

Large-scale synchrony of gap dynamics and the distribution of understory tree species in maple–beech forests

Dominique Gravel · Marilou Beaudet ·
Christian Messier

Received: 13 November 2008 / Accepted: 17 July 2009 / Published online: 8 August 2009
© Springer-Verlag 2009

Abstract Large-scale synchronous variations in community dynamics are well documented for a vast array of organisms, but are considerably less understood for forest trees. Because of temporal variations in canopy gap dynamics, forest communities—even old-growth ones—are never at equilibrium at the stand scale. This paucity of equilibrium may also be true at the regional scale. Our objectives were to determine (1) if nonequilibrium dynamics caused by temporal variations in the formation of canopy gaps are regionally synchronized, and (2) if spatiotemporal variations in canopy gap formation affect the relative abundance of tree species in the understory. We examined these questions by analyzing variations in the suppression and release history of *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh. from 481 growth series of understory saplings taken from 34 mature stands. We observed that (1) the proportion of stems in release as a function of time exhibited a U-shaped pattern over the last 35 years, with the lowest levels occurring during 1975–1985, and that (2) the response to

this in terms of species composition was that *A. saccharum* became more abundant at sites that had the highest proportion of stems in release during 1975–1985. We concluded that the understory dynamics, typically thought of as a stand-scale process, may be regionally synchronized.

Keywords Canopy gaps · Synchrony · Northern hardwoods · Sapling dynamics · Growth release

Introduction

Large-scale synchronous variations in the dynamics of forest tree species are neither common nor well documented (Koenig and Knops 1998; Clark and McLachlan 2003; Liebhold et al. 2004). Understanding the factors responsible for spatial covariation of species dynamics has important implications for predicting species distribution, abundance and extinction risk (Lande et al. 2003). Theory and empirical data suggest three different mechanisms are behind spatially synchronized fluctuations in population densities (Liebhold et al. 2004): (1) dispersal of individuals from a source population; (2) population dependence on an exogenous factor that is spatially synchronized (the Moran effect), and; (3) trophic interactions with other organisms that are spatially synchronized. Since forest trees are organisms with relatively limited dispersal, the most likely mechanism is the second one, although some forest communities are also affected by interactions with other organisms such as insects and pathogens.

In many forest understories, light is the major constraint on tree growth and survival, and an important axis for differentiating ecophysiology, architecture, and demography among different tree species. Consequently, there have been extensive efforts in forests worldwide to document

Communicated by Miguel Franco.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-009-1426-6) contains supplementary material, which is available to authorized users.

D. Gravel · M. Beaudet · C. Messier
Département des Sciences Biologiques, Centre d'Étude de la Forêt
(CEF), Université du Québec à Montréal, C.P. 8888,
Succ. Centre-Ville, Montréal, QC H3C 3P8, Canada

Present Address:

D. Gravel (✉)
Département de Biologie, Chimie et Géographie,
Université du Québec à Rimouski, 300 Allée des Ursulines,
Rimouski G5L 3A1, Canada
e-mail: dominique_gravel@uqar.qc.ca

canopy disturbance regimes and the resulting heterogeneity of understory light conditions (e.g., Runkle 1981; Brokaw 1982; Canham et al. 1990; Kneeshaw and Bergeron 1998). Most efforts have concentrated on the characterization of natural disturbance regimes at a single location (e.g. Lorimer 1980; Glitzenstein et al. 1986) because canopy gap dynamics are thought to be largely based on tree-by-tree replacement processes. The causes of the deaths of individual or groups of trees can, however, have a much wider spatial coverage, suggesting that the synchronization of forest dynamics at a regional scale can also occur, for example, as a result of the strong spatial synchrony of insect outbreaks (e.g., Bjornstad et al. 2002). Less well known, however, is whether the aftermath of such impacts on canopy gap dynamics (Bouchard et al. 2006) is also spatially structured. For instance, extreme climatic events can impact on crown dieback (Payette et al. 1996), in some cases causing tree death (Olano and Palmer 2003). Severe storms are also direct agents of disturbance, breaking branches and trees to form new canopy gaps, as for example in the severe 1998 ice storm in eastern North America (Beaudet et al. 2007b). Such storms leave long-term legacies in terms of the structure and composition of forest landscapes (Woods 2004). Widespread decline episodes are also common (e.g., Drohan et al. 2002) and have been shown to impact on canopy gap dynamics in single stands (Battles and Fahey 2000).

