewed from a transect passing as closely as possible to the center of each forest stand. To determine size, we measured the gap length and width. Gaps were delimited using the trunks of surrounding mature trees as the border. Gaps were thus considered according to the definition of expanded gaps proposed by Runkle (1985). The shape that best described the gaps was the ellipse.

We estimated the age of gaps by cutting three saplings in each gap. We chose stems that appeared to be the oldest in each gap. Our goal was to harvest stems that were present before the formation of the gap. These stems would have been exposed to a marked increase in available light following the gap's creation and should demonstrate a marked increase in annual growth ring width. Moisture probably did not affect the growth rings since most gaps (90%) in our study were located on dry stations (Hébert 2000). Coniferous stems were preferentially harvested since their growth rings were easier to count. We estimated the age of the gap by counting the number of larger growth rings since release (growth rings had to be at least twice as large as previous years to be counted as released). Growth rings were counted using a magnifying glass (1.75×). The age of the gap was determined using the mean age of saplings with a maximum difference of two years. Gaps where all harvested saplings demonstrated an age difference greater than two years were considered to have been created by distinct temporal events and age was not calculated. We also compared the size of gaps with known age versus those of unknown age.

We determined the origin of gaps according to three categories. The first category consisted of gaps caused by broken or uprooted trees. This designation included trees that had died from old age, broken due to deterioration, had large broken branches, or trees uprooted by wind. The second category consisted of gaps caused by insect outbreaks. Insect damage was largely caused by Spruce Budworm and resulting snags could be easily identified (still standing with a broken top). The third category consisted of gaps caused by a combination of both broken or uprooted trees and by insect outbreaks. We compared the size of gaps for each origin using Bonferroni *t*-tests.

Effects of gaps on regenerating woody species

To sample the regenerating woody species, we opted for a paired sampling design in order to compare the vegetation in gaps to that of the surrounding forest.

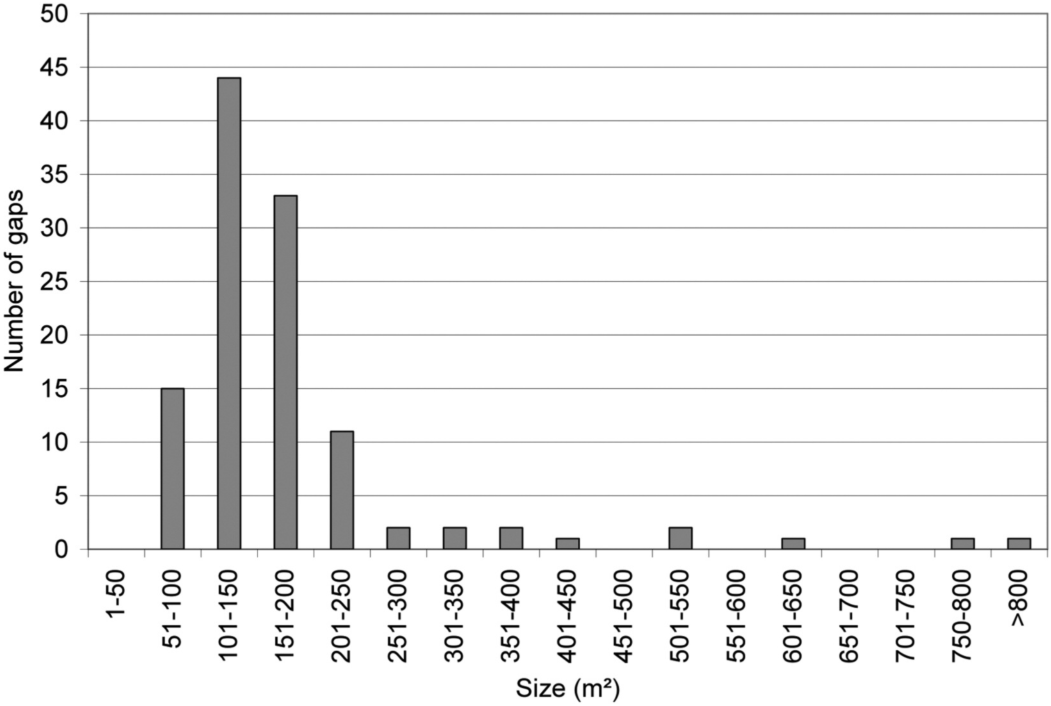

FIGURE 1. Gap size distribution in Balsam Fir-Yellow Birch forests of La Mauricie National Park, Québec.

