

The influence of overstory trees and abiotic factors on the sapling community in an old-growth *Fagus-Acer* forest¹

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Abstract: We examine the influence of overstory trees and abiotic environmental factors on the patterns of spatial variation and species composition in the sapling community of an old-growth *Fagus-Acer* forest in southwestern Québec, Canada. Our main focus was to identify differences in the sapling distribution patterns of *Fagus grandifolia* and *Acer saccharum*, the two codominant species in the overstory, as well as the factors that determine the differences. Using canonical correspondence analysis (CCA), we show that soil moisture has the strongest influence on the spatial variation and species composition of the sapling community. *Acer saccharum* occurred on a wide range of soil moisture conditions, while *Fagus grandifolia* saplings were absent in dry habitats. Another factor that differentiates the distribution patterns of *Fagus grandifolia* and *Acer saccharum* saplings is the relative dominance of *Fagus grandifolia* trees in the overstory, which correlates negatively with pH and Ca availability in the forest floor. *Acer saccharum* saplings were not found on sites where *Fagus grandifolia* trees dominate the overstory, while *Fagus grandifolia* saplings are mostly limited to sites where *Fagus grandifolia* trees have high representation in the overstory. These findings are discussed in light of previous hypotheses on canopy tree replacement patterns in *Fagus-Acer* forests.

Keywords: *Fagus grandifolia*, *Acer saccharum*, forest dynamics, old-growth forest, canonical correspondence analysis.

Résumé : Dans cet article, nous examinons l'influence des arbres formant la strate supérieure d'une forêt et celle des facteurs physiques sur les patrons de variation spatiale et la composition en espèces d'une communauté de gaules. L'étude s'est déroulée dans une forêt ancienne de hêtres et d'érables du sud-ouest du Québec, au Canada. Nous avons surtout cherché à identifier les différences dans les patrons de répartition des gaules de *Fagus grandifolia* et *Acer saccharum*, les deux espèces dominantes de la strate supérieure, de même que les facteurs qui en sont responsables. Selon une analyse des correspondances canoniques, l'humidité du sol est la caractéristique du milieu qui influence le plus la répartition spatiale et la composition en espèces de la communauté de gaules. Les jeunes Érables à sucre s'accroissent d'un large spectre de conditions d'humidité du sol. Par contre, aucun gaule d'Hêtre à grandes feuilles n'a été trouvé dans les habitats secs. Un autre facteur qui différencie les patrons de répartition des gaules des deux espèces est la dominance du hêtre dans la strate supérieure. Cette dominance est corrélée de façon négative avec le pH et la disponibilité du calcium dans le sol. En effet, les jeunes érables ne poussent pas là où les hêtres dominent la strate supérieure, alors que les jeunes hêtres ne croissent qu'aux endroits où les hêtres adultes composent l'essentiel de la voûte forestière. Ces résultats sont analysés en tenant compte des hypothèses en vigueur sur les patrons de remplacement des arbres composant la voûte forestière dans les forêts d'érables et de hêtres.

Mots-clés : *Fagus grandifolia*, *Acer saccharum*, dynamique des forêts, forêt ancienne, analyse des correspondances canoniques.

Introduction

Fagus-Acer forest is one of the major forest types found in eastern North America (Braun, 1950; Runkle, 1996). The dynamics within this forest type have been frequently investigated, a particular interest being the replacement patterns and coexistence of the overstory trees (Forcier, 1975; Fox, 1977; Woods, 1979; 1984; Runkle, 1981; 1984; Cypher & Boucher, 1982; Brisson *et al.*, 1994; Kupfer & Runkle, 1996; Poulson & Platt, 1996; Foré, Vankat & Schaefer, 1997; Beaudet *et al.*, 1999; Forrester & Runkle, 2000). Since suppressed shade-tolerant saplings in the understory usually replace the overstory trees in *Fagus-Acer* forests (Woods, 1984), one of the key factors that determines the overstory replacement patterns and future overstory composition is the sapling community in the understory. Investigating the patterns of spatial distribution

and species composition of saplings in the understory, and also identifying the factors that give rise to these patterns, can help understand the dynamics of *Fagus-Acer* forests.

Studies have shown that environmental factors such as soil moisture, light, and nutrients affect the growth and mortality of species that are typically found in *Fagus-Acer* forests (Canham *et al.*, 1996; Walters & Reich, 1996; 2000; Casperson & Kobe, 2001). These differences in species' response to abiotic factors, coupled with the heterogeneous understory environment, are considered to play a significant role in determining the spatial variation and the composition of the sapling community in the forest understory (Brisson *et al.*, 1994; Poulson & Platt, 1996). Biotic factors have also been implicated as determinants of the sapling community in *Fagus-Acer* forests. Canopy trees may affect the sapling community directly by seed dispersal or indirectly by modifying the abiotic environment in the understory (Abrell & Jackson, 1977; Fox, 1977; Woods, 1979; 1984).

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While both abiotic and overstory tree effects may potentially play a significant role in determining the sapling community in *Fagus-Acer* forests, these factors have usually been investigated in isolation from one another. Because the overstory trees influence sapling composition partly through modifications of abiotic environment in the understory (Forcier, 1975; Woods, 1979), it is possible to over-emphasize or misinterpret the effects of these factors if they are investigated separately (Magnan *et al.*, 1994). Additionally, such partial studies provide no information on the relative importance of abiotic and canopy tree effects and their interactions. Identifying the relative importance of different effects and their interactions will help us better understand the mechanisms underlying the organization of the sapling community and its potential influence on overstory dynamics.

The objective of this study therefore is to identify the factors that determine the patterns of spatial variation and species composition of the sapling community within an old-growth *Fagus-Acer* forest by considering both abiotic and canopy tree effects. For the abiotic effects, we pay special attention to edaphic factors; previous studies have mostly focused on only light regime (*i.e.*, gaps) as the abiotic factor determining the organization of the sapling community in *Fagus-Acer* forests (Runkle, 1981; 1984; 1990; Forrester & Runkle, 2000). Little information is available on the effects of edaphic factors, such as soil moisture and nutrient availability, on the dynamics within *Fagus-Acer* forests. We will mainly focus on the saplings of the two canopy codominants, *Fagus grandifolia* (Ehrh.) and *Acer saccharum* (Marsh.).

