

Quantitative and qualitative effects of a severe ice storm on an old-growth beech-maple forest

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Abstract: In a comparison of permanent plots censused in 1997 and again in 2005, we quantified the impact of a severe ice storm on the forest composition and dynamics at 87 circular plots (6-m radius) in an old-growth beech-maple forest in eastern Canada. In 1997, *Acer saccharum* and *Fagus grandifolia* accounted for 78% of the stand basal area. Stand basal area was reduced from 49.1 m²/ha immediately before the ice storm to 31.5 m²/ha eight growing seasons later; total tree density (> 1-cm DBH) decreased from 6,350 to 3,875 stems/ha. *Acer saccharum* and *Fagus grandifolia* still dominated in 2005; they accounted for 74% of the stand basal area. Detrended correspondence analysis of relative dominance ratios at each plot in 1997 and 2005 showed that species composition did not change much during this period for either the understory (1 cm ≤ DBH < 10 cm) or canopy trees (DBH ≥ 10cm). The ice storm did not lead to recruitment of numerous saplings (DBH ≥ 1 cm), but rather perhaps contributed to the growth of already-established saplings. We conclude that the ice storm of 1998 substantially decreased stand basal area and stem density, but did not act to change the overall species composition and diversity of this old-growth beech-maple forest.

Introduction

Ice storms are recurrent, often substantial disturbances in the forests of northeastern and central North America. Return times of ice glaze vary between several to as many as 100 years (Bragg et al. 2003; Cortinas et al. 2004), with ice accumulation sometimes exceeding several centimeters (Proulx and Greene 2001; Bragg et al. 2003). Ice accumulation on trees causes breakage of twigs, branches or even trunks due to mass loading. Many researchers report large biomass loss from forest stands due to ice storms (Bruederle and Stearns 1985; Boerner et al. 1988; Jacobs 2000; Hooper et al. 2001), but studies show that tree's susceptibility to ice damage varies depending on factors such as the size of the tree (e.g., Proulx and Greene 2001; Lafon 2004), the species (e.g., Bruederle and Stearns 1985; Boerner et al. 1988; Rebertus et al. 1997; Hopkin et al. 2003), and the landscape features (Millward and Kraft 2004). The differences in tree's susceptibility to ice storm is believed to have a significant impact on the post-storm stand structure and species composition (Oliver and Larson 1996; Hooper et al. 2001; Greene et al. 2006).

Earlier studies investigating the impact of ice storms have reported contrasting views on how ice storms may affect species composition and diversity in forest stands. The first view is based on the observation that early successional, shade intolerant species are generally more susceptible to ice loading than the late successional species. The damage sustained by any intolerant overstory tree would allow the more tolerant, late successional species to capture the canopy gaps, thereby promoting the stand to dominance by the later successional species (Carvell et al. 1957; Lemon 1961). A contrasting view is that an extensive damage to the canopy creates large gaps allowing more light to reach the forest floor, which allows reproduction and establishment of early

successional species. The rapid reproduction and growth of the shade intolerant species would effectively shift the forest into an earlier successional stage (Downs 1938; Siccoma et al. 1976), and potentially increasing species diversity. Some studies, however, have shown that either scenario may occur, depending on stand structure, species composition, landscape features, as well as upon storm intensity (Sicamma et al. 1976; Whitney and Johnson 1984; De Steven et al. 1991).

Beech-maple forests, where *Acer saccharum* Marshall and *Fagus grandifolia* Ehrh codominate, are widely distributed forest type in eastern North America (Braun 1950; Runkle 1996), and lies in a region where ice storms occur frequently (Changnon 2003). Beech-maple forests are one of the most studied deciduous forests, where various researchers have examined the mechanisms giving rise to the development and the dynamics of this forest type, with particular emphasis on the patterns found in the two dominant species (e.g., Fox 1977; Woods 1979, 1984; Brisson et al. 1994; Poulson and Platt 1996; Beaudet et al. 1999; Forrester and Runkle 2000; Arie and Lechowicz 2002). As with many other forest types, disturbance is believed to play a major role in shaping the structure and the species composition of this forest type. The influence of ice storms on the maintenance of beech-maple codominance has been previously suggested primarily based on information on differences in the species' susceptibility to ice damage immediately after the ice storm (e.g., Bruederle and Stearns 1985; Melancon and Lechowicz 1987; Duguay et al. 2001). However, these conclusions may be underestimating the mortality caused by the storm, because the susceptibility assessed immediately after the ice storm does not take longer- term post-storm mortality into account. Tree mortality years after the storm is somewhat expected given that the damage to the crown decreases the photosynthetic capacity of an individual, thereby making it

difficult for these individuals to maintain a positive carbon balance. Thus to infer any kind of change in stand structure and species composition following ice storms, a longer term monitoring that exceeds investigation of their immediate impact is warranted. Such a study has been previously reported by De Steven et al. (1991), who examined the changes in species composition in beech-maple forests 16 years after an ice storm. They found that stands with a leeward aspect during an ice storm (less damage) displayed an increase in dominance of *Acer saccharum*, while forests with a windward aspect (more damage) experienced increase in the recruitment of intolerant species. Thus, from what little literature there is available, the changes in species composition in beech-maple forest after ice storms appear to be dependent on the intensity of the damage.

