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## Environmental correlates of canopy composition at Mont St. Hilaire, Quebec, Canada<sup>1</sup>

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ARIEI, K., B.R. HAMEL, AND M.J. LECHOWICZ (Department of Biology, McGill University, 1205 Av. Docteur Penfield, Montréal, QC, H3A 1B1). Environmental correlates of canopy composition at the Gault Nature Reserve in southwestern Quebec, Canada. *J. Torrey Bot. Soc.* 132: 90–102. 2005.—The environmental basis for variation in canopy composition was investigated in an extensive old-growth forest at Mont St. Hilaire, Quebec, Canada. Based on 144 permanent plots, spatial variation in canopy tree species and the effect of environmental variables on canopy composition were examined using canonical correspondence analysis (CCA). Slope and the amount of direct solar radiation received during the growing season, both of which are good indicators of soil moisture, were the main factors explaining plot-to-plot variation in canopy composition. *Quercus rubra*, *Betula papyrifera*, *Ostrya virginiana* and *Pinus strobus* predominated on plots with high insolation and steeper slope, while species such as *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, and *Tilia americana* occurred on sites with gentler slope and lower insolation during the growing season. Additionally, plots with greater dominance of *Acer saccharum* in the canopy had higher soil nitrogen availability, and plots with greater dominance of *Fagus grandifolia* had lower Ca availability.

Key words: temperate deciduous forest, nutrient availability, soil moisture, canonical correspondence analysis (CCA), distribution pattern, codominance.

Mont St. Hilaire (MSH), located approximately 32 km east of Montreal, Canada, is a hill complex that rises prominently from the surrounding St. Lawrence River Valley. It has an area of approximately 10 km<sup>2</sup>, and consists of seven low peaks forming a shallow bowl around a small lake; elevation ranges between 70–415 m a.s.l. MSH is one of ten monadnocks referred to as the Monteregian Hills (Adams 1903, Eby 1984), epizonal intrusions of Cretaceous age that penetrated Ordovician limestones and shales (Webber and Jellema 1965, Feininger and Goodacre 1995). MSH lies within the Upper St. Lawrence

section of the Great Lakes-St. Lawrence Forest Region (Rowe 1972), an area near the northern limit of the temperate deciduous forests of eastern North America.

European immigrants settled in the St. Lawrence River Valley in the vicinity of Montreal beginning in the early 17<sup>th</sup> Century. Due to the continuous influx of settlers and their extensive agricultural practices, almost all of the original forest cover in this region has been cleared in the last 400 years (Rowe 1972, Ricketts et al. 1999). However, the Monteregian Hills were left as stranded forest “islands”, in part due to their unsuitability as agricultural land, although these forests have been used to varying degrees for timber, maple sugar production and recreation (Maycock 1961). Among these forest islands, Mont St. Hilaire (MSH) is the least disturbed by human activities because of its relative inaccessibility and a long period of private ownership (Maycock 1961, Cook 1971). Many trees on MSH exceed 150 years in age and some are over 450 years old (Cook 1971). MSH is considered the largest remnant of primeval forests in the St. Lawrence River Valley; its scientific and cultural significance was recognized in 1978 when it became the first Canadian site to be designated an International Biosphere Reserve under the Man and Biosphere program (MAB) of the United Nations.

There have been several surveys of the flora and vegetation at MSH (e.g., Marie-Victorin 1913, Maycock 1961, Cook 1971), two of which

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have focused on the compositional and spatial patterns of trees on the mountain (Phillips 1972, Enright and Lewis 1985). Phillips (1972) investigated the aspect-related differences in tree composition by sampling and comparing data obtained from eight geomorphic units that were defined prior to the survey (bogs, lowlands, summits, cols, north-slope, south-slope, east-slope, and west-slope). While the data collected by Phillips were quite extensive, site-specific environmental information was not recorded. Therefore, although the results are useful as a broad description of vegetation types found at MSH, relationships between species distribution and environmental conditions are obscure. Enright and Lewis (1985) attempted to identify the vegetation-environment relationships more rigorously by sampling quadrats with site-specific information on environment. The environmental variables they obtained included aspect and soil temperature, which were measured directly at each quadrat, and also estimated values of global radiation (direct and diffuse radiation) and evapotranspiration. While their method was more efficient in identifying the environmental basis of tree distributions at MSH, their sampling locations were restricted to a small corner of the mountain, and half of their localities were likely to have been affected by a fire that had occurred about 40 years prior to their survey. Thus, although there have been attempts to identify the environmental correlates of tree distributions at MSH, we only have a limited and qualitative understanding of these relationships to date.

Numerous studies have shown that species assemblages in various ecosystems typically show distinctive patterns along environmental gradients (e.g., moisture, altitude, etc.). These findings support the mainstream perspective that plant communities are organized by adaptive responses to local environmental heterogeneity (i.e., niche-assembly model: MacArthur 1970, Diamond 1975, Tilman 1982). However, this view of how species assemble has been challenged by the recent development of neutral models (Bell 2000, 2001; Hubbell 2001). These models assume no adaptive differences among the species within the community and ascribe patterns of distribution and abundance entirely on stochastic processes in local dispersal and establishment. Thus at local scales where adaptation and niche-assembly are expected to operate, the neutral theory predicts that patterns of dis-

tribution and abundance may in fact be uncoupled from adaptation.