Methods

STUDY SITE

We assessed the effect of abiotic factors and canopy trees on understory sapling composition in a 10-km² tract of old-growth forest at Mont St. Hilaire in southwestern Québec, Canada (45° 31' N, 73° 08' W). Mont St. Hilaire is a hill complex of plutonic origin (Feininger & Goodacre, 1995), with peaks that rise between 200–300 m above the level floor of the surrounding St. Lawrence River Valley. The forest at Mont St. Hilaire is the largest remaining remnant of the primeval forests in this region; many of the trees

exceed 150 years in age, and a few are over 400 years old (Cook, 1971). Various tree communities occur on the mountain (Maycock, 1961; Enright & Lewis, 1985), but *Acer saccharum* and *Fagus grandifolia* are the common canopy dominants over most of the area. The site is essentially undisturbed by human activities and is protected as an International Biosphere Reserve under the Man and Biosphere program (MAB) of the United Nations.

SAMPLING PROCEDURES

COLLECTING TREE DATA

In the summer of 1997, 92 permanent plots located randomly along seven line transects were sampled; plot elevations range between 145 m and 400 m). Each plot is 113 m² (6-m radius). At each plot, all woody individuals with DBH greater than 2.5 cm were recorded (species, DBH). These data were split into overstory trees data and sapling data based on the size categories used by Cain (1935) and Poulson and Platt (1996). Saplings are defined as individuals with DBH between 2.5 cm and 15 cm, and overstory trees are defined as individuals with DBH greater than 15 cm, which includes both the canopy tree and pole categories in Cain (1935) and Poulson and Platt (1996). For the species included in the analysis, the height of trees with DBH between 2.5 cm and 15 cm (*i.e.*, saplings) is typically 2–10 m (unpubl. data).

The data set that consists of sapling density for each species in each plot is referred to as the sapling matrix (SM; 92 plots × 10 species). The variation in this SM is what we hope to explain in this study. The list of species included in SM and their basic statistics are given in table I. Species that occurred in fewer than 5 plots were not included in the analyses. We focus on the density of the saplings because, for a given species, the likelihood of becoming a canopy component is likely to be higher if the sapling density is higher in the understory.

The data set that consists of overstory tree basal area (cm²) for each species in each plot is referred to as the tree matrix (TM; 92 plots × 4 species). This matrix is used as an explanatory or a covariable matrix in the multivariate analyses. Species that are included in the TM and their basic statistics are listed in table II. While more overstory tree species were recorded in the sampling plots (total of 12 species), only four species were included in the TM. This

TABLE I. List of species included in the sapling data matrix (SM). Their acronyms and basic statistics are shown. Note that stem density of each species in each plot is used in the SM. See text for details.

Species	Acronym	Occurrence (out of 92)	Stem density per plot				Total basal area per plot (m ² ha ⁻¹)	
			Max	Means*	SD*	Median*	Max	Mean*
<i>Acer pensylvanicum</i> L.	Apn	49	29	6.4	6.4	3	7.1	1.0
<i>Acer saccharum</i> Marsh.	Asa	82	65	16.8	14.9	12	9.8	3.1
<i>Acer spicatum</i> Lam.	Asp	12	29	9.2	9.8	5	6.8	1.4
<i>Betula alleghaniensis</i> Britton	Bal	11	6	2.2	1.8	1	1.4	0.4
<i>Betula papyrifera</i> Marsh.	Bpa	8	29	7.4	9.2	5	8.0	2.8
<i>Fraxinus americana</i> L.	Fam	20	9	2.6	2.5	1	5.0	1.2
<i>Fagus grandifolia</i> Ehrh.	Fgr	58	26	7.7	6.9	5	8.4	1.8
<i>Ostrya virginiana</i> (Mill.) K. Koch	Ovg	45	37	6.3	7.6	3	6.4	2.1
<i>Quercus rubra</i> L.	Qrb	10	7	3.3	2.3	3	7.1	2.6
<i>Tilia americana</i> L.	Tam	16	4	1.5	1	1	1.0	0.2

* Calculation based only on the non-zero values.

was done because the rare occurrences of the remaining 8 species, which result in many zeros in the matrix, make them unsuitable to be used as variables in the explanatory or covariable matrix. Of the species included in TM, *Fraxinus americana* L. is the species that occurred least frequently (Table II; 17 plots); any species not included in TM occurred in fewer than 9 plots.

COLLECTING ABIOTIC ENVIRONMENT DATA

A list of abiotic environmental variables included in the analyses is given in table III. The matrix containing these environmental variables is referred to as the abiotic matrix (AM).

SOIL NUTRIENTS

In August 1997, soil samples were gathered at 8 different locations near the center of each plot. After the L-F-H layers were removed from the soil surface, the samples were taken down to 10 cm in depth. Samples taken at each plot were pooled and frozen within hours of collection. They were kept frozen for approximately 3 months before being air-dried and sieved (2 mm) in preparation for soil chemical analysis. Nutrient extractions and analyses of these extracts were carried out by the University of Alberta Soil Chemistry Laboratory. Exchangeable NO₃ and NH₄ were assayed in a KCl extract (Kalra & Maynard, 1991); available P (PO₄) was assayed using an NH₄F-H₂SO₄ extract (method 2 of Bray & Kurtz, 1945); exchangeable potassium, calcium, and magnesium were determined on an NH₄OAc extract at pH 7 (Chapman, 1965); pH was measured on an H₂O extract. For nitrogen, total N (sum of NO₃-N and NH₄-N) was used in the statistical analysis (Table III).

SOIL MOISTURE

Volumetric moisture contents were measured five times during the summer of 1999 (June 14, June 29, July 15,

August 12, August 25) and twice during the summer of 2000 (July 13, August 20). Soil moisture sensors were used to make the measurements (Theta Probe, Type ML2x, Delta-T Devices, Ltd., Cambridge, U.K.). It took two days to make measurements at all plots during each sampling period, and the sampling was done in the same order on all sampling dates to minimize the time required to visit all plots. No rainfall was recorded during the sampling periods. At each plot, moisture content was measured at 5 different locations near the center of the plot. From the five measurements, an average was calculated for each plot.

Although absolute moisture content may vary by year and season, we were interested in the relative moisture content of the plots. At our study site, Rouse and Wilson (1969) have shown that differing rates of snowmelt based on exposure exert an influence on the surface soil moisture regime that is maintained through much of the growing season. Our data are consistent with this expectation. Pairwise Spearman rank correlation coefficients between the moisture content on different sampling dates ranged between 0.68 and 0.93 and were all found to be highly significant (*p* < 0.001). This indicates that the relative moisture contents among the plots are conserved across year and season.

PHYSICAL FACTORS

The slope at each sampling plot was determined using a clinometer (slope was measured for the width of the plot).