Because of temporal variations in canopy gap dynamics, forest communities are never at equilibrium at the scale of a single stand (Poulson and Platt 1996; Woods 2007), even in old-growth forests (Brisson et al. 1994). This pattern could also be true at the regional scale. In this study, we ask if the fluctuating dynamics of canopy gap formation are regionally synchronized by analyzing the suppression and release history of saplings from 34 mature northern hardwood stands in southern Quebec, Canada. More specifically, we test the hypothesis that the formation of canopy gaps is a regionally structured, nonstationary process at regional scales. Under nonsynchronized dynamics, release events should average across several sites, as the high proportion of stems in release at some sites balances the low proportion of stems in release at other sites. We also tested if a characteristic scale of synchrony exists by examining how synchrony among sites decreases with distance between them. Second, because light availability is a major influence on the distribution of tree species, we expected the history of suppression and release to affect the relative abundance of tree species. If this is indeed the case, changes in vegetation composition should also be regionally synchronized. We tested this hypothesis by analyzing the relative abundance of *Acer saccharum* Marsh. (ASA) and *Fagus grandifolia* Ehrh. (FGR) as a function of past suppression and release history. These two shade-tolerant species have been widely studied in attempts to understand

the mechanisms allowing their coexistence (e.g., Woods 1979; Poulson and Platt 1996; Beaudet et al. 1999, 2007a; Gravel et al. 2008), making them good candidates for this analysis. Although our focus was primarily on understory trees, we also performed this analysis on all of the understory woody species found in our forests.

Materials and methods

Study area

In 2003, we sampled 20 stands in the Eastern Townships region and 14 stands in the Portneuf region of southern Quebec (45°30′–47°00′N; 71°00′–72°30′W). These regions are, respectively, located in the *Acer saccharum*—American basswood (*Tilia americana* L.) and *A. saccharum*—yellow birch (*Betula alleghaniensis* Britton) bioclimatic domains (Robitaille and Saucier 1998). Overstories were a mixture of species with ASA as the dominant species, with various proportions of FGR, *B. alleghaniensis*, *Acer rubrum* L., *Ostrya virginiana* (Mill.) Koch, *Fraxinus americana* L., *Tsuga canadensis* (L.) Carr., *Abies balsamea* (L.) Mill., and *Picea rubens* Sarg. For consistency, we only sampled stands that met the following criteria: basal area (BA) >20 m²/ha; presence of trees >30 cm in diameter at breast height (DBH), and; relative BA of FGR (among trees >9 cm in DBH) >5%. Sampling was restricted to stands with no signs of recent disturbance, such as that caused by the 1998 ice storm or logging.

Field sampling

Sampling in the 34 stands was performed at three locations in each stand, 100 m apart along a 200 m transect. The starting locations of the transects and of the first plot were predetermined randomly on the stand map. At each sampling location, all stems (DBH > 9 cm, all species) were recorded in a 400 m² plot (11.28 m radius). Sapling densities (height > 1.3 m–9.0 cm at DBH, all species) were measured in a 100 m² subplot (5.64 m radius). Along each transect, ten ASA and ten FGR saplings (1.1–9.0 cm at DBH) were randomly selected among the three plots for extracting basal stem disks (~20 cm above the ground). Additional large saplings (DBH 5.1–9.0 cm) were harvested (in some cases outside the plots, but along the transect) to ensure a minimum sample of five individuals per species in the large sapling class. We did not distinguish between FGR saplings of seed origin and those of root sprout origin because the proportion of sprouts among stems of height 30 cm to 1 m was only 10.5% across our sites. The response to canopy gaps differs between sprouts and seedlings (Beaudet and Messier 2008; Cleavitt et al.

Table 1 Summary descriptors of release events detected in time series of radial growth

Variable	Species	Minor release		Major release	
		Mean \pm SE	<i>P</i> -value	Mean \pm SE	<i>P</i> -value
Number of release events	ASA	2.02 \pm 0.05	0.001	1.90 \pm 0.06	0.005
	FGR	1.76 \pm 0.05		1.64 \pm 0.06	
Fraction of series in release	ASA	0.40 \pm 0.01	0.013	0.25 \pm 0.01	0.152
	FGR	0.37 \pm 0.01		0.23 \pm 0.01	
Release duration (years)	ASA	9.08 \pm 0.25	0.593	5.28 \pm 0.13	0.075
	FGR	9.61 \pm 0.30		5.21 \pm 0.18	

Minor and major releases correspond to 100 and 200% increases in growth, respectively, sustained for at least four years. Species are compared by ANOVA with regions included in the analysis as a random factor

2008), but this difference vanishes once they reach 1 m in height (Beaudet et al. 1999), and all the trees we measured were larger than that critical size.