In this study, we assessed a 8-year trend in the changes in forest structure and species composition in an old growth beech-maple forest following an extremely severe ice storm that occurred between January 5 and 9, 1998, in Quebec, eastern Ontario, New Brunswick, Nova Scotia, New York, Vermont, New Hampshire and Maine (Kerry et al. 1999; Scarr et al. 2003). This storm was unprecedented not only in its duration and extent, but also in the amount of ice deposited. Glaze ice accumulation was up to 100 mm in the Montreal region (Kerry et al. 1999; Van Dyke 1999), more than double the amount recorded in any previous storms. In 1997, prior to the storm, we had established 87 permanent plots (6-m radius) in an old-growth beech-maple forest at Mont St. Hilaire (MSH) to examine forest dynamics. We took advantage of this pre-storm survey to assess the effects of the 1998 ice storm on the tree community in 2005, eight growing seasons after the disturbance event. Given previous studies, we predicted that the ice storm of 1998 reduced the relative dominance of *Fagus grandifolia* during this period for two reasons: First, previous studies at the study site assessing the impact of the ice storm have

shown that *Fagus grandifolia* was more damaged by the storm than *Acer saccharum* (Melancon and Lechowicz 1987; Duguay et al. 2001), second *Acer saccharum* has a higher growth rate under higher light conditions (Poulson and Platt 1996). Additionally, given the intensity of the ice storm and the results by De Stevens et al. (1991), we also predicted shade intolerant species to increase their presence within the stand. More specifically, we attempted to answer the following questions: (1) Did the ice storm decrease the stand basal area and tree density? If so, by how much? (2) Was the susceptibility to the ice storm different between *Acer saccharum* and *Fagus grandifolia*? (3) Did species composition and diversity change after the ice storm?

Study site

MSH is located approximately 32 km east of Montreal, in southern Quebec, eastern Canada (45°31'N, 73°08'W). MSH is a rugged hill complex standing abruptly above the floor of the St. Lawrence River Valley. The monthly mean temperature in this region ranges between -10.2°C (February) and 20.6°C (August) with the annual mean temperature 5.9°C. Annual precipitation is 1,017 mm (Environment Canada 2002). All climatic data are for St. Hubert Airport [1928 – 1990], 45°31'N, 73°25'W, on the valley floor approximately 20 km west of MSH.

Forests in this region were cleared by European settlers beginning in the mid-17th century, but there were few human disturbances in the forests at MSH. Many of the trees exceed 150 years in age and a few are over 400 years old (Cook 1971). The forests are dominated by deciduous broad-leaved trees such as *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis* Britton, *Acer rubrum* L., *Tilia americana* L., *Fraxinus americana* L., *Populus grandidentata* Michx., and *Quercus rubra* L. and conifers such as

Pinus strobus L. and *Tsuga canadensis* (L.) Carrière (Maycock 1961). Various tree communities occur in relation to local relief and aspect (Arii et al. 2005), but *Acer saccharum* and *Fagus grandifolia* are the common canopy dominants.

Materials and methods

We established 87 permanent circular plots (6-m radius) throughout the mountain in 1997 to examine forest dynamics. These plots were placed on four transects (Arii and Lechowicz 2002). We precisely recorded the geographical coordinates of each plot using a GPS and permanently marked the plot centers. Elevation of the plots ranged between 126 m and 400 m a.s.l., and slope ranged between 0 and 37 degrees. Aspect of the plots also varied in NSWE direction. At each plot, species were identified and diameter at breast height (DBH) was measured for all trees greater than 1-cm DBH in 1997. We re-measured trees in late summer 2005. However, trees were not tagged in the initial census of 1997. Therefore, the precise mortality could not be calculated in this study.

The difference in the susceptibility to the ice storm of 1998 between *Acer saccharum* and *Fagus grandifolia* was examined on the basis of the reduction of the basal area alone, not the density, because the recruitment of trees growing to > 1-cm DBH after the ice storm of 1998 might affect a change in tree density. Total basal area per plot is less affected by recruitment even if many trees recruited over 1-cm DBH. Thus, the change in basal area per plot during 1997 to 2005 was used to compare the species difference in the susceptibility to the ice storm between *Acer saccharum* and *Fagus grandifolia* (stand-level susceptibility). Total basal area per plot in 2005 was regressed against that in 1997 for *Acer saccharum* and for *Fagus grandifolia*, and then the slope and intercept of regressions were compared between the two species by *F*-test and analysis of covariance

(ANCOVA), respectively (Sokal and Rohlf 1995).

Species diversity of each plot was expressed by Shannon-Wiener H' index and Simpson D index. These indices were calculated for each plot in each of 1997 and 2005, and were compared between 1997 and 2005 by paired t -test.

Changes in species composition of all the plots between 1997 and 2005 were examined by detrended correspondence analysis (DCA). Relative dominance ratio of each species at each plot was used for the analysis. The relative dominance ratio (RDR_i) of species i was calculated as,

$$RDR_i = (RD_i + RB_i)/2,$$

where RD_i and RB_i are relative density and relative basal area of species i , respectively, at each plot. The relative dominance ratio of each species was calculated separately for the canopy trees ($DBH \geq 10$ cm) and the understory trees ($1 \text{ cm} \leq DBH < 10$ cm) in each of the 1997 and 2005 data set. Based on this calculation, detrended correspondence analyses were conducted separately for the canopy and understory trees, but both 1997 and 2005 data were included in each of these analyses. Therefore, the axis scores of each plot for both 1997 and 2005 can be shown in the same ordination diagram. Regression analysis was used to detect if species composition changed between 1997 (pre-storm) and 2005 (eight growing seasons post-storm). The DCA score of the axis 1 (or 2) in 2005 was regressed against that in 1997. If relative dominance of each species did not change much or in any consistent trend during the eight years, the regression line should be a 1:1 line. The relationship between the axis score of 1997 and that of 2005 was assessed by reduced major axis regression using the program (S)MATR (Falster et al. 2003).

Results

A total 17 tree species were recorded in 1997 (Table 1). *Acer saccharum* and *Fagus grandifolia* dominated the forest, accounting for 78% of the stand basal area and 75% of the total density in 1997. However, the standard deviation of basal area and density among the 87 plots was large for each species including *Acer saccharum* and *Fagus grandifolia* (Table 1), indicating that each species did not uniformly distribute throughout the mountain.