We inventoried woody species using two plots of 1 m by 4 m positioned at the center of the halves of the longest diagonal of the gap. Two plots of 4 m^2 were also positioned under the forest cover. They were located 10 m from the border of the gap, in the axis of the longest diagonal of the gap. If the plots overlapped another gap, they were relocated perpendicularly to the longest gap diagonal. In each plot, all woody stems measuring over 20 cm in height were identified to species. We noted all stems having more than half of their base inside the plot and offering available twigs up to 2 m height from the ground. Spruces were not distinguished at the species level. Canadian Yew (*Taxus canadensis*) stems were counted as individual when separated above the ground.

For data analysis, we grouped the two plots of each gap together. The two corresponding plots under the forest cover were grouped as well. We used the Shapiro-Wilk test to verify data normality. Since standard transformations were unsuccessful, we used the Wilcoxon signed ranks test for paired data to compare vegetation in gaps and under the forest cover.

To determine the effects of gap characteristics on the regenerating woody species, we build a general model using an analysis of variance (ANOVA) on the number of stems and on the number of species. The analysis included the size, age and origin of gaps, as well as the interactions between the variables. Statistical analyses were done with the SAS software (SAS Institute Inc 2003). We considered the results of the statistical tests significant when $P < 0.05$.

Results

Gap characteristics

The mean size of the gaps was 184.5 ± 14.6 (mean ± standard error) m^2. The smallest encountered gap was 51 m^2 in size, whereas the largest was 1415 m^2 (Figure 1). However, the latter is unusual since the second largest gap measured 760 m^2. Ninety percent of the gaps had a size ≤ 250 m^2 and 67% of gaps were between 101 and 200 m^2.

Mean age of gaps was 7.8 ± 0.4 (mean ± standard error) years. Moreover, the majority of gaps (77%) were between 4 and 9 years old. The youngest gap encountered was 3 years old, while the oldest was 17 years old (Figure 2). We were able to estimate the age of only 73 of the 119 gaps sampled. Of the remaining gaps, we did not have enough data for 29 gaps (when coniferous stems were absent or not old enough, we still harvested deciduous stems in replacement, but we were often unable to read the growth rings in the laboratory), and 17 gaps had too much variation in the