Growth measurement

All saplings were measured for annual radial growth. Stem disks were air-dried and sanded. Annual radial growth was measured to a precision of 0.001 mm under 40 \times magnification with an electronic micrometer (Velmex Inc, Bloomfield, NY, USA) coupled to a digital meter (Acurite III, Jamestown, NY, USA). Growth measurements were taken along one radius per disk, located 30 $^\circ$ from the longest radius. Visual examination of the disks was done prior to measurement along at least two additional radii where annual rings were clearly readable in order to identify partial and false rings. The growth increment of partial rings was set at 0 mm. Partial and missing rings are relatively common for maple and beech (Canham 1990; Lorimer et al. 1999). Lorimer et al. (1999) reported that the mean number of partial or missing rings of a suppressed 40-year-old maple was five. The series could not be cross-dated, however, because (1) they were too short, (2) no wood anomalies were apparent that could be used for the skeleton plot method, and (3) understory maple and beech saplings generally undergo multiple episodes of suppression and release (Canham 1990) that mask climatic signals and therefore prevent accurate cross-dating (Lorimer et al. 1999). Because the series were not cross-dated, we could not precisely date the occurrence of any particular event. However, this lack of fine precision should not impact our results because of the relatively coarse time resolution of our method for detecting release events (a four-year window for gap duration, as in Canham (1990)). Our analysis focuses on the shape of a temporal pattern, not on dating of events. The consequence of imprecise dating is to make the pattern more compact than it is in reality. Assuming that there is no reason to expect the occurrence of missing rings to differ between regions, this should not affect the

synchrony of release and suppression events. Moreover, ASA and FGR had similar suppression periods (Table 1), suggesting no bias with more missing rings for any one species. We focused on the last 41 years (1963–2003) to ensure a minimal representation of three stems per species/site (there were, on average, seven growth series per species/site with >41 years of growth). The analysis was performed on a total of 251 ASA and 230 FGR saplings.

Identification of release periods

Because of the potential for growth trends to bias the interpretation of sudden growth events that indicate “release,” we developed a novel method to identify release events. This method was based on an iterative assessment of the suppression and release history that best fitted the data when accounting for a growth trend using a maximum likelihood algorithm (see Appendix I in the “[Electronic supplementary material](#)”). To select the best method of release identification, we compared the data fit for the method we developed with four other release identification methods. We used the Akaike information criterion (AIC) to discriminate among models for a subsample of series (see details in Appendix I). According to the AIC, our iterative method performed best on the subsampled series and hence was used for the identification of release events in this study. We distinguished between minor and major release episodes, defined as increases of 100 and 200%, respectively, in radial growth sustained over a minimum of four years (Canham 1990). At each site, we calculated the fraction of stems in release during each year to get a time series for the occurrence of release events. Note that, for any method, the first and last three years of the series must be removed to avoid a biased evaluation of the release status (consequently, the series of suppression/release last 35 years).

There are two potential sources of bias in this approach. First, we followed the suppression and release histories of trees that are currently alive and part of the sapling stratum. Such a retrospective approach thus misses the trees that

were part of the sapling population 40 years ago that either died or were recruited to the canopy. One empirical study suggests this could potentially bias the evaluation of suppression and release history by over-representing release events (Landis and Peart 2005). These two selection mechanisms could result in a time series for the proportion of stems in release that is not constant over time. To ensure that the pattern we observed was not an artefact of our methodological approach (inherent to such a retrospective study), we simulated the process of mortality and recruitment from an initial population of saplings subjected to growth release. More specifically, the question we addressed was: in a constant environment, does the elimination of stems by growth and mortality processes create a suppression and release history that is not constant over time? This simulation and its results are described in the supplementary material (Appendix II in the “[Electronic supplementary material](#)”). The simple simulation we performed shows that the proportion of stems in release is constant over time despite two strong selection mechanisms (Fig. AII.1), allowing us to infer that the pattern in suppression and release history we observed is robust against these two selection processes. In a constant environment, such a retrospective study is not biased if, at any given moment, each individual has the same probability of being released by a canopy gap. In the absence of records on growth out of the sapling category and mortality, this is a reasonable assumption to make.

A second source of potential bias in retrospective dendrochronological studies stems from the fact that because measured saplings have been increasing in size over time, they may have gained better access to understory light and therefore benefited from an increased release probability over time. We tested this hypothesis by comparing the proportion of largest stems in release over time to the proportion of the smallest stems in release. The stems from the two groups had very similar trends (Fig. AII.2). If there was a strong size effect affecting the probability of release, the largest stems should show a pronounced increase in the proportion of release in the 1990–2000 period, which we did not observe. Moreover, radial growth in our time series was only weakly related to stem size, suggesting that the detection of release events is independent of size (Gravel et al., unpublished manuscript). Consequently, we are confident that the pattern we observed is not an artefact of our methodological approach.