The stand basal area decreased from 49.2 to 31.5 m²/ha during 1997 to 2005 (36% reduction, Table 1). The total density decreased from 6,350 to 3,875 trees/ha (39% reduction, Table 1). The total density and basal area decreased in most plots (Fig. 1). The reduction of basal area and density was observed in all species, except for the density of *Betula alleghaniensis* (Table 1). The degree of reduction of the density and basal area differed between the two dominant species (*Acer saccharum* and *Fagus grandifolia*); the reduction of the density was much greater in *Acer saccharum* than in *Fagus grandifolia* (49.2% versus 27.2%, Table 1), but the reduction of the basal area was greater in *Fagus grandifolia* than in *Acer saccharum* (46.6% versus 35.7%, Table 1). Total basal area per plot in 2005 at any basal area in 1997 was lower in *Fagus grandifolia* than in *Acer saccharum*, i.e., the slope of regression was not different between the two species (F -test, $F_{1,170} = 0.72$, $P = 0.397$) and the intercept of regression for *Fagus grandifolia* was significantly lower than that of *Acer saccharum* (ANCOVA, $F_{1,171} = 11.8$, $P < 0.001$, Fig. 1d, 1f).

Tree density decreased in most size classes, except for DBH 5 – 10 cm and 10 – 15 cm (Fig. 2a). The largest reduction of tree density was observed at the smallest size class (DBH 1 – 5 cm) for the two dominant species, and the absolute number of the

reduction at this size class was four times greater in *Acer saccharum* than in *Fagus grandifolia* (1,543 trees/ha versus 395 trees/ha, Fig. 2b, 2c). In contrast, the density of *Acer saccharum* increased at DBH 10 – 15 cm class, and that of *Fagus grandifolia* increased at DBH 5 – 10 cm class (Fig. 2b, 2c). The shape of the DBH frequency distribution in 2005 significantly differed from that in 1997 for *Acer saccharum* (Kolmogorov-Smirnov two-sample test, $P < 0.001$, Fig. 2b). Mean DBH increased and the skewness of the DBH frequency distribution decreased in *Acer saccharum* (Fig. 2b). Although the shape of the DBH frequency distribution of *Fagus grandifolia* also differed significantly between 1997 and 2005 (Kolmogorov-Smirnov two-sample test, $P < 0.001$), mean DBH and skewness were almost unchanged (Fig. 2c).

Change in species composition between 1997 and 2005 was examined by detrended correspondence analysis. The overall distribution of plot scores in the ordination diagram was similar between 1997 and 2005 for both the canopy (Fig. 3a, 3c) and understory trees (Fig. 3b, 3d). In particular, plots dominated by *Fagus grandifolia* prior to the ice storm continued to be occupied by *Fagus grandifolia* after the storm, while plots dominated by *Acer saccharum* also remained dominated by *Acer saccharum* post-storm, both in the canopy (Fig. 3c) and in the understory (Fig. 3d). The change in the relative dominance of species during 1997 to 2005 was also analyzed by regression analysis. In both the canopy and understory trees, the relationships between the axis-1 score of 1997 and that of 2005 and between the axis-2 score of 1997 and that of 2005 were close to a 1:1 line; the 95% confidence intervals included 1 for the slope and 0 for the intercept (Fig. 4, Table 2). Species diversity indices (Shannon-Wiener H' index and Simpson D index) were not significantly different between 1997 and 2005 (paired t -test, $P > 0.05$, Fig. 5). Therefore, these results indicated that the species composition and

diversity did not change much or in any consistent trend during 1997 to 2005.

Discussion

The ice storm of 1998 had a significant impact on the total basal area and density, where we observed 36% and 39% reductions in stand basal area and density, respectively, in the eight years following the ice storm. At MSH, there was an immediate biomass loss of about 7 to 10% due to the breakage of trunks and branches (Hooper et al. 2001). The probability of mortality of the trees that suffered such damage is likely to be higher after the storm because crown loss decreases photosynthetic production, which then leads to difficulties in maintaining carbon balance in individual trees. Additionally, the reduction in carbon gain lowers a tree's resistance to fungi and insects, which could also increase the probability of mortality (Rhoads et al. 2002). Hopkin et al. (2003) showed that individuals with severe crown damage (>75 % of crown lost) had 74 % chances of dying within 3 years after the storm, with significant amount of mortality recorded during the first growing season after the storm. We believe the large reductions in stand basal area and density are evidence of the ongoing, deleterious impact of the ice storm.

Assuming that the reduction of the canopy-tree density (DBH > 10 cm) during 1997 to 2005 in this study was due to the death of trees, annual mortality is estimated to be 2.3%/year. In a sample of two 1-ha plots where individual trees were tagged at MSH, annual mortality was 3.2%/year from 1998 through 2000 for hardwood trees and conifers (DBH > 10 cm) (B. R. Hamel, personal communication). If we assume that the mortality rate in the plots we studied was also 3.2%/year between 1998-2000, the mortality between 2001-2005 can be calculated as 1.7%/year. Annual mortality of deciduous hardwood trees and conifers (DBH > 10 cm) is usually ca. 1% in natural forests without

the effects of large disturbances such as ice storms (Parker et al. 1985; Runkle 1990), which suggests that mortality rate remained high years after the ice storm of 1998. Annual mortality after the ice storm of 1998 was estimated as 7.2%/year during 1998 to 2001 in pine plantations (canopy height ranged from 15 to 20 m) in eastern Ontario (Ryall and Smith 2005), and 1.3%/year during 1998 to 2002 for hardwood trees (DBH 23 – 46 cm) in northern United States (Shortle et al. 2003). Thus, the estimated mortality in this study is within the reported values.