STATISTICAL ANALYSIS

Canonical correspondence analysis (CCA) and partial canonical correspondence analysis (pCCA) were used to investigate the effect of overstory trees (TM) and abiotic environmental factors (AM) on the sapling composition (SM) in the understory (ter Braak, 1986; 1988). CANOCO (ver. 4.0, ter Braak & Šmilauer, 1998) was used to perform the analyses. Density values in the SM were square-root

TABLE II. List of species included in the overstory tree data matrix (TM). Their acronyms, basic statistics and transformations used are shown. Note that basal area of each species in each plot is used in the TM, but stem density is also reported. See text for details.

Species	Acronym	Occurrence (out of 92)	Total basal area per plot (m ² ha ⁻¹)				Density per plot		Transformation
			Max	Means*	SD*	Median*	Max	Mean*	
<i>Acer saccharum</i> Marsh.	Asa ₁₅	70	83.9	24.5	19.2	20.6	7	2.7	log ₁₀ (x+1)
<i>Fraxinus americana</i> L.	Fam ₁₅	17	15.1	6.6	4.1	5.8	4	1.5	log ₁₀ (x+1)
<i>Fagus grandifolia</i> Ehrh.	Fgr ₁₅	48	66.3	16.3	15.3	12.8	7	2.5	log ₁₀ (x+1)
<i>Quercus rubra</i> L.	Qrb ₁₅	40	48.8	21.3	13.0	18.9	11	3.1	log ₁₀ (x+1)

* Calculation based only on the non-zero values.

TABLE III. List of abiotic environmental variables included in the abiotic variables matrix (AM). Their acronyms, basic statistics, and transformations used are shown.

Variable	Acronym	Units	Means	SD	Max	Min	Median	Transformation
N (NO ₃ -N+NH ₄ -N)	N	ppm	45.3	29.0	162	9	36	log ₁₀ (x+1)
P (PO ₄ -P)	P	ppm	12.1	17.1	105.0	0.1	5.3	log ₁₀ (x+1)
K	K	ppm	167.0	80.4	438	31	158	log ₁₀ (x+1)
Mg	MG	ppm	318.0	155.7	924	159	231	log ₁₀ (x+1)
Ca	CA	ppm	2476	1917	9942	190	1780	log ₁₀ (x+1)
pH	PH	-	4.98	0.55	6.6	3.6	4.9	log ₁₀ (x)
Moisture	MST	m ³ m ⁻³	0.07	0.06	0.31	0.01	0.05	arcsin (x ^{1/2})
Slope	SLP	%	14.3	9.43	36	0	13	none

transformed prior to analysis, and the downweight function in CANOCO was used to reduce the effects of rare species (weighted total density is used as weights instead of total density; see ter Braak & Šmilauer, 1998 for details). Transformations used for the variables included in TM and AM are given in Tables II and III. We used unimodal models over linear models (*i.e.*, redundancy analysis [RDA]) since the standard deviation in unimodal models exceeded 2 SD (ter Braak, 1995). For each CCA/pCCA run, significance of the sum of all canonical eigenvalues and the significance of the first two ordination axes were tested using Monte Carlo permutation tests (1,000 permutations) (ter Braak & Šmilauer, 1998; Legendre & Legendre, 1999).

Because a high correlation was found among the moisture content measurements taken on different dates, preliminary analysis was done to avoid the redundancy among these measurements. Preliminary CCA was conducted using SM as the main matrix and moisture measurements as the explanatory matrix. Note that moisture measurements taken on different dates are considered as separate environmental variables in the explanatory matrix. The results showed that all the environmental variables (moisture measurements taken on different dates) correlate positively with the first CCA axis, which indicates that inclusion of all moisture variables may be superfluous. Thus, we used the following two steps to choose only one soil moisture variable (*i.e.*, measurement taken on a single day) for the analysis. First, moisture content variables with missing values were dropped. Second, CCA with forward selection was done to choose the best moisture content variable to be used in AM. This procedure resulted in choosing the measurements taken on August 25, 1999 (Table III; MST). Note that when all the moisture measurements were used in CCA, the eigenvalue of the first canonical axis was 0.253; when measurements taken on August 25, 1999 were the only moisture variable, the eigenvalue was 0.213. This indicates that addition of moisture measurements taken on different dates in the analysis does not significantly increase the amount of variation explained. While the use of an August moisture measurement was chosen statistically, August measurement may be the best measurement to use as an environmental variable from a biological perspective as well: soil moisture is most limiting at Mont St. Hilaire in the late summer months (Rouse & Wilson, 1969).

VARIATION EXPLAINED BY ALL EXPLANATORY VARIABLES

CCA was performed on sapling data (SM) using all variables in TM and AM as explanatory variables. This was done to determine how much of the total variation is explained by all environmental variables combined and to examine which variables best explain the sapling variation. We will refer to the variation explained by both TM and AM simultaneously as total explained variation. Note the difference between total variation and total explained variation: total variation is the sum of total explained variation and unexplained variation.

VARIATION PARTITIONING

Total sapling composition variation (total variation) was partitioned into four components using a series of CCA and partial CCA (pCCA) (ter Braak, 1986; 1988; Borcard,

Legendre & Drapeau, 1992; Legendre & Legendre, 1999): a) pure overstory tree (TM) variation, the fraction of the total variation that can be explained by TM variables independently of variables in AM; b) pure abiotic (AM) variation, the fraction of the total variation that can be explained by AM variables independently of variables in TM; c) shared variation, the fraction of the total variation explained by the interaction of the two factors; and d) unexplained variation, the fraction of the total variation explained neither by TM nor by AM. The use of the terms pure and shared follows Magnan *et al.* (1994).

The procedure of partitioning the total variation into four components involves the following steps: (1) compute the variation accounted for by TM and AM together (total explained variation); (2) compute the variation accounted for by TM after removing the effects of AM (pure TM variation); (3) compute the variation accounted for by AM after removing the effects of TM (pure AM variation); (4) subtract (2) and (3) from (1) to obtain the shared variation; and (5) subtract the total explained variation in step (1) from the total variation to obtain the unexplained portion of the variation. (For more details on the partitioning procedure, see Borcard, Legendre & Drapeau, 1992.)