Statistical analysis

To determine whether the overall time series of occurrence of release events was nonstationary, we fitted a second-order polynomial to the time series of the fraction of stems in release, accounting for the effects of region (random

factor) and species (including interaction terms). We tested whether there was a characteristic scale of synchrony by assessing the correlation of the time series of fraction of stems in release between all possible (561) pairs of sites. A second-order polynomial was fitted to test the relationship between the geographic distance between pairs of sites and their correlation. Finally, we tested whether temporal variation in release events affected the composition of tree species in the understory using redundancy analysis (RDA), a multivariate form of multiple regression (Legendre and Legendre 1998). RDA is a constrained ordination method that models the structure of several dependent variables while accounting for a multivariate set of explanatory variables. It allows easy representation in a two-dimensional plot of a multivariate analysis and the partitioning of the variance. It first models each dependent variable with respect to the independent variables and then performs ordination for all dependent variables with respect to the modeled relationships with the independent variables. The dependent variables were, in the first analysis, the relative density and relative BA of ASA saplings (vs. ASA + FGR) per site, and, in a second analysis, the Hellinger-transformed abundances (Legendre and Gallagher 2001) of all the species recorded among saplings. The independent variables were the proportion of stems in minor release at each site (the two species combined since there were no differences between them in the shape of the temporal pattern) at five-year intervals. The results were similar with major release (not shown). The significance of the RDA was tested against the distribution of the F statistic based on 10,000 permutations of the residuals (Legendre and Legendre 1998).

Results

We compared the principal descriptors of release history (i.e., number of releases per series, fraction of time in release, average release duration) between species with ANOVA (Table 1). There were on average 2.02 and 1.76 minor release events per series for ASA and FGR ($P < 0.001$), respectively, occurring throughout 40 and 37% of the lifespan of individuals ($P = 0.013$), for average durations of 9.08 and 9.61 years ($P = 0.593$). The comparisons of descriptors between species were similar, with generally lower values, for major releases (Table 1).

Across the 34 stands, the proportion of stems under minor and major release followed a marked nonlinear pattern over time (Fig. 1). The proportion of stems in minor release ranged between 50 and 60% for the 1960s, decreased to 20–35% in the 1980s, and then increased to 50–60% during 1998–2003. The pattern was U-shaped for both species. The polynomial model successfully described

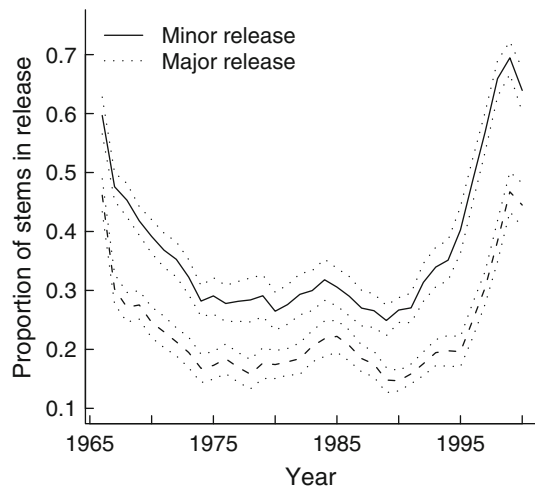


Fig. 1 Proportion of saplings under minor (>100% increase in radial growth) and major (>200% increase) release over time. *Acer. saccharum* (ASA) and *Fagus. grandifolia* (FGR) data were pooled to allow the standard error to be plotted (dotted lines)

this pattern ($P < 0.001$), with much of the variation accounted for by the first- and second-order terms (for year: F value = 41.64, $P < 0.001$; for year²: F value = 529.48, $P < 0.001$). There was a significant difference between species for the intercept (F value = 14.71, $P < 0.001$; ASA had the highest fraction of stems in release), but this effect accounted for little variance compared to that modeled by the second-order term. The shape of the pattern was the same between species (no significant interaction of species in the first- and second-order terms) and between the two regions.

Synchrony among sites occurred at all scales of our sampling design (Fig. 2; illustrated for minor release, but results were similar for major release). The maximum distance between sampled stands was >200 km. The correlation between series was not related to distance (polynomial regression, $P = 0.236$ for the first-order term and $P = 0.115$ for the second-order term). Relationships within regions were not statistically significant for both regions.

The density of understory saplings in the 34 stands varied between 1,633 and 4,767 stems/ha (all species combined). For ASA and FGR, the density ranged from 33 to 2,833 stems/ha and from 233 to 4,767 stems/ha, respectively. The relative abundance of ASA ranged from 3 to 91%. The first RDA performed on the abundance of ASA relative to FGR, calculated from both sapling density and BA, revealed that the proportion of stems in minor release at different times during the last 35 years contributed significantly to spatial variability in sapling composition at the time of sampling ($R^2 = 0.404$, $P = 0.027$ Fig. 3a). The relative abundance of ASA in 2003 was positively correlated to the proportion of stems in minor release during the 1975, 1980 and 1985 periods (i.e., when release events were