The reduction of the tree density at the smallest size class (DBH 1 – 5 cm) indicates that newly recruited saplings grown to > 1-cm DBH were infrequent after the ice storm. By contrast, tree densities at DBH 5 – 10 and 10 – 15 cm mostly increased, suggesting that the ice storm promoted the growth of saplings that were present in the understory prior to the storm (i.e., advance regeneration). This probably occurred because larger canopy trees are generally more prone to ice storm damage (e.g., Rebertus et al. 1997; Duguay 2001; Hopkin et al. 2003; Lafon 2004), which created gaps in the canopy. This allowed more light to reach the understory saplings after the storm, leading to an increase in tree density at DBH 5 – 10 and 10 – 15 cm. The growth of these saplings to sub-canopy trees, however, may have created a closed, but a lower canopy relatively quickly. Arie (2002) showed that gap fraction measured at a height of 60 cm increased from 7.7% in 1997 to 16.6% in 1998 due to the damage by the ice storm, but the gap fraction recovered to the pre-storm levels by 2000. This relatively quick closure of the gaps may have limited the recruitment of saplings to the smallest size class (DBH 1 – 5 cm).

The degree of reduction of the density and basal area differed between the two dominant species; the reduction of the density was much greater in *Acer saccharum* than

in *Fagus grandifolia* (49.2% versus 27.2%), but the reduction of the basal area was greater in *Fagus grandifolia* than in *Acer saccharum* (46.6% versus 35.7%). We believe this discrepancy was found primarily because of how the understory trees of *Acer saccharum* and *Fagus grandifolia* are distributed at MSH. In general, *Acer saccharum* understory trees tend to be found densely under a relatively open canopy, while *Fagus grandifolia* understory trees, which are mostly of sprout-origin, is found close to a “parent tree”. Thus while *Fagus grandifolia* understory trees may have been sheltered by the parent tree, the understory trees of *Acer saccharum* could have received considerable amount of ice glaze. Because these understory trees of *Acer saccharum* are abundant, it may have resulted in substantial reduction in the density of *Acer saccharum*, despite the lower reduction in basal area. If we examine the only the larger sized tree, we find that *Fagus grandifolia* was damaged more by the ice storm of 1998. This result is in agreement with many of the previous studies (Melancon and Lechowicz 1987; Duguay et al. 2001; Rhoads et al. 2002; Hopkin et al. 2003), however, it is not clear why the susceptibility to ice storms was higher in *Fagus grandifolia* than in *Acer saccharum*. Rebertus et al. (1997) reported that an ice storm damaged more trees in lower slopes for a given species, probably because cold-air drainage allows ice to persist longer there. At MSH, *Fagus grandifolia* is distributed mainly on the lower slopes near the lake located in the center of MSH, while *Acer saccharum* dominates the upper slopes or hilltops (Arii et al. 2005); therefore, this difference in elevation could have caused more damage on *Fagus grandifolia*. However, we found no significant difference in percent reduction of basal area per plot between high elevation (> 280 m a.s.l.) and low elevation (< 280 m a.s.l.), for both *Acer saccharum* and for *Fagus grandifolia* (data not shown), probably because of the small elevation range in this study site (126 m to 400 m a.s.l.). Thus, the

plot elevation is unlikely to have brought about the species difference in the susceptibility to the ice storm. *Fagus grandifolia* may also experience heavier damage if they are infected with beech bark disease (Rhoads 2002), but at MSH, there are no notable cases of the disease. An alternative reason why species differences in susceptibility may arise is the occurrence of branch sprouting. Previous studies have shown that branch sprouting is more commonly observed in *Acer saccharum* than in *Fagus grandifolia* after ice storms (Duguay et al. 2001; Brommit et al. 2004). The ability of *Acer saccharum* to branch sprout may have allowed individuals to fix enough carbon to maintain a positive carbon balance, which may have led to differences in mortality after the storm.

If we assume that spatial distribution of *Acer saccharum* and *Fagus grandifolia* were random, the species difference in susceptibility to ice storms may have large effects on the species dominance after ice storms, i.e., repetition of ice storms accelerates the exclusion of the species with higher susceptibility to ice storms. Given that *Fagus grandifolia* suffered more damage at our study site, we expected *Acer saccharum* to become more dominant (De Stevens et al. 1991; Lafon 2004). However, our study showed that plots dominated by *Acer saccharum* prior to the storm continued to be dominated by *Acer saccharum* after the storm, while the plots dominated by *Fagus grandifolia* also remained to be dominated by *Fagus grandifolia*, both in the canopy and in the understory. This pattern may arise due to the spatial segregation of *Fagus grandifolia* and *Acer saccharum* at our study site, which is brought about primarily by edaphic factors (Arii and Lechowicz 2002). If the two species are spatially segregated, the differences in susceptibility will not yield significant changes in species dominance, as the damaged trees will simply be replaced by its own species. Thus the spatial pattern of *Fagus grandifolia* and *Acer saccharum* may have resulted in little changes in

dominance after the ice storm.

While the ice storm of 1998 caused significant damage to the trees and opened up the canopy (Hooper et al. 2001), we did not detect any significant increase in the shade-intolerant species; all species showed a decrease in both basal area and density. The only exception is *Betula alleghaniensis*, which showed an increase in density, however, the difference is minimal and it is not expected to influence species composition. In a beech-maple forest studied by De Stevens et al. (1991) shade-intolerant species showed an increase in abundance, particularly at locations hard hit by the storm. This is contrary to our finding but their study site included many shade intolerant species in the canopy prior to the storm, which may have allowed them to capture the opened canopy (De Stevens et al. 1991). At our site, beech and sugar maple dominated the canopy prior to the storm, and this may have limited the successful colonization and establishment of the shade-intolerant species after the storm.