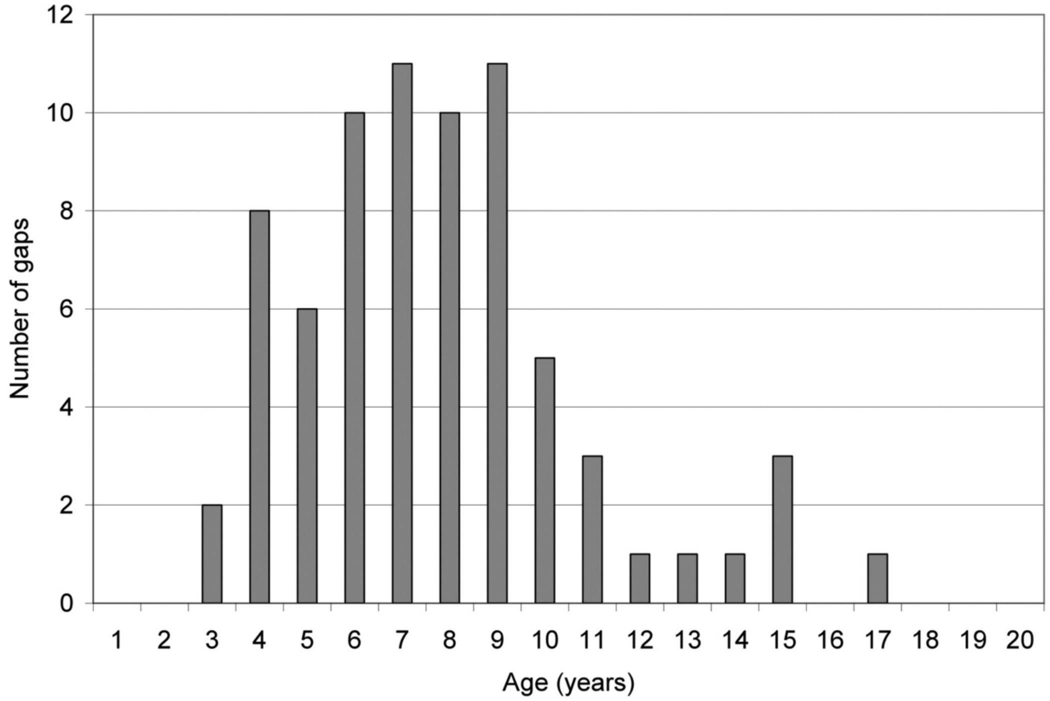

FIGURE 2. Gap age distribution in Balsam Fir-Yellow Birch forests of La Mauricie National Park, Québec.

age, which suggests that at least 14% of gaps were created from distinct temporal events. However, gap size did not significantly differ (Z = 0.340, $P = 0.734$) between gaps of known age (171.2 m² ± 11.9, $n = 69$) and gaps of unknown age (204.5 m² ± 31.8, $n = 46$). There was also no significant difference (Z = -1.507, $P = 0.132$) in gap size between 3-7 year-old gaps (193.6 m² ± 20.9, $n = 35$) and 8-17 year-old gaps (148.1 m² ± 9.9, $n = 34$).

For the origin of gaps, broken or uprooted trees were responsible for the majority of gaps (56%). The combination of broken or uprooted trees and insect outbreaks represented the second most frequent cause of gap creation (36%). Insect outbreaks alone (8%) seem to play a relatively weak role, especially when they are not in combination with broken or uprooted trees. The size of gaps did not differ significantly among origins (Figure 3). The majority of gaps resulting from insect outbreaks were, like the others, of small dimension (about two or three trees).

Effects of gaps on regenerating woody species

A total of 25 woody species was encountered in the plots (Table 1). Species such as Red Maple, Yellow Birch, Mountain Maple (*Acer spicatum*), Hobblebush (*Viburnum alnifolium*) and Beaked Hazelnut (*Corylus cornuta*), had significantly more abundant regenerating stems in gaps. Only one species, Canada Yew, had significantly more abundant regenerating stems under the forest cover. Other species, such as Balsam Fir, Sugar Maple, White Cedar (*Thuja occidentalis*), Spruces, American Beech (*Fagus grandifolia*), Striped Maple (*Acer pensylvanicum*) and the American Fly-honeysuckle (*Lonicera canadensis*), had regenerating stems as abundant in gaps as under the forest cover. When considering all species, significantly more stems/ha were found in gaps than under the forest cover.

In general, gap characteristics did not influence the regenerating woody species (Table 2). The size, age, or origin of gaps, as well as the interactions among these variables, did not affect significantly the total number of stems found in the gaps, nor the number of species found in gaps. Gaps had a mean number of regenerating woody species of 5.6 ± 0.1 (mean ± standard error; minimum = 2 species; maximum = 9 species).

Discussion

Gap characteristics

A relatively large portion of the forest consisted of gaps, suggesting that gap dynamics play a major role in the regeneration process of Balsam Fir-Yellow Birch forests. In mixed forest stands of La Mauricie National Park, Hébert (2000) reported that gap density was 1173.7 ± 76.3 (density ± standard error) gaps/km².