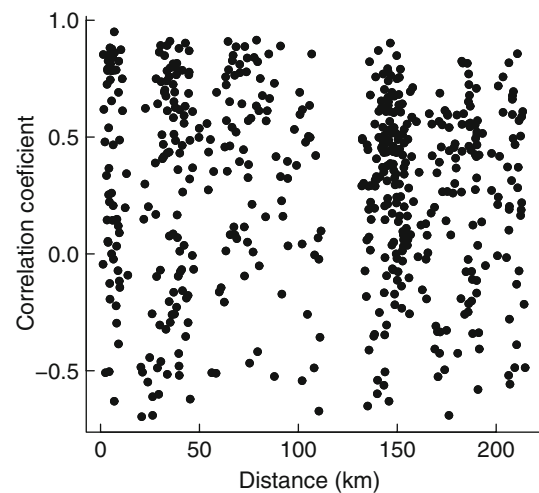


Fig. 2 Correlation between time series of the fractions of stems in minor release against the distance (km) between sites

infrequent), but was negatively correlated to the 1990, 1995 and 2000 periods (when release events were frequent Fig. 3a). The ordination of the proportion of release at five-year intervals illustrates the contrast between the 1975–1985 periods and the remaining periods. The proportion of stems during that period was not correlated to the 1970 period, was weakly correlated to the 1990–1995 periods, and was correlated to the 2000 period. The ordination also showed that the higher the proportion of stems in release during 1975–1985, the more abundant ASA was relative to FGR in 2003. In contrast, ASA was least abundant at sites with an elevated proportion of release during the 1990–2000 periods. A RDA using all-species abundance in the sapling layer, however, showed that the pattern was less clear than in the previous analysis (Fig. 3b). The overall proportion of the variance explained in the second analysis was lower ($R^2 = 0.285$, $P = 0.050$). The abundance of ASA was uncorrelated to that of *Acer pensylvanicum* L. and *Viburnum alnifolium* Michx. and weakly negatively correlated to that of FGR. *Acer spicatum* Lam. and *B. alleghaniensis* were positively correlated to the proportion of stems in release in the 2000 period and *A. pensylvanicum* and *V. alnifolium* to those in the 1990 and 1995 periods. The abundance of ASA in 2003 was positively correlated with the proportion of stems in release during the 1975–1985 periods, while the abundance of FGR was positively correlated with proportion of stems in release during the 1970 and 1990 periods.

Discussion

The temporal pattern in release events we observed was consistent among all sites, with no distinction between

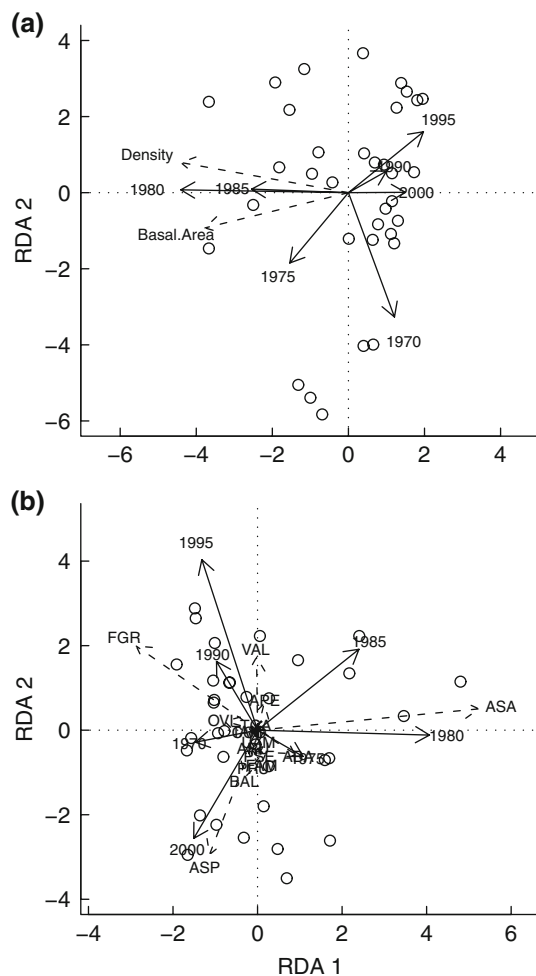


Fig. 3 Biplots from a redundancy analysis (RDA) of vegetation composition as a function of the proportion of stems in minor release (ASA and FGR combined). The angle between arrow pairs is a measure of the correlation between the variables that they represent. Arrows pointing in the same direction are strongly positively correlated, arrows pointing in opposite directions are negatively correlated, and perpendicular arrows are not correlated. The length of each arrow is proportional to the contribution of the corresponding variable to the analysis. Points represent each of the 34 sites. **a** ASA and FGR relative abundance among saplings, calculated from stem density and basal area; **b** all understory woody species (with Hellinger transformation of abundance data). ABA, *Abies balsamea*; ASA, *Acer saccharum*; ASP, *Acer spicatum*; APE, *Acer pensylvanicum*; BAL, *Betula alleghaniensis*; FGR, *Fagus grandifolia*; OSV, *Ostrya virginiana*; VAL, *Viburnum alnifolium*. Years correspond to the endpoints of five-year periods

regions or species. We know of no other study that has documented similar patterns at such a large spatial scale. The synchrony we observed did not decline with distance between sites at the 200 km spatial scale we studied. This would suggest that synchrony in sapling release events occurs at a scale even larger than the region we sampled.