This study concluded that (1) the severe ice storm of 1998 substantially decreased the stand basal area and total density of this forest, (2) the susceptibility to the ice storm was higher in *Fagus grandifolia* than in *Acer saccharum* (large sized trees), and (3) the ice storm had little influence on species composition and diversity, the dominance of *Acer saccharum* and *Fagus grandifolia* was maintained after the ice storm, most likely because of the spatial segregation between the two species. Thus, our working hypothesis, that the severe ice storm of 1998 might reduce the relative dominance of *Fagus grandifolia*, was rejected. While some of earlier studies suggest increase in shade intolerant species, effectively shifting the forest into an earlier successional stage after an ice storm (Downs 1938; Siccama et al. 1976), we did not observe this pattern. Rather, the ice storm appeared to accelerate the turnover of the canopy trees, dominated by *Fagus*

grandifolia and *Acer saccharum*.

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Figure legends

Fig. 1. Changes in tree density and basal area per plot between 1997 and 2005 for total (a, b), *Acer saccharum* (c, d), and *Fagus grandifolia* (e, f) in an old-growth beech-maple forest on Mont St. Hilaire, eastern Canada. A dotted line indicates a 1:1 line.

Fig. 2. Frequency distribution of DBH for total (a), *Acer saccharum* (b), and *Fagus grandifolia* (c) in an old-growth beech-maple forest on Mont St. Hilaire, eastern Canada. Solid and open bars indicate the tree density in 1997 and that in 2005, respectively. M_{97} and M_{05} are mean DBH in 1997 and that in 2005, respectively, and S_{97} and S_{05} are the skewness of the DBH frequency distribution in 1997 and that in 2005.

Fig. 3. Ordination of plots and species by detrended correspondence analysis for canopy trees and understory trees. Relative dominance ratio of each species at each plot was used for the analysis. (a) and (b) represent species and site scores (dots) for analysis based on canopy trees and understory trees, respectively. Species abbreviation is the same as in Table 1. (c) and (d) are diagrams illustrating the changes in site scores before and after the ice storm. The origin of the arrow gives the site scores prior to the ice storm (1997), where as the head indicates the post-storm values (2005).

Fig. 4. Relationships between the axis score of 1997 and that of 2005 for canopy trees (a, b) and understory trees (c, d). Regression equations are listed in Table 2.

Fig. 5. Shannon –Wiener H' index (a) and Simpson D index (b) in 1997 and 2005.

Vertical bars indicate positive standard deviation.