The objective of this study is to examine the canopy tree-environment relationship by using a plot size at which adaptation and niche-assembly rules are more likely to operate. Previous studies on canopy tree-environment relationship at MSH lack site-specific environmental information to examine this (Phillips 1972), or lack spatial representation of MSH (Enright and Lewis 1985). We identify the environmental correlates of variation in canopy composition at MSH by using canonical correspondence analysis (CCA), and by testing its significance using Monte Carlo permutation tests. Our data come from a set of long-term monitoring plots that were established in the last few years. For the environmental variables, factors such as soil moisture and nutrient availability were measured directly at the plots and augmented by physical environmental variables derived from a digital elevation model (DEM) for MSH. We discuss our findings in light of what is known about canopy tree-environment relationships in the region.

**Materials and Methods.** **STUDY SITE.** *Physical characteristics of MSH.* Mont St. Hilaire (MSH) is located approximately 32 km east of Montreal, in southwestern Quebec, Canada (45°31'N, 73°08'W; Fig. 1). The mean annual temperature in this region is 5.9 °C (minimum and maximum monthly mean temperatures are -10.2 °C (Feb.) and 20.6 °C (Aug.), respectively), and mean total annual precipitation is 1017 mm (Environment Canada 2002, all climatic data are for St. Hubert Climate Station (1928–1990), 45° 31' N, 73° 25' W, on the valley floor approximately 20 km west of MSH). The mean annual freeze-free period is 140 days (Wilson 1971, based on data for the period 1931–1960). Mont St. Hilaire originated in a series of three intrusions of magma into Ordovician-age sedimentary rocks. The three intrusions each have a distinct composition and chemistry and differ in age. The first group (133 million years old) consists mostly of melagabbro, perkinite and pyroxenite. The intrusives of the second group (120 million years old) are mostly gabbro, nepheline syenite, diorite and monzonite. Finally, the eastern side of the mountain (12 million years old) is mostly peralkaline nepheline syenites and porphyrites. No extensive soil survey has been conducted at MSH to date, and the information we have on soil characteristics remains very limited. Although the information is based on a small set

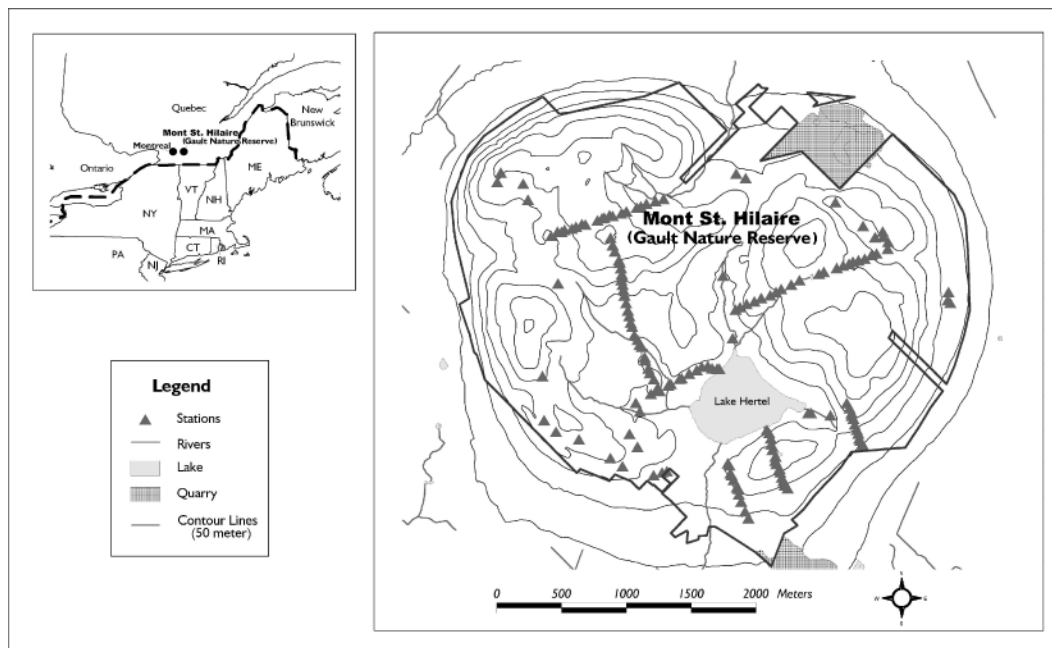


FIG. 1. Map of Mont St. Hilaire (Gault Nature Reserve). The triangles in the diagram indicate plot locations.

of plots in a localized area, the soil type and the soil texture at MSH have been found to be mainly ferro-humic podzol and sandy loam, respectively (Beaumont 1980, Grenon et al. 1999). Soil depth is known to vary by location (slopes, hill tops, valley bottoms), and the C horizon is believed to be mainly absent, except at lower elevations and in valley bottoms (Beaumont 1980, Grenon et al. 1999).

*Trees found at MSH.* MSH lies in a region where the dominant forest community is composed chiefly of *Acer saccharum* Marshall and *Fagus grandifolia* Ehrh., with *Betula alleghaniensis* Britton, *Acer rubrum* L., *Tilia americana* L., *Fraxinus americana* L., *Populus grandidentata* Michx., and *Quercus rubra* L. (Rowe 1972), although there is a fairly diverse range of forest communities found in the St. Lawrence River Valley and adjacent areas (e.g., Dansereau 1943, Dansereau 1959, Walther 1963, Op de Beeck 1972, Bouchard and Maycock 1978, Bouchard 1979, Gagnon and Bouchard 1981, Gavin and Bouchard 1983, Domon et al. 1986, St-Jacques and Gagnon 1988, Gauthier and Gagnon 1990, Lamontagne et al. 1991, Brisson et al. 1992, Anseau 1993, Meilleur et al. 1994). Various tree communities are also found at MSH (Maycock, 1961, Phillips 1972, Enright and Lewis, 1985), but *Acer saccharum*, *Fagus gran-*

*difolia* and *Quercus rubra* are the three dominant species (Table 1). Maycock (1961) provided a list of species that are found on the mountain, 41 species of trees on the mountain reach canopy or subcanopy positions (see footnote in Table 1).