Our study was not specifically designed to identify the cause(s) of this marked U-shaped pattern. Nevertheless, some possible causes can be ruled out a posteriori. First, the

stands we sampled had no recent sign of logging (neither fresh nor old decaying stumps). Given the extensive history of logging throughout the study regions, it is reasonable to assume that our sampling sites may have been partially logged in the early or mid-twentieth century (Majcen 1994; Brisson and Bouchard 2003; Boucher et al. 2006). However, we found saplings older than 100 years old at most sites, which suggests that recruitment has been continuous for a long time. Second, the catastrophic ice storm that hit southern Quebec in 1998 is too recent to explain the increase in release frequency that started in the early 1990s observed in this study. Moreover, the Portneuf region was not hit by the ice storm, but still showed the same 1990s increase in release frequency. A third potential cause of the U-shaped pattern that can be ruled out is the influence of beech bark disease (Krasny and DiGregorio 2001); the disease has not yet significantly impacted Quebec's deciduous forests (Duchesne et al. 2005). Finally, the U-shaped pattern of release frequency was not related to the decline episode that affected southern Quebec forests during the 1980s (Payette et al. 1996), since the 1980s correspond in our record to the period with the lowest frequency of release.

Nevertheless, a number of potential causes remain, and different factors may have impacted the stands at different time periods. The occurrence of extreme climatic events such as severe droughts (Payette et al. 1996; Olano and Palmer 2003) and insect outbreaks (Payette et al. 1996) are known to periodically affect canopy opening at large scales. Further research is needed to determine if and how such factors, or other ones, may have generated such a synchronous temporal U-shaped pattern of release across such a large regional scale.

Even though we could not identify the underlying cause(s) of the observed pattern, our findings have important implications for forest dynamics and ecosystem functioning at large spatial scales. In the case of ASA and FGR, short- and long-term changes in their relative abundance have been reported in both managed and old-growth forests, some in favor of ASA (e.g., Runkle 1990; Fain et al. 1994; Poulson and Platt, 1996), and others in favor of FGR (e.g., Brisson et al. 1994; Woods 2000; Duchesne et al. 2005). These changes have been attributed to site-level and exogenous temporal variations in canopy gap dynamics (Poulson and Platt 1996; Beaudet et al. 1999). Numerous reports over the last few decades have indicated an unexpected increase in the abundance of FGR saplings relative to sugar maple in various regions of the ranges of these species (Ostrowsky and McCormack 1986; Schwarcz et al. 2001; Forrester et al. 2003; Hane 2003; Duchesne et al. 2005). While changes in soil properties have been hypothesized to be responsible for changes in the recruitment dynamics of ASA and FGR at some sites (Kobe et al. 2002; Lovett and Mitchell 2004; Duchesne et al. 2005), this

hypothesis was not supported by Gravel et al. (unpublished manuscript) for these same study sites. The results presented here suggest an alternative cause of this recent widespread change in the regeneration dynamics of northern hardwoods.

The response to light availability is a major niche axis differentiating ASA and FGR (Pacala et al. 1996). Obviously, fluctuations in light availability would result in corresponding fluctuations in recruitment dynamics. The traditional model for the coexistence of ASA and FGR (Poulson and Platt 1996) predicts that ASA will have greater recruitment (in absolute number of individuals) than FGR under high light conditions because of its greater fecundity and ability to maintain an abundant seedling bank (Marks and Gardescu 1998). Under low light, mortality is expected to be higher for ASA than for FGR (Kobe 1996), but growth release should be more important for ASA than for FGR (Canham 1990). During periods of low light both species should decrease in density, but the decline should be slower for FGR than ASA due to its higher survival rate, leading to an increase in its relative abundance. In this study, we showed that the relative abundance of ASA was associated with the temporal pattern of release frequency, suggesting that the lower frequencies of release observed in the 1975–1985 period may have limited the current abundance of ASA.

Our results suggest that large-scale temporal variations in canopy gap dynamics could at least partly explain the recent increase in FGR in the understory of eastern North American temperate deciduous forests (Duchesne et al. 2005; Gravel 2007). FGR may have had a more favorable response than ASA to the rising frequency of release during 1990–2000. Increased FGR growth during this period likely allowed a rapid transition from the seedling to the sapling stage, a possible explanation for the doubling of FGR sapling density recorded in the last ten years in the Quebec forest inventory data (Gravel 2007) and reported by Duchesne et al. (2005). The decreased ASA abundance at sites which had few release events during 1975–1985 is similar to the phenomenon observed in an old-growth forest in Quebec where extended periods of low light conditions resulted in a recruitment failure of ASA in the sapling layer, despite extremely high densities of ASA seedlings (Beaudet et al. 1999). At that same site, the 1998 ice storm greatly affected the canopy, leading to a sudden but short-lived increase in understory light, but no shift in the species hierarchy was observed (Beaudet et al. 2007b). We hypothesize that the large-scale synchrony of low light conditions during the 1980s reduced the abundance of ASA saplings by a greater degree than for FGR, therefore affecting the ability of ASA to respond to the subsequent canopy opening that occurred in the 1990s. Conversely, FGR was relatively less affected by the slow-growth conditions of the 1980s and therefore

managed to capitalize on the canopy opening to increase in abundance during the 1990s.