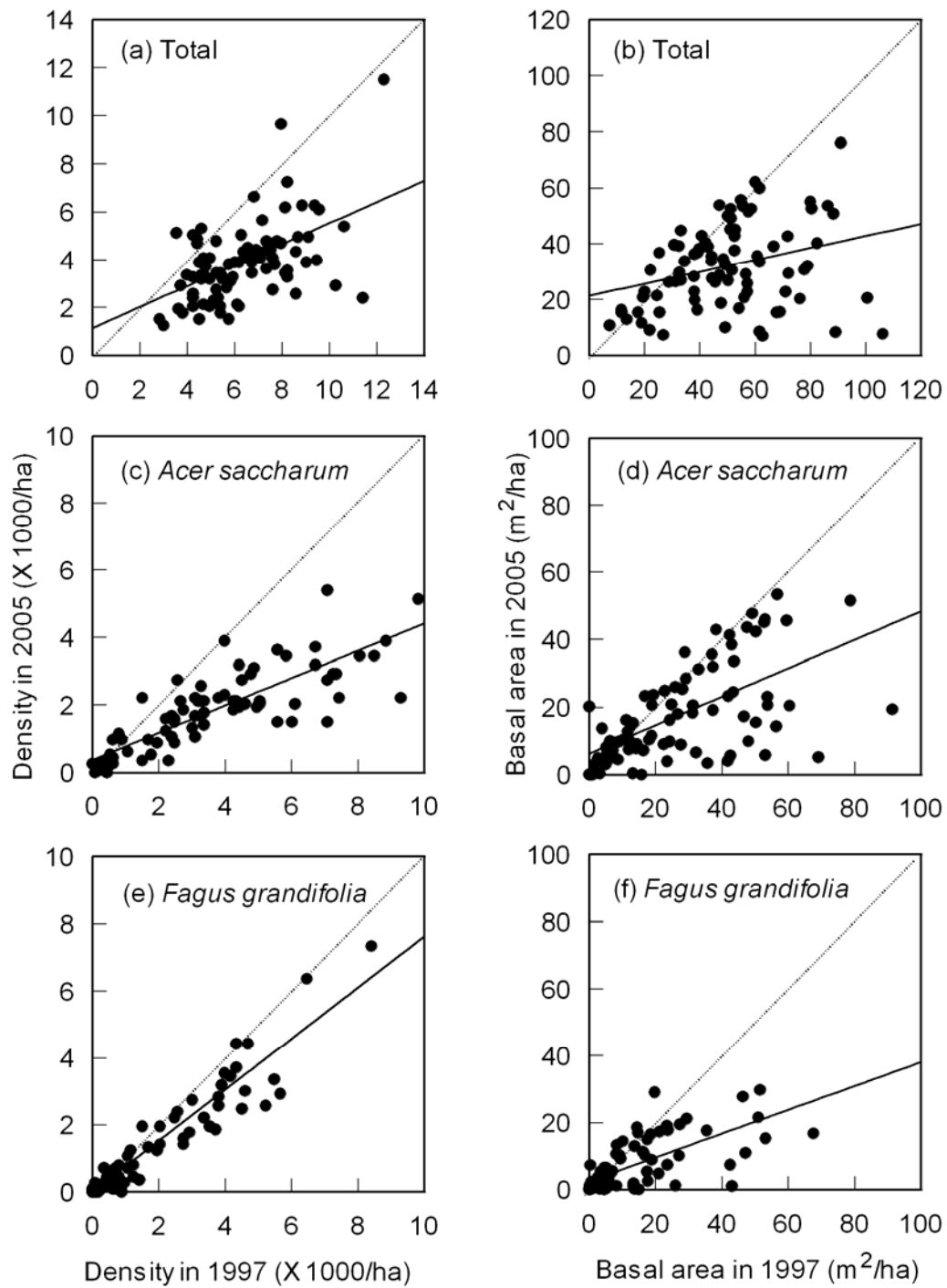


Fig. 1

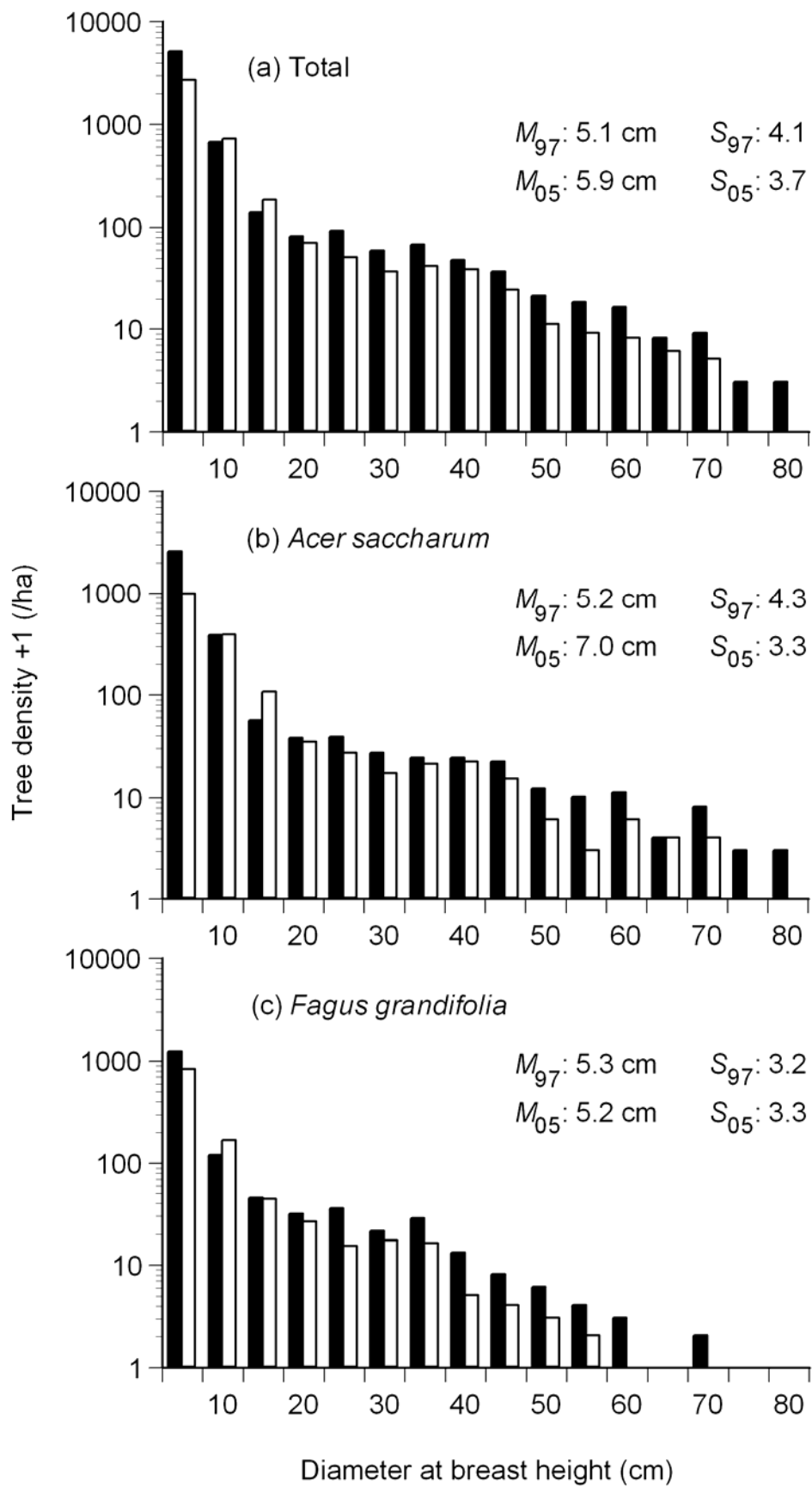


Fig. 2

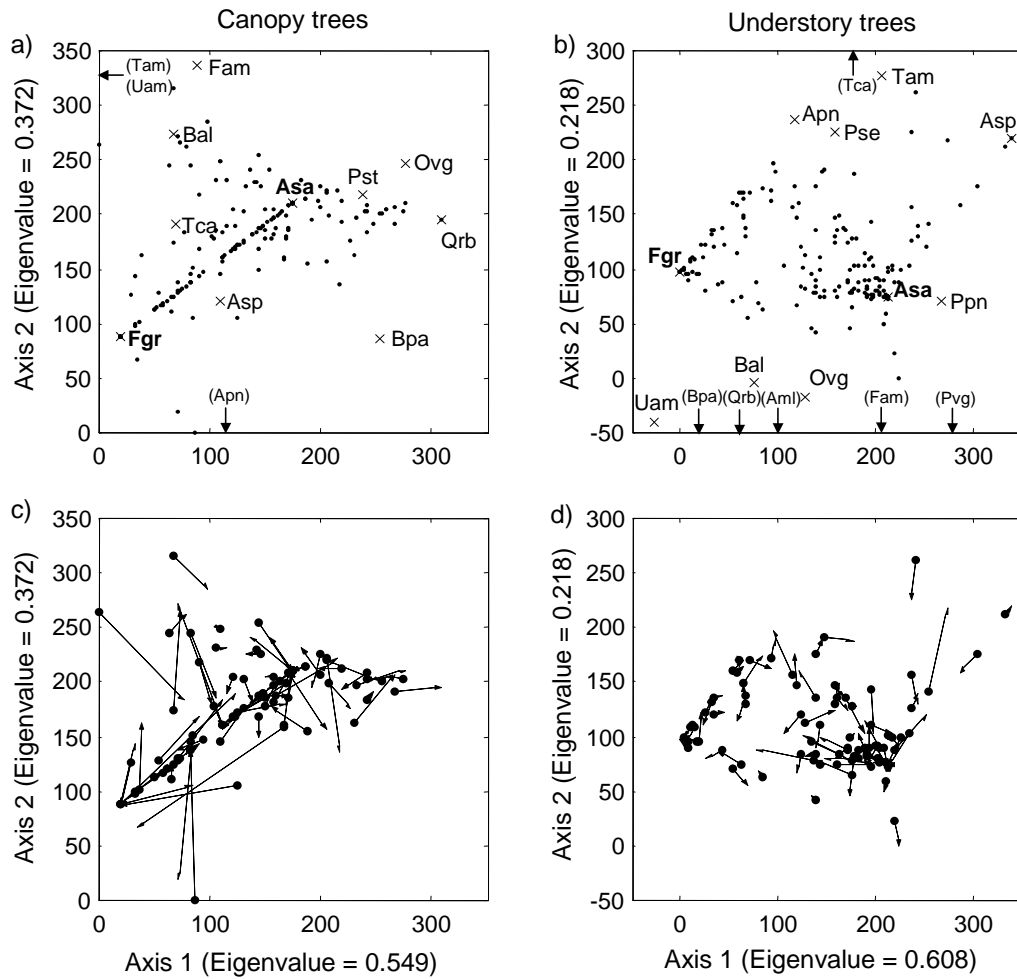


Fig. 3

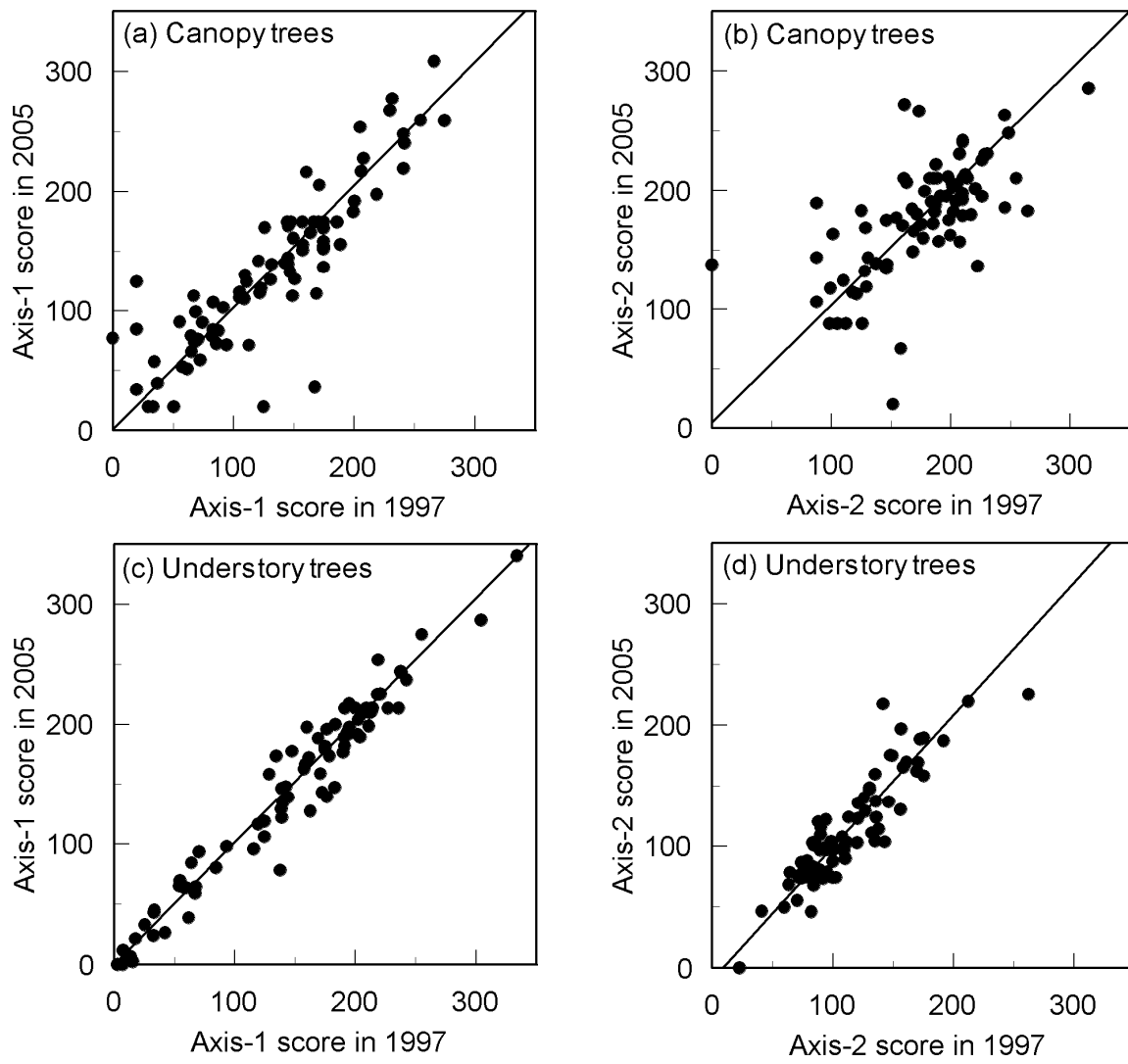


Fig. 4

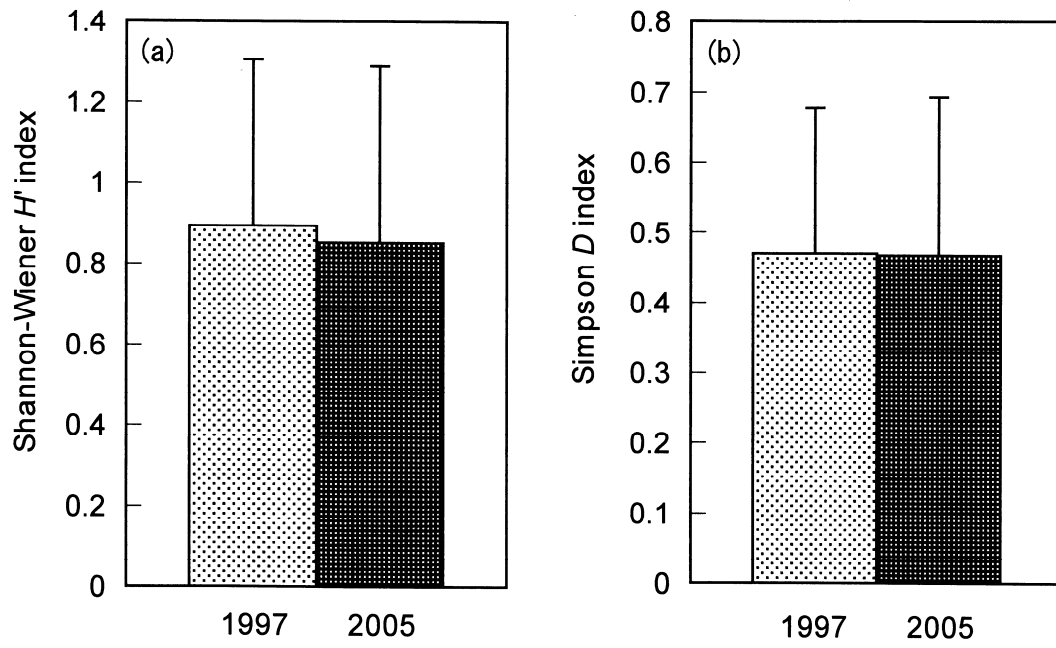


Fig. 5.

Table 1. Changes in basal area and density of trees (larger than 1-cm DBH) between 1997 and 2005 at 87 circular plots (6-m radius, total 0.984 ha) in an old-growth beech-maple forest in Mont St. Hilaire, eastern Canada. Numbers in parentheses indicate standard deviation among the 87 plots.

Species	Abbreviation	Basal area (m ² /ha)		Density (trees/ha)	
		1997	2005	1997	2005