*DATA COLLECTION. Tree data.* We established 144 permanent plots to sample forest variation over the mountain (Fig. 1). Of the 144 plots, 114 were established in the summer of 1997, and were placed on seven different transects. The seven line transects were placed so that (1) we can minimize time required to visit all the plots (this is important when making abiotic variable measurements at these plots, such as soil moisture), (2) the transects go through various vegetation types classified by Phillips (1972) (note that the aerial photograph interpretation, in which Table 1 is based on, was not available at the time of plot setup). The remaining 30 plots were established in the summer of 2000, and were setup to augment some of the underrepresented canopy types found at MSH. Each plot is circular and has a 6-m radius; average tree density per plot is 7.1 (DBH  $\geq$  10 cm).

We recorded the geographical coordinates of each plot using a GPS. At each plot, we recorded all woody individuals with DBH greater than

Table 1. Total area covered by the major canopy tree species based on interpretation of an aerial photograph of our study site. The digital map of forest cover for MSH was created by a private company (DESFOR, Région Montérégie, Verchères, Québec). The digital map was based on a interpretation of infrared aerial photographs (scale 1:15 000) taken in 1994 (Centre de la Nature du Mont Saint-Hilaire 2002). The map identifies 128 different polygons (i.e. cover types), 119 of which are forested (minimum polygon surface area was set to 1 hectare). For each polygon, species that had less than 10% cover were not recorded. Thirteen different species were recognized for the entire map. Using the area (m<sup>2</sup>) and the relative cover of the canopy trees in each polygon, we calculated the total area covered by each canopy tree species at MSH.

Species	Total covered area (ha)	Relative cover (%)	Cumulative cover (%)
<i>Acer saccharum</i> Marshall	339.8	32.1	32.1
<i>Fagus grandifolia</i> Ehrh.	209.2	19.8	51.9
<i>Quercus rubra</i> L.	174.0	16.4	68.4
<i>Betula alleghaniensis</i> Britton	50.9	4.8	73.2
<i>Fraxinus americana</i> L.	30.9	2.9	76.1
<i>Pinus strobus</i> L.	18.4	1.7	77.8
<i>Tilia americana</i> L.	7.6	0.7	78.6
<i>Tsuga canadensis</i> (L.) Carrière	7.3	0.7	79.2
<i>Ostrya virginiana</i> (Miller) K. Koch	5.9	0.6	79.8
<i>Acer rubrum</i> L.	4.4	0.4	80.2
<i>Betula papyrifera</i> Marshall	4.2	0.4	80.6
<i>Populus tremuloides</i> Michx.	2.2	0.2	80.8
<i>Alnus rugosa</i> (Du Roi) Spreng.	0.9	0.1	80.9
Unidentified species*	138.5	13.1	94.0
<b>Others</b>			
Rocky summits and cliffs	30.6	2.9	
Ponds, lakes	32.4	3.1	
Buildings	0.4	0.0	
<b>Total area</b>	<b>1057.6</b>		

\* Species unidentified in the aerial survey include *Abies balsamea*, *Acer nigrum*, *Betula populifolia*, *Carya ovata*, *Carya cordiformis*, *Fraxinus americana*, *Fraxinus nigra*, *Juglans cinerea*, *Populus grandidentata*, *Picea glauca*, *Pinus resinosa*, *Populus deltoidea*, *Populus balsamifera*, *Prunus pennsylvanica*, *Prunus serotina*, *Thuja occidentalis*, *Ulmus americana* *Ulmus rubra*.

10 cm (species, DBH). We converted the data to importance values; for each plot, the importance value of species *i* (IV<sub>*i*</sub>) is calculated as:

$$IV_i = \left( \frac{BA_i}{BA_{tot}} \right) + \left( \frac{DN_i}{DN_{tot}} \right) \quad (0 \leq IV_i \leq 2)$$

where, BA<sub>*i*</sub> = total basal area of species *i* in a plot, BA<sub>tot</sub> = total basal area in a plot, DN<sub>*i*</sub> = stem density of species *i* in a plot, DN<sub>tot</sub> = total stem density in a plot. The tree species identified in the plots appear in Table 2, all of which are native species typically found in the forests of the St. Lawrence River Valley (Walther 1963, Op de Beek 1972, Rowe 1972).

**Soil nutrients.** In August 2000, we took soil samples to 10 cm depth at eight different locations near the center of each plot, first removing the L-F-H layers. We pooled samples taken at each plot and froze them within hours of collection. The samples were kept frozen 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 Soil Chemistry Laboratory at Université La-

val. Mg, Ca and K were assayed in the Mehlich III extractant (Mehlich 1984), and were analyzed with the ICP (Inductively Coupled Plasma) method (Plasma 40, Perkin-Elmer Instruments, Boston, MA, U.S.A.). NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> were assayed in a 2M KCl extract (Page et al. 1982) and analyzed with a QuikChem 4000 (Lachat Instruments, Milwaukee, WI, U.S.A.): NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> were analyzed using the QuikChem Method 12-107-06-2-A (Lachat Instruments 1990) and the QuikChem Method 12-107-04-1-B (Lachat Instruments 1992), respectively. Basic statistics of the measurement values are given in Table 3.