IDENTIFYING THE VARIABLES THAT BEST REPRESENT EACH VARIATION COMPONENT

By examining the ordination diagrams resulting from analyses (2) and (3) above, we identified variables that may best account for pure TM variation and pure AM variation. We also attempted to identify variables that best represent the shared variation component; however, this is not easily done because this variation is not derived directly from CCA or pCCA. To estimate the variables that may best account for the shared variation, we examined ordination results from analysis (1) and attempted to identify any relationship between abiotic and overstory tree variables. Abiotic variables that account for the shared variation component should correlate with one or more overstory tree variables, and vice versa.

NOTE ON THE PERCENTAGE OF VARIATION EXPLAINED

Økland (1999) has suggested that percentage of variation explained, which is a ratio of variation explained to total inertia (or total explained variation divided by the total variation), may underestimate how much the variation components truly contribute to the total variation and has proposed a shift in focus from the variation explained to total inertia ratio to the relative amounts of variation explained. In this study, we mainly focused on the relative importance of different ordination axes and variation components on the total explained variation, rather than on the total variation.

Results

The total variation of the sapling composition data was 1.591, and the sum of all canonical eigenvalues (total explained variation) was 0.725. A Monte Carlo permutation test for the sum of all canonical eigenvalues showed that there is a significant relationship between plot-to-plot variation in the sapling composition data and the explanatory variables ($p = 0.001$). The first two CCA axes explain 78%

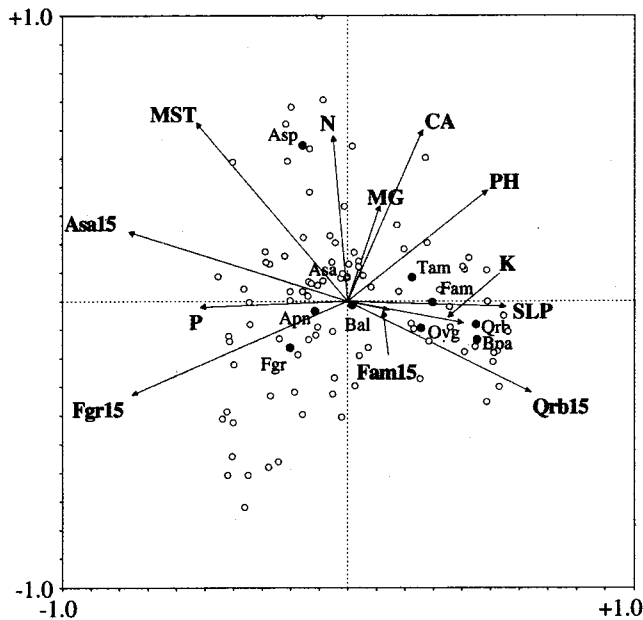


FIGURE 1. Ordination diagram (biplot scaling) based on CCA using all variables in overstory tree matrix (TM) and abiotic variable matrix (AM) as explanatory variables. Refer to tables I-III for explanation of acronyms.

of the total explained variation, and both axes are significant based on the Monte Carlo permutation test ($p = 0.001$). Figure 1 shows the ordination diagram resulting from this CCA; figures 2 and 3 show the density of saplings and basal area of canopy trees in ordination space, respectively.

The first CCA axis accounts for 48% of the total explained variation (eigenvalue = 0.345) and correlates positively with Qrb₁₅ and negatively with Asa₁₅ and Fgr₁₅ (Table IV, Figure 1). The effects of these overstory tree variables on the first axis can be considered as combined effects of two gradients represented by one or two of the overstory tree variables that are also correlated with some abiotic environmental variables. The first gradient correlates positively with Qrb₁₅ and negatively with Asa₁₅; this gradient is likely to reflect a soil moisture gradient, as it is correlated negatively with MST (figure 1; this gradient will be referred to as the MST gradient). The second gradient is represented by Fgr₁₅, which correlates negatively with pH and Ca (Figure 1; this gradient will be referred to as the Fgr₁₅ gradient). Given the spread of the species scores along the two gradients, MST gradient appears to explain more sapling variation than the Fgr₁₅ gradient.

Along the MST gradient, *Quercus rubra* (Qrb) and *Betula papyrifera* (Bpa) occur only on the drier plots, while *Acer spicatum* (Asp) occurs on the wettest (Figures 1 and 2). The species scores of the two focal species, *Fagus grandifolia* (Fgr) and *Acer saccharum* (Asa), are both found near the origin of the diagram along the MST gradient (Figure 1). However, *A. saccharum* saplings are found on a wider range of moisture conditions than *F. grandifolia* saplings (Figure 2). Species scores for *F. grandifolia* and *Acer pensylvanicum* (Apn) are positioned at the higher extreme along the Fgr₁₅ gradient (Figure 2); thus, they are the two species that are found abundant at plots where *F. grandifolia* trees have higher representation in the canopy (Figures 2 and 3). Saplings of other species rarely occur on sites domi-

nated by *F. grandifolia*. Note that *A. saccharum* saplings, although they are abundant on most plot locations, are not found on sites where *F. grandifolia* trees are found in the overstory (Figures 2 and 3).

The second CCA axis in figure 1 accounts for an additional 31% of the total explained variation (eigenvalue = 0.224) and is represented by soil moisture (MST), Ca, and N (Table IV). Upon inspection of the species scores along the second axis, it is clear that *A. spicatum* has a significant influence on this axis (Figure 1). To evaluate the influence of *A. spicatum*, we ran a CCA without *A. spicatum* in the data set. The results show that the second axis decreases its importance after *A. spicatum* is removed (eigenvalues of the second axis with and without *A. spicatum* are 0.224 and 0.153, respectively) and soil moisture (MST) is represented more weakly along the second axis (Figure 4a). Despite the removal of *A. spicatum*, the general interpretation of other species along environmental gradients does not change (compare the relationship between the species scores and environmental gradients in Figures 1 and 4a). Our two focal species have opposed species scores along the second axis (Figure 1). *Acer saccharum* saplings are found on sites with higher N and Ca availabilities than *F. grandifolia* saplings; however, Ca availability better separates the two species (Figure 1).

VARIATION PARTITIONING

The result of the variation partitioning procedure is given in table V. It shows that pure TM variation accounts for 20% of the total explained variation ($p = 0.001$), while pure AM variation ($p = 0.001$) and shared variation each account for 40% of the total explained variation.