Conclusion

Regionally synchronized large-scale temporal variations in release frequency are hypothesized to have had a major influence on the recruitment dynamics of ASA–FGR forests. That variations in release frequency (likely a function of small-scale disturbance frequency) were the main factor affecting the relative abundance of ASA and FGR among sites would probably not be particularly revealing at the local scale (Poulson and Platt 1996; Gravel et al. 2008); however, this is a surprising result when considered at the regional scale. Forest communities are never at equilibrium at the scale of a single stand (Woods 2000); this nonequilibrium could also be true at the regional scale. Conceptual models of species coexistence in forest communities generally account for variation over time in the rate of canopy gap formation at the stand scale (Poulson and Platt 1996). However, links between stand-scale rates of gap formation and larger spatial-scale variation in disturbance regimes are less well understood. Disturbance regimes are known to result from the complex interplay of allogeneic and exogenous factors, and many processes at the regional scale can potentially affect the latter. Future research should aim to better identify such processes in order to improve our understanding of how these affect disturbance regimes and forest dynamics at multiple spatial and temporal scales.

Acknowledgments We thank D. Fréchette and D. Sénécal for assistance in the field and laboratory. Access to study sites was made possible by Domtar and the Unité de Gestion de Portneuf. Thanks to C. Drever, Miguel Franco and two anonymous reviewers for helpful comments on earlier versions of the manuscript. Financial support was provided by Fonds d'Action Québécois sur le Développement Durable, Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT, Programme des Actions Concertées), and the Natural Sciences and Engineering Research Council of Canada (NSERC). This work was conducted in compliance with the laws of Canada.

References

- Battles JJ, Fahey TJ (2000) Gap dynamics following forest decline: a case study of red spruce forests. *Ecol Appl* 10:760–774
- Beaudet M, Messier C (2008) Beech regeneration of seed and root sucker origin: a comparison of morphology, growth, survival, and response to defoliation. *For Ecol Manage* 255:3659–3666
- Beaudet M, Messier C, Paré D, Brisson J, Bergeron Y (1999) Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Bois-des-Muir old-growth forest, Québec. *Écoscience* 6:264–271
- Beaudet M, Brisson J, Gravel D, Messier C (2007a) Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and