**Soil moisture.** We measured volumetric moisture contents twice during the summer of 2000 (July 13, August 20) using frequency-domain reflectometers (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 done in the same order on all sampling dates to minimize the time required to visit all plots. There was no rainfall during the sampling periods. At

Table 2. List of species identified in the 144 permanent plots at Mont St. Hilaire. Their acronyms and basic statistics are shown.

Species	Acronym	Frequency (out of 146 plots)	Stem density (per plot)				Basal area (m <sup>2</sup> ha <sup>-1</sup> )					Importance value				
			Max	Median	Mean	S.D.	Min	Max	Median	Mean	S.D.	Min	Max	Median	Mean	S.D.
<i>Acer pensylvanicum</i> L.	Apn	10	4	1	2.0	1.4	0.7	5.3	1.4	2.2	1.7	0.11	1.22	0.28	0.43	0.36
<i>Acer saccharum</i> Marshall	Asa	123	12	3	3.0	2.0	0.7	84.0	13.3	19.5	18.5	0.07	2.00	0.83	0.95	0.58
<i>Acer spicatum</i> Lam.	Asp	3	2	1	1.3	0.6	0.9	1.6	1.0	1.1	0.4	0.31	0.86	0.36	0.51	0.30
<i>Betula alleghaniensis</i> Britton	Bal	15	2	1	1.1	0.3	1.1	35.8	3.6	8.1	10.4	0.12	1.22	0.24	0.36	0.30
<i>Betula papyrifera</i> Marshall	Bpa	20	7	1	1.6	1.6	0.7	8.4	3.8	4.0	2.9	0.10	0.81	0.22	0.31	0.22
<i>Carya ovata</i> (Miller) K. Koch	Cov	2	1	1	1.0	0.0	0.8	1.2	1.0	1.0	0.3	0.15	0.30	0.22	0.22	0.10
<i>Fraxinus americana</i> L.	Fam	37	10	2	2.3	2.0	0.8	27.3	6.8	7.9	5.9	0.13	1.74	0.49	0.54	0.37
<i>Fagus grandifolia</i> Ehrh.	Fgr	67	11	2	3.1	2.2	0.8	66.3	12.2	15.0	14.7	0.14	2.00	0.66	0.82	0.57
<i>Juglans cinerea</i> L.	Jcn	1	1	1	1.0	n/a	3.7	3.7	3.7	3.7	n/a	0.25	0.25	0.25	0.25	n/a
<i>Ostrya virginiana</i> (Miller) K. Koch	Ovg	28	5	1	1.8	1.1	0.7	5.6	1.1	2.0	1.5	0.07	0.93	0.21	0.28	0.22
<i>Populus grandidentata</i> Michx.	Pgr	2	1	1	1.0	0.0	0.8	1.3	1.1	1.1	0.4	0.13	0.21	0.17	0.17	0.06
<i>Pinus strobus</i> L.	Pst	5	2	1	1.2	0.4	1.0	23.2	3.6	7.7	9.0	0.13	0.43	0.24	0.26	0.13
<i>Prunus pensylvanica</i> L.f.	Ppn	1	1	1	1.0	n/a	0.7	0.7	0.7	0.7	n/a	0.17	0.17	0.17	0.17	n/a
<i>Prunus serotina</i> Ehrh.	Pse	1	1	1	1.0	n/a	9.8	9.8	9.8	9.8	n/a	0.56	0.56	0.56	0.56	n/a
<i>Prunus virginiana</i> L.	Pvg	1	3	3	3.0	n/a	3.1	3.1	3.1	3.1	n/a	0.45	0.45	0.45	0.45	n/a
<i>Quercus rubra</i> L.	Qrb	56	15	3	3.4	2.8	0.7	48.8	17.0	19.2	12.6	0.15	2.00	0.96	0.97	0.51
<i>Tilia americana</i> L.	Tam	9	3	1	1.3	0.7	0.9	15.6	3.2	5.9	5.2	0.13	1.27	0.28	0.39	0.36
<i>Tsuga canadensis</i> (L.) Carrière	Tca	11	6	2	2.7	1.9	3.5	29.2	7.1	12.7	9.9	0.15	2.00	0.78	0.92	0.58
<i>Thuja occidentalis</i> L.	Toc	1	1	1	1.0	n/a	3.0	3.0	3.0	3.0	n/a	0.24	0.24	0.24	0.24	n/a
<i>Ulmus americana</i> L.	Uam	1	1	1	1.0	n/a	27.0	27.0	27.0	27.0	n/a	0.81	0.81	0.81	0.81	n/a

\* Minimum, maximum, mean and S.D. are calculated based on non-zero values.

Table 3. List of environmental variables included in the analysis. Their acronyms, basic statistics, and transformations used are shown. Note that aspect, a nominal variable, is not shown in the table.

Variable	Units	Acronym	Transformation	Mean	S.D.	Median	Range
Total Nitrogen	ppm	TN	Log <sub>10</sub> (x)	89	75	60	16–584
Mg	ppm	MG	Log <sub>10</sub> (x)	167	121	124	21–632
Ca	ppm	CA	Log <sub>10</sub> (x)	2748	2675	2027	179–14 054
K	ppm	K	Log <sub>10</sub> (x)	174	89	153	37–487
pH	—	PH	—	4.8	0.5	4.8	3.6–6.3
Moisture (Jul. 13)	m <sup>3</sup> m <sup>3</sup>	MST1	arcsin(x <sup>1/2</sup> )	0.34	0.20	0.29	0.07–1.00
Moisture (Aug. 20)	m <sup>3</sup> m <sup>3</sup>	MST2	arcsin(x <sup>1/2</sup> )	0.35	0.24	0.26	0.10–1.00
Elevation	m	ELV	—	249	64	239	126–400
Insolation (direct)	kWh m <sup>-2</sup>	IDIR	—	658	55	670	419–728
Insolation (diffuse)	kWh m <sup>-2</sup>	IDIF	—	690	26	699	591–741
Slope	degrees	SLP	—	14	9	13	0–37

each plot, we determined average soil moisture from five random locations near the center of the plot.