VARIABLES THAT REPRESENT THE PURE AM VARIATION

Figure 4b shows the species-environment pCCA ordination diagram using AM as the explanatory matrix and TM as the covariable matrix (*i.e.*, pure AM variation). The first axis accounts for 53% of pure AM variation. The diagram shows that *A. spicatum* has an extremely high first axis score, which is represented well by soil moisture. However, if *A. spicatum* is removed from the analysis, much of the remaining species variation can be explained by a N-Ca gradient. This finding is similar to the results found for the second axis in figure 1, and the species occurrence along the first axis in figure 4b is similar to the second axis in figure 1. Because the effects of overstory trees were mainly reflected on the first axis in figure 1, the second axis, which is orthogonal to the first axis, may indeed be represented mostly by the variables that explain the pure AM variation. Note that the best separation of species scores of our two focal species occurs on a Ca gradient.

VARIABLES THAT REPRESENT THE PURE TM VARIATION

Figure 4c shows the species-environment pCCA ordination diagram using TM as the explanatory matrix and AM as the covariable matrix (*i.e.*, pure TM variation). The first axis represents approximately 69% of pure TM variation and is negatively correlated with Fgr₁₅; the second axis was found to be non-significant. Although Fgr₁₅ was also highly correlated with the first axis in figure 1, this effect of Fgr₁₅ is correlated with abiotic variables. Therefore, the effect of

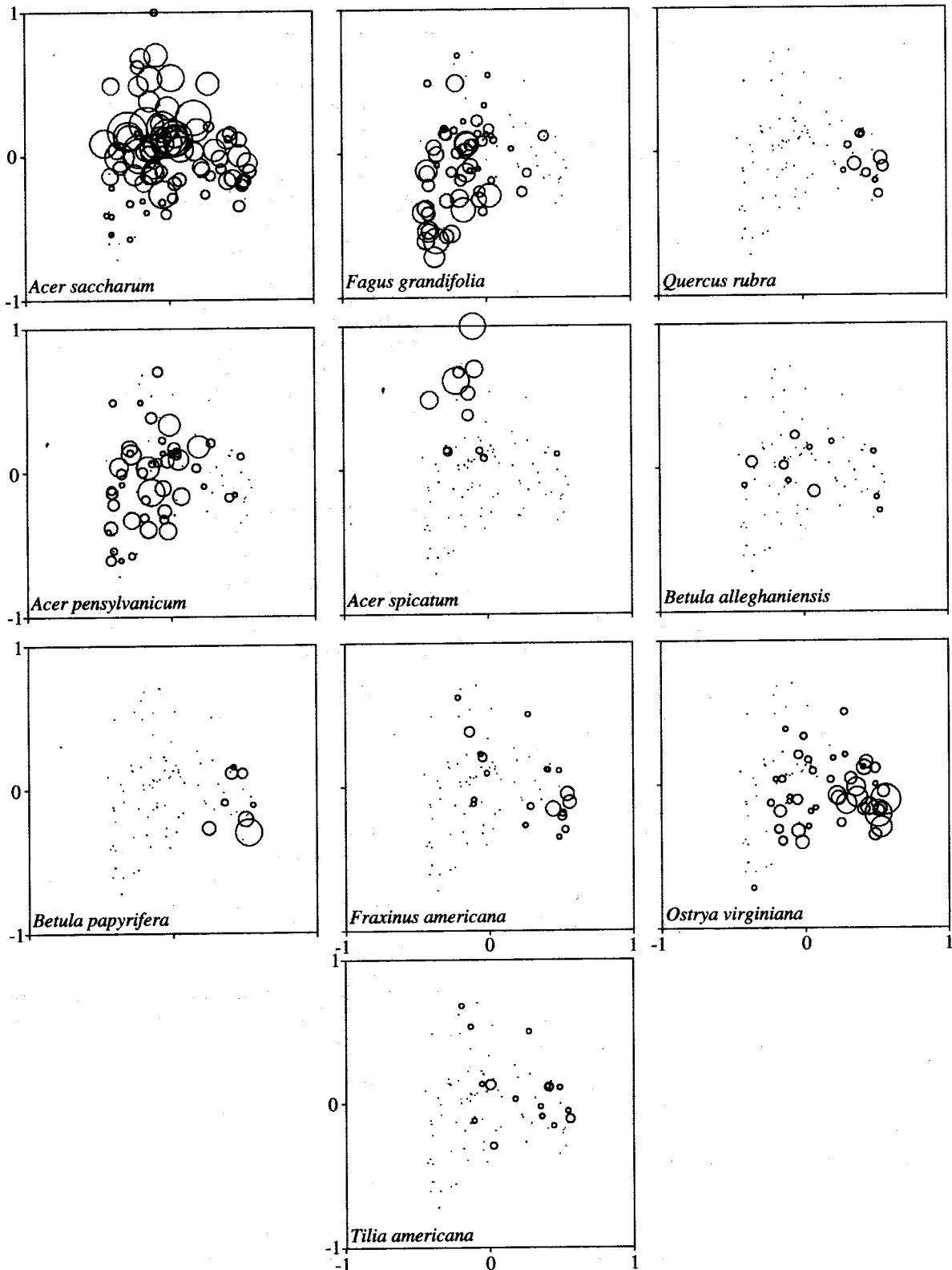


FIGURE 2. Density of saplings in ordination space for each species. Density (square-root transformed) of saplings at each site is superimposed on the site scores given in figure 1. Bigger symbols indicate greater stem density.

Fgr_{15} in figure 4c, which is the effect of Fgr_{15} not correlated with abiotic variables, may account for a considerable portion of the remaining variation that was not explained by the first two axes in figure 1.

Based on the ordination diagram in figure 4c, *F. grandifolia* saplings occur on sites where *F. grandifolia* trees are more present in the overstory, while *A. pensylvanicum*, *A. saccharum*, *A. spicatum*, and *Betula alleghaniensis* (Bal)

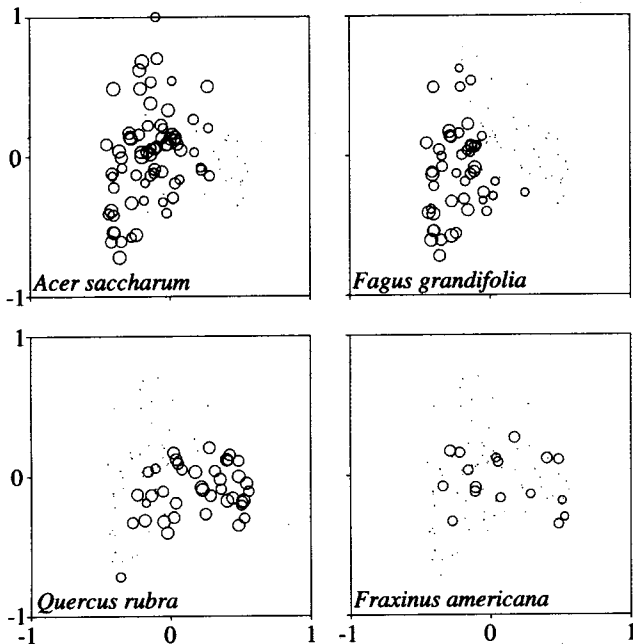


FIGURE 3. Basal area of canopy trees in ordination space for each species. Basal area (log-transformed) of trees at each site is superimposed on the site scores given in figure 1. Bigger symbols indicate greater basal area.