Knowing the mean size of a gap, we can now determine that gap occupied 21.7 ± 2.2 (proportion ± standard error) % of the forest area. Our result on the size of gaps and on the proportion of the forest comprised of gaps compare well with other studies done in other ecosystems (Table 3), including the study of Kneeshaw and Bergeron (1998) carried out in the Balsam Fir-White Birch domain. In our study, the fact that we had no gaps < 50 m^2 probably indicates that in Balsam Fir-Yellow Birch forests, a gap of at least 50 m^2 is created when a tree dies.

The oldest gap encountered was 17 years old, suggesting that in the Balsam Fir-Yellow Birch forest, the process of gap formation and closure occurs within approximately 20 years. Runkle (1990) found that the majority of gaps were 6 years old or younger in a deciduous forest dominated by the genus *Acer* and *Fagus*. However, some gaps were up to 21 years old. Age provides a good idea of the duration of a gap, and can provide insight into the turnover rate of the mature Balsam Fir-Yellow Birch forest. With an approximate time of 20 years to reach half canopy height and a mean proportion of 21.7% of the land occupied by gaps, this suggests a full canopy turnover rate of about 184 years.

We noted that some gaps might have been created by distinct temporal events. Runkle (1985) also reported this phenomenon. For example, a gap could initially be created by only one tree fallen from the canopy. A few years later, another tree from its border could fall, thus increasing the initial size of the gap. The date of reaction (larger growth rings) of the stems in this gap created by two different episodes would differ significantly. Individual variation between stems could also explain why age was not determined for all gaps. Each stem may react differently. One may be located in a shadier part of the gap or one may stay in the shade longer than the others because of more developed stems surrounding it for example. The fact that gap size was not related to gap age indicates that gap size is probably relatively stable in Balsam Fir-Yellow Birch forests.

Three reasons could explain the weak influence of Spruce Budworm outbreaks on gap creation. The first reason is that when a coniferous tree dies, it does not clear much space in the canopy. The other deciduous trees in the canopy take advantage of the small gap by simply lengthening the branches in their crown, thus rapidly closing the opening (Runkle and Yetter 1987). The second reason why insect outbreaks do not play a larger role is that mixed stands are less susceptible to Budworm outbreak than pure Balsam Fir stands (Su et al. 1996; Cappucino et al. 1998). Finally, the third reason is that the study was not conducted in a period of severe outbreak. Results show that the majority of gaps were between 4 and 9 years old. In Québec, the last severe outbreak took place from about 1973 to 1985 (Blais 1983; Hardy et al. 1983; Gray et al. 2000).

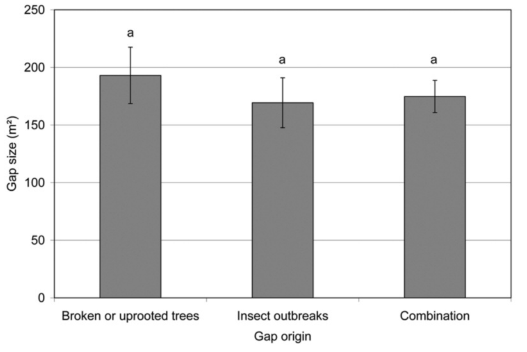

FIGURE 3. Gap size (mean ± standard error) of gaps created by broken or uprooted trees (n = 64), by insect outbreaks (n = 10), and by a combination of broken or uprooted trees and insect outbreaks (n = 41) in Balsam Fir-Yellow Birch forests of La Mauricie National Park, Québec. Means with the same letter were not significantly different.

Even though Spruce Budworm is not active solely within the context of a severe outbreak, more gaps would potentially be created during an outbreak, relatively few of these would still be visible. Kneeshaw and Bergeron (1999) also reported that the Spruce Budworm can be a factor in the creation of small gaps.