*Physical environmental factors.* We calculated the physical environmental factors used in this study (elevation, slope, aspect, insolation) for each sampling plot using a digital elevation model (DEM) of MSH (minimum pixel size is 5 × 5 m). To create the DEM, we interpolated a digital map (Ministère des Ressources Naturelles 1999; scale 1:20 000, 10 m contour line intervals) using Idrisi32 Release 2 (Clark Labs, Worcester, MA, U.S.A.). Arcview 3.2 and the Spatial Analyst extension 2.0a (Environmental Systems Research Institute, Inc., Redlands, CA, U.S.A.) were used to calculate elevation, aspect and slope for each sampling plot. Insolation was estimated with Solar Analyst extension 1.0 (Helios Environmental Modeling Institute, Vermont, KS, U.S.A.). Insolation is defined as cumulative energy (kWh) per square meter for every hour of sunshine received during the growing season (1 April to 30 September). Various factors are taken into account to calculate insolation, which includes latitude, elevation, aspect, shadows cast by surrounding topography, daily and seasonal shifts in solar angle, and atmospheric attenuation. Transmittivity of the atmosphere was fixed at 0.5. We divided global insolation into direct and diffuse insolation by fixing the diffuse insolation proportion to 0.53. This value is estimated using the equations provided in Frazer et al. (1999) and by using the hourly global radiation data measured at weather stations on the island of Montreal between 1961 and 2001 by Environment Canada (1961–1986—Jean Brebeuf weather station 45° 30' N, 73° 37' W; 1961–1986 and 1987–2001—Dorval Airport weather station 45° 28' N, 73° 45' W). We used

only 34 years of data between 1961 and 2001, because some years had incomplete data.

We converted the aspect data (0–359°) to a nominal variable with five classes, which are defined as follows. The plots that had less than 5° slope were classified as “Flat (F)”. Plots with more than 5° slope were classified as facing East (E), South (S), West (W), or North (N). “East” plots had aspect in the range 45–135°, south plots 135–225°, West plots 225–315°, and North plots 0–45° and 315–359°.

**STATISTICAL ANALYSIS.** We used canonical correspondence analysis (CCA) to investigate the relationship between environmental variables and tree composition. CANOCO (ver. 4.0, ter Braak and Šmilauer 1998) was used to perform the analyses, and the “downweight” function in CANOCO was used to reduce the effects of rare species. Only species that occurred in more than 3 plots were included in the analyses. Environmental variables were transformed (Table 2) and standardized to zero mean and unit variance prior to analysis. This standardization makes the canonical coefficients comparable to each other, but does not influence other aspects of the analysis (ter Braak 1986). Significance of the sum of all canonical eigenvalues and the significance of the first two ordination axes were tested using Monte Carlo permutation tests provided in CANOCO (1000 permutations under the full model; ter Braak and Šmilauer 1998, Legendre and Legendre 1999).

With our data set, permutation tests of sum of all canonical eigenvalues and of the first two ordination axes requires special attention, because the layout of our sampling plots raises concerns for autocorrelation. If autocorrelation is detected, completely random permutations yield invalid tests (ter Braak and Šmilauer 1998). For

Monte Carlo permutation under the full model, residuals of a linear model are the permutable units (Kempthorn 1952, Legendre and Legendre 1999), and if the residuals resulting from a CCA are autocorrelated, our permutation test results are invalid. Thus prior to running the permutation tests, residuals were tested for autocorrelation using the following steps: 1) *Create distance class matrices ( $\mathbf{D}_x$ )*. Calculate the geographical distances between every sampling plots based on latitude, longitude, and elevation of the plots. Use the distances to create “distance class matrices ( $\mathbf{D}_x$ )” (e.g., for distance class 1 ( $\mathbf{D}_1$ ), pairs that belong to the first geographic distance class are coded 1, whereas the remainder of matrix contain zeros). The interval for each distance class was set at 20 m, except for the first distance class, which ranged between 0–40 m (sample size in the 0–20 m distance class was too small to be analyzed). 2) *Calculate the residual matrix of a CCA ( $\mathbf{Y}_{res}$ )*. Because  $\mathbf{Y}_{res}$  is not readily available in CANOCO, we obtained  $\mathbf{Y}_{res}$  by programming CCA in Matlab following the calculations provided in Legendre and Legendre (1999, p.594). 3) *Use  $\mathbf{D}_x$  and  $\mathbf{Y}_{res}$ , and calculate the Mantel statistic ( $r_M$ ) for each distance class matrices*. PC-ORD (ver. 4.0, McCune and Mefford 1999) was used to calculate  $r_M$ , and  $P$ -values of each  $r_M$  were obtained by permutation tests (9999 permutations). Significance of  $P$ -values for each distance class was tested using progressive Bonferroni correction (Legendre and Legendre 1999, p.671).