TABLE IV. Canonical coefficients and intra-set correlation coefficients of explanatory variables for the first two CCA-axes (all variables in TM and AM are used simultaneously as explanatory variables).

Variable	Canonical coefficients		Correlation coefficients	
	Axis 1	Axis 2	Axis 1	Axis 2
Asa ₁₅	-0.38	0.08	-0.77	0.24
Fam ₁₅	0.07	-0.03	0.14	-0.03
Fgr ₁₅	-0.39	-0.24	-0.75	-0.33
Qrb ₁₅	0.19	0.07	0.64	-0.32
N	-0.12	0.39	-0.05	0.58
P	-0.13	-0.08	-0.51	-0.02
MG	-0.47	-0.45	0.11	0.33
CA	0.39	0.88	0.26	0.60
K	0.23	-0.48	0.40	-0.08
PH	0.14	-0.05	0.49	0.39
SLP	-0.04	0.20	0.55	-0.02
MST	-0.03	0.48	-0.53	0.62

occur on sites with intermediate occurrence of *F. grandifolia* trees. Based on the occurrence of species along this gradient, we believe this may represent a light-availability gradient, a variable not included in our analysis. However, the variation explained by pure TM variation is small relative to the other variation components.

VARIABLES THAT REPRESENT THE SHARED VARIATION COMPONENT

In figure 1, the overstory tree variables, which were highly correlated with the first ordination axis, are also correlated with some abiotic environmental variables. This implies that the abiotic and overstory tree variables that are correlated may explain a significant portion of the shared variation component. Additionally, the fact that these variables were reflected on the first ordination axis may explain why the shared variation explained a high proportion of the

total explained variation (40%). The correlation between the overstory tree variables and abiotic variables can also be examined by comparing the ordination diagram in figure 1 with an ordination diagram based on a CCA that uses abiotic factors as the only explanatory variables (Figure 4d). When the two ordination diagrams are compared, the relationships among the abiotic variables (relative directions of the arrows) and the occurrence of species (saplings) scores along the abiotic variables are almost identical (note that the two diagrams are rotated 180°). Additionally, the sum of canonical eigenvalues of the first two axes in figure 4d is 0.476, which is 85% of the sum of canonical eigenvalues of the first two axes in figure 1. This suggests that much of the information in figure 1 is being preserved in figure 4d even though the overstory tree effects have been removed and that overstory tree effects are indeed correlated with some or a set of abiotic environmental variables.

Many of the previous studies attempting to identify the factors that give rise to the patterns of spatial distribution and species composition of saplings have been done 1) by examining the overstory-understory relationships or 2) by investigating the occurrence of saplings along one or a few environmental gradients. It is clear in the preceding results that some variables in the TM (overstory effects) and AM (abiotic environmental effects) are collinear and that these collinear variables account for a considerable fraction of the total explained variation. We therefore emphasize the nature and the implications of this collinearity in the following discussion.

Discussion

While various factors may contribute to the patterns of spatial variation and species composition of the sapling community, our results show that soil moisture has the strongest influence on the overall pattern. Soil moisture is negatively correlated with *Q. rubra* in the overstory (Qrb₁₅) and positively with *A. saccharum* in the overstory (Asa₁₅). This relationship is in agreement with previous studies on the distribution patterns of adult trees along moisture gradients. *Quercus rubra* trees are often found on dry sites at the northern edge of its distribution, while *A. saccharum* trees are typically found on more mesic sites (Walther, 1963; Op de Beek, 1972; Anderson *et al.*, 1990). The occurrence of saplings (*i.e.*, species scores) along the soil moisture gradient agrees with a study that investigated the distribution patterns of saplings along moisture gradients in the forests of the St. Lawrence Lowlands in Québec and Ontario (Op de Beek, 1972); this study included stands on Mont St. Hilaire.

Soil moisture also partially explains the differences in spatial patterns of our two focal sapling species, *F. grandifolia* and *A. saccharum*. While *A. saccharum* tends to occur across the full range of soil moisture conditions we have sampled, *F. grandifolia* saplings are completely absent on the drier sites. Both species are generally known to be drought intolerant, but *F. grandifolia* is known to be more sensitive than *A. saccharum* to reduced moisture (Tubbs & Houston, 1990), which may explain their absence at the drier sites.

However, on mesic sites, moisture does not distinguish the distribution patterns of *F. grandifolia* and *A. saccharum*