Effects of gaps on regenerating woody species

We distinguished three regeneration strategies of woody species: (1) species with more abundant regenerating stems in gaps; (2) species with more abundant regenerating stems under the forest cover; (3) species with regenerating stems as abundant in gaps as under the forest cover. Whitmore (1989), in a discussion on the general groups of forest trees, identified only the two first categories.

In general, species with more abundant regenerating stems in gaps are usually associated with light. They need a lot of light to enable seeds to germinate and for young stems to survive. As a result, gaps are beneficial by enabling the massive recruitment of new stems. Connell (1989) and Schupp et al. (1989) wrote a good discussion on the origin of colonizing species and on the challenges they must overcome. Soil resources probably also change in gaps. Our results indicated that Yellow Birch is using this strategy, where gaps enable the species to reproduce and to reach the canopy. The abundance of Yellow Birch appears relatively low in comparison to Mountain Maple, but Yellow Birch survives much longer and reaches the canopy.

We found only the Canada Yew in the category of species with more abundant regenerating steams under the forest cover. Canada Yew is a shade-demanding species (Marie-Victorin 1995). It cannot endure light and therefore does not regenerate in gaps. We even observed cases of Canadian Yew mortality in gaps.

Species with regenerating stems as abundant in gaps as under the forest cover are relatively shade tolerant.

TABLE 1. Abundance of regenerating woody species (number of stems/ha) in gaps and under the forest cover of Balsam Fir-Yellow Birch forests in La Mauricie National Park.

Species	Gap		Forest cover		Wilcoxon signed ranks test	
	Mean	Standard error	Mean	Standard error	Z	*P*
Abies balsamea	7973	811	7248	792	-0.890	0.373
Acer pensylvanicum	4212	883	3487	606	-0.169	0.866
Acer rubrum	4842	762	2458	375	-2.661	0.008
Acer saccharum	4338	764	3655	759	-1.339	0.181
Acer spicatum	16765	1396	7553	674	-5.909	0.000
Amelanchier sp.	336	125	273	130	-0.713	0.476
Betula alleghaniensis	3078	507	620	138	-5.222	0.000
Betula papyrifera	74	34	53	38	-0.343	0.732
Cornus alternifolia	53	38	0	0	-1.342	0.180
Cornus stolonifera	21	21	53	38	0.816	0.414
Corylus cornuta	4569	1024	914	260	-4.104	0.000
Diervilla lonicera	147	56	116	79	-0.465	0.642
Fagus grandifolia	368	172	252	91	-0.141	0.888
Fraxinus americana	11	11	0	0	-1.000	0.317
Lonicera canadensis	1218	318	746	163	-0.296	0.767
Picea sp.	578	134	672	156	0.640	0.522
Sambucus pubens	210	120	0	0	-2.271	0.023
Shepherdia canadensis	32	23	0	0	-1.342	0.180
Sorbus americana	189	64	74	34	-1.617	0.106
Taxus canadensis	4149	1134	8015	1819	2.187	0.029
Thuja occidentalis	1366	323	1912	446	1.087	0.277
Tsuga canadensis	32	23	63	36	0.647	0.518
Viburnum alnifolium	6733	1538	1964	483	-3.560	0.000
Viburnum cassionides	42	30	32	32	0.000	1.000
Viburnum edule	0	0	11	11	-1.000	0.317
Coniferous stems	14098	1435	17910	1908	1.299	0.194
Deciduous stems	47238	2394	22261	1694	-8.493	0.000
All species	61336	2484	40171	2542	-6.686	0.000

TABLE 2. General model built to determine the effect of various variables on the total number of stems (R^2 = 0.07) and on the number of regenerating woody species (R^2 = 0.20) in gaps of Balsam Fir-Yellow Birch forests in La Mauricie National Park.