- Fagus grandifolia* in the understory of an old-growth forest. *J Ecol* 95:458–467
- Beaudet M, Brisson J, Messier C, Gravel D (2007b) Effect of a major ice storm on understory light conditions in an old-growth *Acer Fagus* forest: pattern of recovery over seven years. *For Ecol Manage* 242:553–557
- Bjornstad ON, Peltonen M, Liebhold AM, Baltensweiler W (2002) Waves of larch budmoth outbreaks in the European Alps. *Science* 298:1020–1023
- Bouchard M, Kneeshaw DD, Bergeron Y (2006) Forest landscape composition and structure after successive spruce budworm outbreaks. *Ecology* 87:2319–2329
- Boucher Y, Arseneault D, Sirois L (2006) Logging-induced change (1930–2002) of a preindustrial landscape at the northern range limit of northern hardwoods, eastern Canada. *Can J For Res* 36:505–517
- Brisson J, Bouchard A (2003) In the past two centuries, human activities have caused major changes in the tree species composition of southern Quebec, Canada. *Écoscience* 10:236–246
- Brisson J, Bergeron Y, Bouchard A, Leduc A (1994) Beech-maple dynamics in an old-growth forest in southern Québec, Canada. *Écoscience* 1:40–46
- Brokaw NVL (1982) The definition of tree-fall gap and its effect on measures of forest dynamics. *Biotropica* 14:158–160
- Canham CD (1990) Suppression and release during canopy recruitment of *Acer saccharum* and *Fagus grandifolia*. *Bull Torrey Bot Club* 117:1–7
- Canham CD, Denslow TS, Platt WJ, Runkle JR, Spies TA, White PS (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can J For Res* 20:620–631
- Clark JS, McLachlan JS (2003) Stability of forest biodiversity. *Nature* 423:635–638
- Cleavitt NL, Fairbairn M, Fahey TJ (2008) Growth and survivorship of American beech (*Fagus grandifolia* Ehrh.) seedlings in a northern hardwood forest following a mast event. *J Torrey Bot Soc* 135:328–345
- Drohan PJ, Stout SL, Petersen GW (2002) Sugar maple (*Acer saccharum* Marsh.) decline during 1979–1989 in northern Pennsylvania. *For Ecol Manage* 170:1–17
- Duchesne L, Ouimet R, Moore JD, Paquin R (2005) Changes in structure and composition of maple-beech stands following sugar maple decline in Québec, Canada. *For Ecol Manage* 208:223–236
- Fain JJ, Volk TA, Fahey TJ (1994) Fifty years of change in an upland forest in south-central New York: general patterns. *Bull Torrey Bot Club* 121:130–139
- Forrester JA, McGee GG, Mitchell MJ (2003) Effects of beech bark disease on above ground biomass and species composition in a mature hardwood forest, 1985–2000. *J Torrey Bot Soc* 130:70–78
- Glitzenstein JS, Harcombe PA, Streng DR (1986) Disturbance, succession, and maintenance of species diversity in an east Texas forest. *Ecol Monogr* 56:243–258
- Gravel D (2007) Coexistence et dynamique d'espèces forestières tolérantes à l'ombre: le cas de l'érable à sucre et du hêtre à grandes feuilles (Ph.D. dissertation). Université du Québec à Montréal, Montréal, Canada
- Gravel D, Beaudet M, Messier C (2008) Partitioning the factors of spatial variation in regeneration density of shade-tolerant tree species. *Ecology* 89:2879–2888
- Hane EN (2003) Indirect effects of beech bark disease on sugar maple seedling survival. *Can J For Res* 33:807–813
- Kneeshaw DD, Bergeron Y (1998) Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79:783–794
- Kobe RK (1996) Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecol Monogr* 66:181–201
- Kobe RK, Likens GE, Eagar C (2002) Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest. *Can J For Res* 32:954–966
- Koenig WD, Knops JMH (1998) Scale of mast-seeding and tree-ring growth. *Nature* 396:225–226
- Krasny ME, DiGregorio LM (2001) Gap dynamics in Allegheny northern hardwood forests in the presence of beech bark disease and gypsy moth disturbances. *For Ecol Manage* 144:265–274
- Lande R, Engen S, Saether BE (2003) Stochastic population dynamics in ecology and conservation (Oxford Series in Ecology and Evolution). Oxford University Press, Oxford
- Landis RM, Peart D (2005) Early performance predicts canopy attainment across life histories in subalpine forest trees. *Ecology* 86:63–72
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P, Legendre L (1998) Numerical ecology (Developments in Environmental Modelling, vol 20), 2nd English edn. Elsevier, Amsterdam
- Liebhold A, Koenig WD, Bjornstad ON (2004) Spatial synchrony in population dynamics. *Annu Rev Ecol Evol Syst* 35:467–490
- Lorimer CG (1980) Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61:1169–1184
- Lorimer CG, Dahir SE, Singer MT (1999) Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. *Plant Ecol* 143:189–202
- Lovett GM, Mitchell MJ (2004) Sugar maple and nitrogen cycling in the forests of eastern North America. *Frontiers Ecol Environ* 2:81–88
- Majcen Z (1994) Historique des coupes de jardinage dans les forêts inéquiennes au Québec. *Revue Forestière Française* 46:375–384
- Marks PL, Gardescu SA (1998) A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. *J Torrey Bot Club* 125:287–296
- Olano JM, Palmer MW (2003) Stand dynamics of an Appalachian old-growth forest during a severe drought episode. *For Ecol Manage* 174:139–148
- Ostrofsky WD, McCormack ML (1986) Silvicultural management of beech and the beech bark disease. *North J Appl For* 3:89–91
- Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol Monogr* 66:1–43
- Payette S, Fortin M-J, Morneau C (1996) The recent sugar maple decline in southern Quebec: probable causes deduced from tree rings. *Can J For Res* 26:1069–1078
- Poulson TL, Platt WJ (1996) Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology* 77:1234–1253
- Robitaille A, Saucier J-P (1998) Paysages régionaux du Québec méridional. Les Publications du Québec, Ste-Foy
- Rubino DL, McCarthy BC (2004) Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21:97–115
- Runkle JR (1981) Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041–1051
- Runkle JR (1990) Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. *Can J For Res* 20:632–641
- Schwarz PA, Fahey TJ, Martin CW, Siccama TG, Bailey A (2001) Structure and composition of three northern hardwood-conifer forests with differing disturbance histories. *For Ecol Manage* 144:202–212
- Woods KD (1979) Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *Oikos* 33:31–39

Woods KD (2000) Long-term change and spatial pattern in a late-successional hemlock–northern hardwood forest. *J Ecol* 88:267–282

Woods KD (2004) Intermediate disturbance in a late-successional northern hardwood forest. *J Ecol* 92:464–476

Woods KD (2007) Predictability, contingency and convergence in late succession: slow systems and complex datasets. *J Veg Sci* 18:543–554