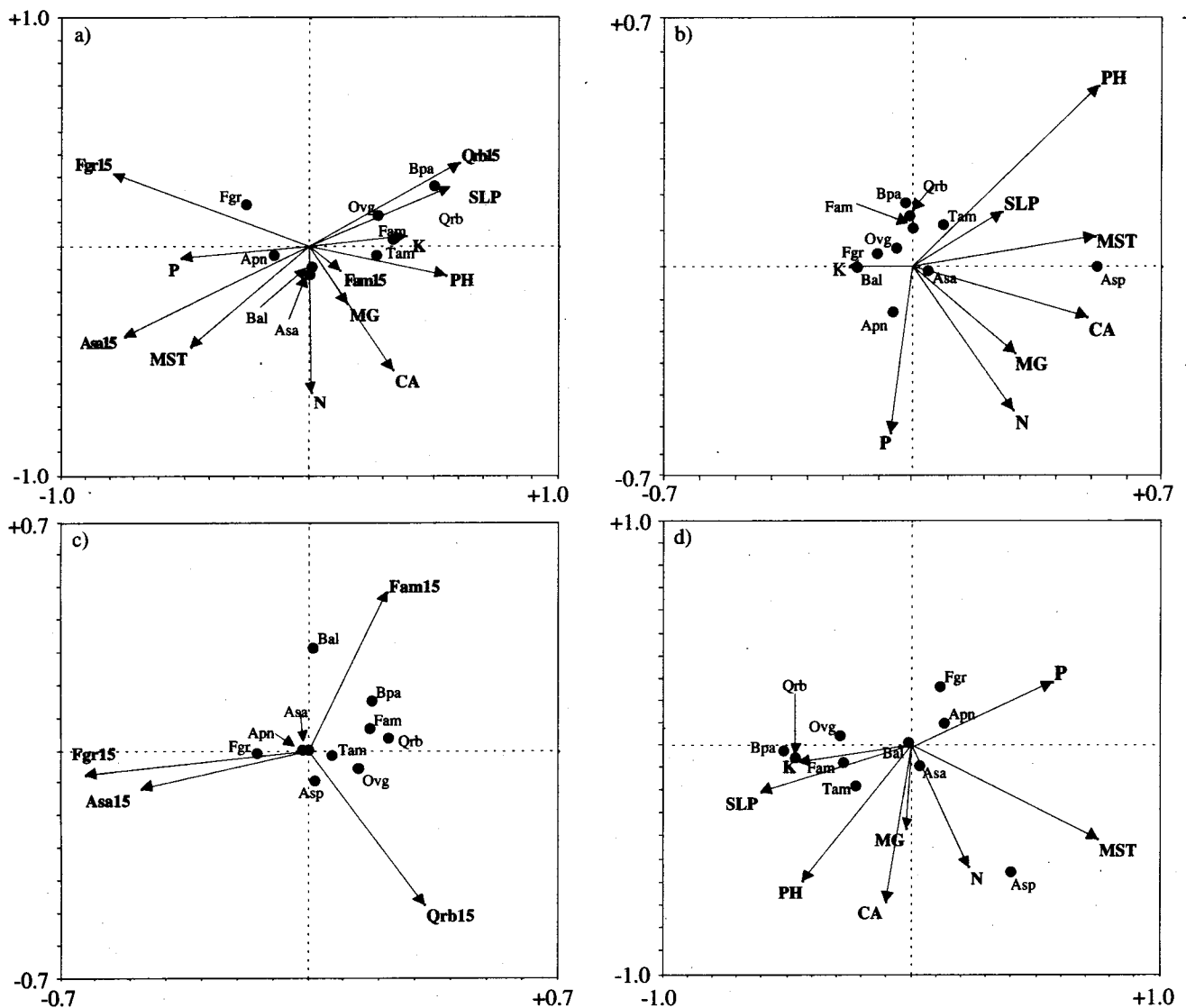


FIGURE 4. a) Species-environment ordination diagram (biplot scaling) based on CCA using all variables in overstorey tree matrix (TM) and abiotic variable matrix (AM) as explanatory variables, but with *Acer spicatum* excluded from the sapling matrix (SM) (refer to text for details). b) Species-environment ordination diagram (biplot scaling) based on a pCCA using variables in abiotic variable matrix (AM) as the explanatory variables and variables in overstorey tree matrix (TM) as the covariable variables (accounts for pure AM variation). c) Species-environment ordination diagram (biplot scaling) based on a pCCA using variables in overstorey tree matrix (TM) as the explanatory variables and variables in abiotic variable matrix (AM) as the covariable variables (accounts for pure TM variation). d) Species-environment ordination diagram (biplot scaling) based on CCA using all variables in abiotic variable matrix (AM) as explanatory variables. Refer to tables I-III for explanations of acronyms.

saplings. On these sites, relative dominance of *F. grandifolia* trees in the overstorey (*Fgr*₁₅) appears to have considerable influence; *F. grandifolia* saplings are found on sites with more *F. grandifolia* trees in the canopy, while *A. saccharum* saplings are mostly absent on such sites.

One of the hypotheses to explain the coexistence and the replacement patterns in *Fagus-Acer* forests is reciprocal replacement (Fox, 1977; Woods, 1979; Runkle, 1981), which suggests that seedlings and saplings of each species tend to grow and survive better under canopies of the other species than under conspecific adults. We found no evidence of such reciprocal replacement patterns; *Fagus grandifolia* saplings are found only at sites where *F. grandifolia* overstorey trees are abundant, suggesting "self-replacement". *Acer saccharum* saplings are found abundant at most locations at the study site, except at sites where *F. grandifolia*

trees are found more abundant in the overstorey; these are the sites where the reciprocal replacement hypothesis predicts *A. saccharum* saplings should be abundant.

Our results show that the effects of *F. grandifolia* overstorey trees are correlated with pH and Ca availability. While a naturally occurring pH and Ca availability gradient may have given rise to the changes in relative dominance of *F. grandifolia* in the overstorey, *F. grandifolia* trees are also known to influence edaphic conditions in the understorey. Leaf litter of *F. grandifolia* has low pH (Finzi, Canham & Van Breeman, 1998), and as the pH is lowered, availability of Ca decreases (Ellis & Mellor, 1995). Additionally, *Fagus* leaf-litter is low in Ca concentration (Gosz, Likens & Bormann, 1973; Côté & Fyles, 1994a,b) and also has high levels of lignin and polyphenols (Melillo, Aber & Muratore, 1982; Aber, Melillo & McClaugherty, 1990), which can

complex with Ca and increase leaching of these elements (Davies, 1971). Therefore, pH and Ca availability may be decreased in stands with frequent occurrence of *F. grandifolia* trees. From this study, we are unable to determine whether the edaphic conditions gave rise to changes in relative dominance of *F. grandifolia* or *F. grandifolia* overstorey trees influenced the edaphic conditions. However, our results do show that low pH and Ca availability are found at sites where *F. grandifolia* trees are dominant in the overstorey, as also has been reported in other studies (Van Breeman, Finzi & Canham, 1997; Finzi, Canham & Van Breeman, 1998).

Kobe *et al.* (1995) and Kobe (1996) found that mortality of *A. saccharum* saplings was higher in non-calcareous soils than calcareous soils under deep shade (less than 5% of the full sun). *Acer saccharum* has been found to achieve maximum dominance at sites with high pH and Ca content in northern Michigan (Woods, 2001), and deficiencies in Ca have also been linked to the widespread dieback of *A. saccharum* in southern Québec and adjacent regions (Liu, Ellsworth & Tyree, 1997). Thus the low pH and Ca availability under *F. grandifolia* trees may decrease the growth and survivorship of *A. saccharum* saplings and therefore may explain the lack of regeneration of *A. saccharum* saplings at sites where *F. grandifolia* trees are frequently found.