Factors	Total number of stems/ha			Number of species		
	df	F	*P*	df	F	*P*
Age of gaps (years)	1	0.14	0.71	1	0.41	0.53
Origin of gaps (see note below)	2	0.17	0.85	2	0.27	0.76
Size of gaps (m^2)	1	0.60	0.44	1	0.51	0.48
Age*Origin	2	0.08	0.92	2	0.27	0.76
Age*Size	1	0.35	0.56	1	0.78	0.38
Origin*Size	2	0.27	0.77	2	0.75	0.48
Age*Origin*Size	2	0.11	0.90	2	0.53	0.59

Note: the three possible categories for the origin of gaps were broken or uprooted trees, insect outbreaks, and a combination of the two.

Their seeds can germinate under the forest cover and young stems survive (Canham et al. 1994). However, they will never be able to reach the canopy if they remain under the forest cover (Canham 1985, 1988). These species need gaps to reach the canopy, but not to reproduce. Our results indicated that this was the case for Balsam Fir.

One important question is also to determine whether there are enough gaps to ensure the maintenance of canopy composition. Yellow Birch lives up to 300 years. Since the turnover rate is below this life expectancy, continued recruitment of this species is possible because mature trees are likely to witness the creation of a gap to allow recruitment. For Balsam Fir, life expectancy is shorter than the turnover rate, with a life span generally close to 100 years. This could be a problem if Balsam Fir was relying on gaps to reproduce, because mature trees would not survive long

TABLE 3. Reports on gap characteristics found in the scientific literature in various forest ecosystems.

Study	Ecosystem	Gap size and proportion of the forest stands in gaps
Brokaw (1985)†	Tropical forest	Gap size = 20 m^2 to 705 m^2.
Cumming et al. (2000)	Boreal forest	Gap size = 52 m^2. Proportion = 3.6% to 16.6%.
Kneeshaw and Bergeron (1998)	Mixed forest	Proportion = 26.1% to 32.0%.
Krasny and DiGregorio (2001)	Deciduous forest	Gap size = 159 m^2 to 380 m^2. Proportion = 19.7% to 31.9%.
Krasny and Whitmore (1992)	Deciduous forest	Gap size = 209 m^2. Proportion = 20.7%.
Ott and Juday (2002)	Boreal forest	Gap size < 200 m^2. Proportion, mean = 27.4%. Proportion, range = 18.1% to 43.9%.
Pham et al. (2004)	Boreal forest	Gap size = 75 m^2 to 106 m^2. Proportion = 54.0%.
Runkle (1981)	Deciduous forest	Gap size, mean = 200 m^2. Gap size, range = 28 m^2 to 2009 m^2.
Runkle (1982)	Deciduous forest	Proportion, mean = 21.0%. Proportion, range = 6.7% to 47.0%.
Runkle (1990)	Deciduous forest	Gap size = 100 m^2 to 400 m^2. Proportion = 14.1%.
Uhl et al. (1988)†	Tropical forest	Gap size < 200 m^2.

† These authors used canopy gaps instead of extended gaps.