**Results.** The total variation of the tree composition data was 3.08, and the sum of all canonical eigenvalues (total explained variation) was 0.828. The residuals from the CCA were found to be spatially uncorrelated (Fig. 2). The 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 tree composition and the environmental variables ( $P = 0.001$ ). The first two CCA axes were also significant based on the Monte Carlo permutation test (first axis eigenvalue = 0.450,  $p = 0.001$ ; second axis eigenvalue = 0.167,  $P = 0.001$ ). The first axis correlates positively with direct insolation and slope, and negatively with total nitrogen, diffuse insolation, and soil moisture (Fig. 3a, Table 4a). Species such as *Quercus rubra*, *Pinus strobus*, *Ostrya virginiana*, and *Betula papyrifera* are found on sites with higher axis 1 values, while *Acer sac-*

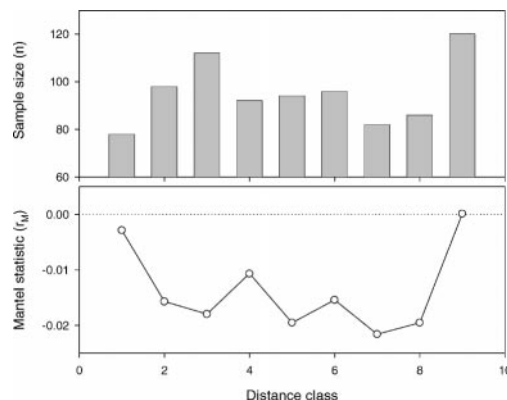


FIG. 2. Mantel correlogram for the residual matrix ( $\mathbf{Y}_{res}$ ). Open circles indicate that Mantel statistics ( $r_M$ ) are not significant after progressive Bonferroni correction ( $\alpha = 0.05$ ). The interval for each distance class is 20 m, except for the first distance class, which has a range between 0–40 m. The histogram in the upper panel shows the sample size in each distance class.

*charum*, *Fagus grandifolia* and *Betula alleghaniensis* are found at sites with lower axis 1 values. The second CCA-axis is negatively correlated with Ca availability, elevation and total nitrogen (Table 4a). Of the three most commonly occurring species at MSH (Table 1), *Fagus grandifolia* is found at sites with low elevation and with low Ca availability, while *Acer saccharum* is found on sites with higher total nitrogen content. Aspect is also a good indicator of different stand types (Fig. 3a). South facing plots are mainly dominated by *Quercus rubra*, north and east facing plots by *Acer saccharum*, and “flat” plots by *Fagus grandifolia*. West facing plots are codominated by *Acer saccharum* and *Quercus rubra*.

To highlight the effects of the important environmental variables, forward selection of the environmental variables was done (ter Braak and Šmilauer 1998). The procedure selected the following four variables: direct insolation, slope, Ca and total nitrogen (Table 4b, Fig. 3b). The sum of all canonical eigenvalues was 0.539 ( $P = 0.001$ ), which is 65% of the value obtained when all environmental variables are used as explanatory variables in the CCA. The first two CCA axes were significant based on the Monte Carlo permutation test (first axis eigenvalue = 0.399,  $P = 0.001$ ; second axis eigenvalue = 0.097,  $P = 0.002$ ). The relative coordinates of the species scores, as well as their relative position along the environmental gradients, do not differ overall with the CCA ordination diagram based on all environmental variables. This in-

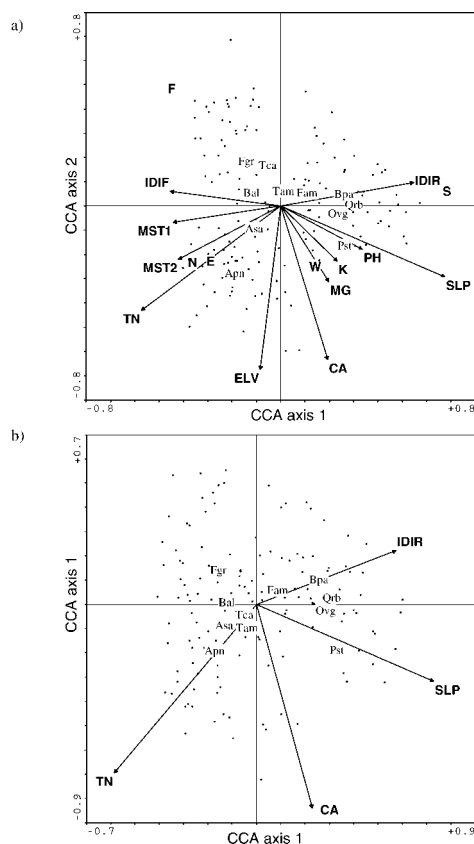


FIG. 3. CCA-ordination diagram of the sampling plots. a) Diagram based on CCA with all environmental variables included in the analysis. Note that aspect classes are given as a point at the centroid (the weighted average) of the sites belonging to that class (ter Braak 1995, ter Braak and Šmilauer 1998). F = flat, N = north, E = east, S = south, W = west. b) Diagram based on CCA with the variables selected by forward selection. Species that occur in less than five samplings plots are not shown in the diagram. For acronyms, see Tables 1 and 2.

indicates that the four variables selected have strong influence on the species composition of the sampled plots.

**Discussion.** Our results show significant relationship between the local environment and canopy tree species composition. While our survey was not specifically designed to test the neutral model, our results do not support the neutral model prediction that patterns of distribution and abundance are uncoupled from adaptation to the local environment. A recent study in Amazonian and Panamanian forests showed that neutral models could account for patterns of tree diversity at scales between 0.2 and 50 km<sup>2</sup>, but was

unable to do so at either larger and smaller scales (Condit et al. 2002). At the spatial scale we have used in this study, adaptation and niche-assembly rules appear to play important roles in determining the abundance and composition of canopy tree communities.