It is often argued that light is the main controlling factor in determining the patterns of understory vegetation in eastern deciduous forests of North America (Shugart, 1984; Kobe *et al.*, 1995; Finzi & Canham, 2000), and in *Fagus-Acer* forests temporal variation in understory light conditions has been considered to be a key factor in explaining the patterns of canopy replacement and coexistence of *F. grandifolia* and *A. saccharum* (Runkle, 1984; Poulson & Platt, 1996). Poulson and Platt (1996) have suggested that *F. grandifolia* tends to gain importance when the disturbance is infrequent (low light conditions persist for extended periods of time) and *A. saccharum* tends to gain importance when it is frequent (gaps are created and light availability temporarily increases). This hypothesis is based on the fact that *F. grandifolia* survives for longer periods of time and grows more rapidly upward in the shaded understory than *A. saccharum*, while *A. saccharum* grows more rapidly upward in gap conditions (Canham, 1988; Poulson & Platt, 1989). This known difference in species' response to light coupled, with the frequency of disturbances, which create temporal and spatial variations in understory light conditions, is the mechanistic basis of the disturbance hypothesis.

At our study site, relatively large-scale ice storms have occurred approximately every 20 years for the past 60 years (major storms have been recorded in 1942, 1961, 1983, 1998). The ice storm damage creates gaps in the canopy, and while there is spatial variation in the gaps created, the damage is widespread, which is unlike the gaps created by treefalls (Runkle, 1984; Hooper, Arie & Lechowicz, 2001). Given the frequency of disturbance, the disturbance hypothesis suggests that our study site should be advantageous for *A. saccharum* saplings, and as expected, most of the study plots have high density of *A. saccharum* saplings in the understory. However, this pattern does not apply at all sites: *A. saccharum* saplings are almost absent at sites where *F. grandifolia* trees are dominant in the overstorey. This exception suggests that edaphic conditions under an overstorey

with *F. grandifolia* (low pH and Ca availability) may indeed have a strong influence on the distribution pattern of *A. saccharum* saplings. There may be two reasons why this pattern was not detected at the study site where Pouson and Platt (1996) conducted their study. The first is that the soil at their study site is highly calcareous, and the second is the possibility that "climatic harshness" amplifies the influence of low pH and Ca availability on the growth and survival of *A. saccharum* toward the northern range of its distribution.

Another factor that may be important in explaining the abundant occurrence of *F. grandifolia* saplings (or the absence of *A. saccharum* saplings) at sites where *F. grandifolia* trees dominate is their ability to propagate clonally by root sprouts. The occurrence of root sprouts is considered to gain importance with increasing latitude (Held, 1983; Melançon & Lechowicz, 1987), and indeed *F. grandifolia* sprouts have been found to occur extensively at our study site (Kitamura *et al.*, 2000; Arie, unpubl. data), as well as in other *Fagus-Acer* forests in southwestern Québec (Beaudet *et al.*, 1999). Beaudet *et al.* (1999) have shown that *F. grandifolia* sprouts (up to 3 m) grow considerably faster than adjacent *A. saccharum* saplings in an old-growth *Fagus-Acer* forest in Québec. This suggests that during the inter-disturbance periods, *F. grandifolia* saplings of sprout origin could gain considerable height advantage over *A. saccharum* saplings in the understory, which may benefit *F. grandifolia* saplings when a gap opens. Additionally, we found that *F. grandifolia* sprouts grow just as fast as *Acer* saplings after gap openings created by an ice storm (Arie, unpubl. data). Thus, at sites where root sprouts occur in greater density (*i.e.*, sites where *F. grandifolia* trees mainly dominate the overstorey), *A. saccharum* saplings may not benefit from having frequent disturbances. At the study site where Poulson and Platt (1996) conducted their study, root sprouting was not found to be important. Therefore, in conjunction with the edaphic conditions, the extensive occurrence of root sprouts may explain why *A. saccharum* saplings are not found at sites where *F. grandifolia* trees dominate the overstorey, despite the frequent occurrence of disturbance at our study site.

CONCEPTUAL MODEL FOR *FAGUS-ACER* DYNAMICS

In summary, we provide a conceptual model explaining how *F. grandifolia* saplings can self-replace despite a frequent occurrence of canopy disturbance. The model can be viewed as an addendum to the model proposed by Poulson and Platt (1996) for locations with frequent disturbances. Consider an early successional forest where *F. grandifolia* and *A. saccharum* begin to establish (from seed). Because the light level is still relatively high beneath the early successional canopy, *A. saccharum* seedlings/saplings generally will perform better than *F. grandifolia* seedlings/saplings, except at sites where the conditions are less favorable for *A. saccharum* (*e.g.*, more acid soil). At sites where *A. saccharum* saplings perform well, they will eventually dominate the overstorey, and frequent canopy disturbance will ensure continuous regeneration of *A. saccharum* at these locations (Poulson & Platt, 1996). At locations where *A. saccharum* seedling/sapling growth is retarded, *F. grandifolia* saplings will capture a greater proportion of the overstorey, which will make the conditions less suitable by modifying the

edaphic conditions. Furthermore, adult beech trees will produce root sprouts. These factors lead to local dominance by *F. grandifolia* saplings/trees and ensure self-replacement of *F. grandifolia* at these sites.

It should be noted that even at locations where conditions are favorable for *A. saccharum*, if several *F. grandifolia* seedlings/saplings of seed origin are able to establish by chance and grow into overstory trees, they may be able to slowly replace the neighboring stands over time by root sprouts. At our study site, we have observed numbers of small patches consisting of almost pure *F. grandifolia* stands, both in the overstory and understory, in an area where *A. saccharum* dominates the overstory. These patches may suggest the rare occasions where *F. grandifolia* of seed origin are able to establish by chance and grow into overstory trees at sites more favorable for *A. saccharum*.

Conclusion

Our study has shown that the soil moisture gradient, which correlates negatively with relative dominance of *Q. rubra* overstory trees and positively with *A. saccharum* overstory trees, contributes the most in explaining the patterns of spatial variation and species composition of the sapling community in an old growth *Fagus-Acer* forest. *Acer saccharum* was found to occur on a wide range of soil moisture conditions, while *F. grandifolia* saplings were not found on the dry sites. The relative dominance of *F. grandifolia* in the overstory, which correlates negatively with pH and Ca availability, also explained the differences in the spatial distribution patterns of *A. saccharum* and *F. grandifolia* saplings at our study site. *A. saccharum* saplings were not found on sites where *F. grandifolia* dominates the overstory, while *F. grandifolia* saplings are mainly limited to sites dominated by *F. grandifolia* overstory trees. These findings do not support existing hypotheses for canopy tree replacement patterns in *Fagus-Acer* forests.

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