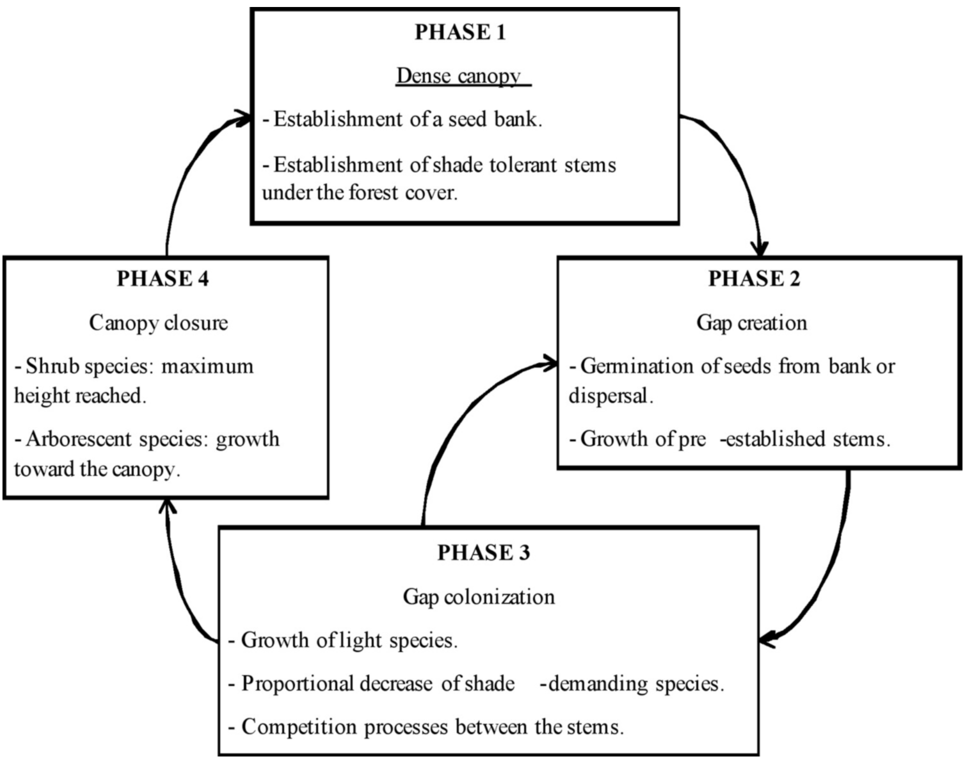

FIGURE 4. Gap dynamics model in Balsam Fir-Yellow Birch forests of La Mauricie National Park, Québec.

enough to witness the creation of a gap. However, there is Balsam Fir recruitment under the forest cover waiting for a gap to be created.

Composition of the regenerating woody species in gaps and under forest cover does not seem to be completely independent. We propose a four-step model of gap dynamics in Balsam Fir-Yellow Birch forests (Figure 4). Phase 1 takes place under the forest cover, where some stems establish. These species' seeds can germinate under the forest cover and young stems survive. They mostly belong to the category of species with regenerating stems that are as abundant in gaps as under the forest cover. Phase 2 consists of gap creation. Here, we observe the growth of pre-established stems that were still under the forest cover at the time of the first phase. We also note germination of seeds from bank or dispersal. In phase 3, we note the proliferation of light-demanding species. These species can hardly regenerate under the forest cover and therefore belong to the category of species with regenerating stems more abundant in gaps than under the forest cover. Shade-demanding species also decrease in gaps, thus corresponding to the category of species with regenerating stems more abundant under the forest cover than in gaps. Phase 4 is when shrub species reach their maximum height. Arborescent species then continue their growth toward the canopy. When the canopy closes, the process then repeats itself (Watt 1947). As Runkle (1985) emphasized, some stems may need more than one gap to reach the canopy, which explains the possible return from phase 3 to phase 2 that we suggested. Once back to the second gap for example, the stems have already grown considerably as opposed to the newly pre-established stems.

Brokaw and Scheiner (1989) reported that the composition of the regenerating species varies according to the size of gap, thus contributing to the biodiversity of the tropical forest. This is not the case in the Balsam Fir-Yellow Birch forests, since the size of gaps generally did not influence the composition of regenerating woody species. Vegetation within gaps also appears to be relatively stable, since gap age generally did not influence regenerating woody species.

Conclusion

Knowledge on the natural regeneration processes of the forest ecosystems is important, especially to reduce the impacts of timber harvest. For instance, the ecosystem management approach relies on exploitation techniques that are based on the natural regeneration processes of the forest stands (Carignan and Villard 2002). In the Balsam Fir-Yellow Birch domain, our study indicates that special attention should be placed on exploitation techniques, such as partial cutting, that tend to imitate gap dynamics (Hébert 2003). Our study also reveals the importance of protected forests in national parks, since they can serve as models to better understand the natural dynamics of the forest ecosystems.

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