The distribution of canopy trees at MSH is mainly organized along gradients of slope and direct insolation, both good indicators of soil moisture regimes. Although no detailed survey has been done, soil depth is believed to be generally shallow at MSH (Rouse and Wilson 1969). This is particularly true on the slopes, which typically lack a C horizon (Beaumont 1980, Grenon et al. 1999). This shallow soil, in conjunction with the sandy loam texture of the soil, results in low water holding capacity on the slopes. Additionally, the bedrock, which is of plutonic origin, is not water permeable, so the infiltrated water readily runs off down the slope. Direct insolation can also have an influence on soil moisture. At MSH, snowmelt based on exposure has been shown to exert a strong influence on the surface soil moisture regime that is maintained throughout much of the growing season (Rouse and Wilson 1969). This may explain why soil moisture is lower at locations receiving higher amounts of direct solar radiation.

Previous studies have shown that soil moisture significantly influences the species composition of canopy trees in the St. Lawrence River Valley, and in the surrounding Conifer-Northern Hardwood region (Maycock 1963, Walther 1963, Op de Beek 1972, Bouchard and Maycock 1978, Gauch and Stone 1979). Our results are consistent with these previous findings; species such as *Quercus rubra*, *Pinus strobus*, *Betula papyrifera*, and *Ostrya virginiana* are found on the drier sites (higher direct insolation, steeper slope), while the wetter sites (lower direct insolation, gentler slope) are mostly dominated by *Acer saccharum* and *Fagus grandifolia*, with minor components such as *Betula alleghaniensis*, *Tilia americana*, and *Tsuga canadensis*.

Aspect was also a good indicator of differences in canopy tree species composition at MSH. Our results show that south-facing plots are mainly dominated by *Q. rubra*, north- and east-facing plots by *A. saccharum*, and "flat" plots by *F. grandifolia*. West-facing plots are co-dominated by *A. saccharum* and *Q. rubra*. These results support the survey conducted by Phillips (1972) who investigated the aspect-related differences in tree composition at MSH. Both Phillips' study and our study found differences in

Table 4. Canonical coefficients and intra-set correlation coefficients of environmental variables for the first two CCA-axes. a) Results for CCA with all the environmental variables used as explanatory variables. The variables with asterisk (\*) represent aspect, a nominal variable. The canonical coefficients for "West" are zero because it is used as a reference of the aspect classes. See ter Braak and Šmilauer (1998) for details. b) Results for CCA using the forward selection procedure in CANOCO to select four variables.

	Canonical coefficients		Correlation coefficients	
	Axis 1	Axis 2	Axis 1	Axis 2
a)				
Total N	-0.60	-0.17	-0.57	-0.43
Mg	0.10	0.90	0.20	-0.31
Ca	0.06	-1.32	0.19	-0.63
K	0.38	0.02	0.23	-0.23
pH	0.17	0.14	0.34	-0.18
Moisture (Jul. 13)	-0.06	-0.32	-0.42	-0.22
Moisture (Aug. 20)	-0.01	0.07	-0.44	-0.07
Elevation	0.00	-0.15	-0.09	-0.68
Insolation (diffuse)	0.07	-0.46	-0.46	0.06
Insolation (direct)	0.35	0.04	0.55	0.10
Slope	0.35	-0.61	0.68	-0.29
West*	0.07	0.01	0.11	-0.22
North*	-0.02	-0.19	-0.34	-0.20
East*	0.09	-0.16	-0.27	-0.19
South*	0.11	-0.23	0.66	0.06
Flat*	0.00	0.00	-0.43	0.45
b)				
Total N	-0.4946	-0.5994	-0.59	-0.70
Ca	0.3517	-0.4963	0.23	-0.84
Insolation (direct)	0.4769	0.1325	0.58	0.22
Slope	0.4852	-0.4282	0.73	-0.32

species composition between west- and east-facing slopes, where east-facing slopes were more similar to species composition found on north-facing slopes. This may reflect the differences in soil moisture regimes between the east- and the west-facing plots, which can be explained by the following two mechanisms; 1) prevailing wind at our study site is from the west (Wilson 1971, Environment Canada 2002), which may increase evaporation on the west-facing plots and 2) east-facing plots receive solar radiation in the morning when the soil temperature is lower; this reduces evaporation from the east-facing plots compared to the west-facing plots, despite receiving similar amounts of solar radiation. As a consequence, east-facing plots have higher soil moisture, which is reflected in the differences in species composition with the west-facing plots (or similar composition with the north-facing plots).

While variables related to topography have significant influence on the differences in forest types, two edaphic factors, total nitrogen and Ca availability, were also found to explain the spatial variation in canopy tree species composition. At sites with high total nitrogen, *A. saccharum* is found to dominate the canopy. Previous stud-

ies have shown that nitrogen pool and mineralization rates are higher at sites dominated by *A. saccharum* than sites dominated by *F. grandifolia* or *Q. rubra* (Boerner and Koslowsky 1989, Findzi et al. 1998a). *Acer saccharum* leaf litter has a lower C:N ratio than that of *F. grandifolia* or *Q. rubra*, which can lead to faster rates of decomposition (Pastor et al. 1984, Findzi et al. 1998a); the differences in the rate of litter decomposition spanning temporal scales of decades to centuries can lead to large differences in N content of soils (Parton et al. 1987). This mechanism may explain why sites dominated by *A. saccharum* have higher total nitrogen content. Our results also show that *F. grandifolia* is more dominant at sites with low Ca availability, which is in agreement with previous studies (e.g. van Breeman et al. 1997, Findzi et al. 1998b, Woods 2000). *Fagus grandifolia* has been shown to modify the edaphic conditions through their leaf litter. *Fagus grandifolia* leaves have low pH (Findzi et al. 1998b), and as the pH is lowered, availability of Ca decreases (Ellis and Mellor 1995). Additionally, *F. grandifolia* leaf-litter is low in Ca concentration (Gosz et al. 1973, Côté and Fyles 1994a,b) and also has high levels of lignin and polyphenols (Melillo et al. 1982,

Aber et al. 1990), which can complex with Ca and increase leaching of this element (Davies 1971). Thus, the Ca gradient may be created by the greater dominance of *F. grandifolia* in the canopy. For both total nitrogen and Ca availability, we have suggested that species composition of the canopy trees may be affecting the availability of these elements, as opposed to soil nutrients affecting the canopy tree composition. Alternatively, successful recruitment of *A. saccharum* and *F. grandifolia* may have been limited to areas with high nitrogen and low Ca availability, respectively. Further investigation is necessary to examine to what extent total nitrogen and Ca availability at our study site is influenced by the relative dominance of *A. saccharum* and *F. grandifolia* in the canopy.

The pH is generally considered to be an important factor influencing the distribution patterns of trees in the deciduous forests of eastern North America. Although pH was excluded during the forward selection procedure in our analysis (Fig. 3), it does not necessarily imply that pH does not explain the species distributions at MSH. In fact, when pH is used as the only explanatory variable in CCA, it explains a significant proportion of the variation in species distribution patterns at MSH (eigenvalue = 0.085,  $P = 0.001$ ). Thus, had pH been the only or one of the few explanatory variables, it would have been considered as one of the important factors that explain the species distribution patterns. The fact that pH was not one of the variables included during the forward selection process implies that much of the variation explained by pH overlapped with variation explained by variables that were selected by forward selection. In our study, slope, which was the first variable to enter the forward selection, appears to overlap with the variation explained by pH (Fig. 3a; examine the arrows of the two variables). Our data set does not provide the mechanism that gave rise to this relationship. However, it may be related to the fact that flat areas are dominated by *F. grandifolia*, whose litter has a low pH.

Although it is not included as an explanatory variable in our study, soil texture is also considered an important factor in determining tree species distribution patterns. The soil texture mainly influences tree species distribution indirectly by affecting soil moisture and soil nutrient availability, both of which were included in our study and were found to influence the tree distributions at MSH. Therefore, including soil texture in our analysis may not have provided additional

explanatory power, as the variation explained by soil texture could have overlapped with variations explained by soil nutrients and moisture. While this may be the case, the spatial variation of soil texture at MSH is believed to be relatively small (soil texture at MSH is mainly sandy loam: Beaumont 1980, Grenon et al. 1999), and therefore may not influence tree species distribution patterns. However, we currently lack sufficient data to verify this assumption; further research on soil properties at MSH is warranted.

Some canopy tree species that are known to occur on the mountain but were not found in our sampling plots include *Acer rubrum*, *Pinus resinosa* Aiton., *Populus tremuloides* Michx., *Carya cordiformis* (Wangenh.) K. Koch., *Abies balsamea* (L.) Miller, *Populus balsamifera* L., *Betula populifolia* Marshall and *Fraxinus nigra* Marshall. The absence of species such as *Acer rubrum*, *Abies balsamea* and *Fraxinus nigra* indicate that wet and wet-mesic sites were underrepresented in our sampling plots. However, these habitats comprise only 1.7 % of the total area of MSH (Phillips 1972) and therefore will only represent a small fraction of the canopy trees found at MSH as a whole. *Pinus resinosa* is found to form dominant stands on west and south facing slopes at MSH (Maycock 1961, Phillips 1972). However, the occurrence of *Pinus resinosa* is low at MSH (Phillips 1972), as well as in forest stands on other Monteregian Hills (Walther 1963) and in the St. Lawrence River Valley (Op de Beek 1972). *Pinus resinosa* stands at MSH are eventually likely to be replaced by other species as is generally found in the Great Lakes region (Rudoff 1990), and in the absence of major disturbances, their presence at MSH will most likely decline. However, given their lifespan, these *Pinus resinosa* stands are likely to persist at MSH for an extended period of time.

**Conclusion.** Overall, our results suggest that variables related to topography, good indicators of soil moisture, are the primary factors differentiating the major forest types found at MSH. *Quercus rubra* dominates the drier sites, while *Fagus grandifolia* and *Acer saccharum* dominate sites with higher soil moisture. Additionally, high total nitrogen was associated with the greater dominance of *A. saccharum* and low Ca availability was associated with greater dominance of *F. grandifolia*. While we were able to identify the environmental correlates of canopy

composition for the commonly occurring species, there are still pockets of unusual stand types found at MSH that were not assessed in the current study (e.g. stands of *Abies balsamea* and *Thuja occidentalis*). Factors that are not considered in this study, such as the spatial and temporal patterns of past disturbances, may be the key factors determining the patterns of these species. Identifying the factors that give rise to these very restricted forest types at Mont St. Hilaire merit further research.

In the years ahead, forest communities found at MSH are expected to undergo significant changes in species composition mainly due to the following three factors. First, as a consequence of global change, species that currently have their distribution limit just south of MSH are expected to expand their range further north (e.g., *Betula lenta*, Iverson and Prasad 1998). Second, *Acer platanoides*, which is a European species widely planted as a street tree, may invade MSH. *Acer platanoides* has already invaded the New England forests and has been shown to decisively outcompete *Acer saccharum* (Webb et al. 2000, 2001), a native tree that is one of the dominant trees found at MSH. Third, indications of beech bark disease have been first observed at MSH in the late 1980s (Martin Lechowicz, unpublished data), which is likely to influence the abundance and distribution of another dominant tree at MSH, *Fagus grandifolia* (DiGregorio et al. 1999). The current study based on well-marked permanent plots provides a good benchmark against which future studies of forest composition can be compared.

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