<i>Acer pensylvanicum</i> L.	Apn	0.88 (1.68)	0.78 (1.24)	970 (1,268)	680 (1,016)
<i>Acer saccharum</i> Marshall	Asa	26.54 (20.47)	17.06 (14.01)	3,205 (2,597)	1,629 (1,238)
<i>Acer spicatum</i> Lam.	Asp	0.26 (0.92)	0.10 (0.28)	195 (519)	159 (447)
<i>Amelanchier</i> spp.	Aml	0.04 (0.16)	0.03 (0.14)	56 (241)	44 (200)
<i>Betula alleghaniensis</i> Britton	Bal	1.26 (5.16)	0.80 (3.47)	47 (131)	53 (168)
<i>Betula papyrifera</i> Marshall	Bpa	0.32 (1.38)	< 0.01 (0.05)	5 (21)	1 (9)
<i>Fagus grandifolia</i> Ehrh.	Fgr	11.94 (15.19)	6.37 (4.46)	1,531 (1,852)	1,114 (1,487)
<i>Fraxinus americana</i> L.	Fam	1.35 (3.54)	1.24 (7.71)	52 (102)	36 (87)
<i>Ostrya virginiana</i> (Miller) K. Koch	Ovg	0.45 (1.13)	0.26 (0.69)	147 (341)	81 (225)
<i>Pinus strobus</i> L.	Pst	0.40 (2.64)	0.26 (2.05)	4 (23)	2 (13)
<i>Prunus pensylvanica</i> L.f.	Ppn	< 0.001 (0.02)	0 (0)	1 (9)	0 (0)
<i>Prunus serotina</i> Ehrh.	Pse	< 0.001 (< 0.01)	0 (0)	1 (9)	0 (0)
<i>Prunus virginiana</i> L.	Pvg	0.02 (0.11)	0.01 (0.04)	36 (269)	13 (99)
<i>Quercus rubra</i> L.	Qrb	4.50 (10.02)	4.20 (10.37)	46 (102)	40 (97)
<i>Tilia americana</i> L.	Tam	0.47 (2.28)	0.34 (1.51)	40 (90)	17 (46)
<i>Tsuga canadensis</i> (L.) Carrière	Tca	0.37 (2.97)	0.05 (0.31)	12 (59)	6 (35)
<i>Ulmus americana</i> L.	Uam	0.31 (2.89)	0 (0)	2 (13)	0 (0)
Total		49.11 (21.39)	31.50 (15.18)	6,350 (1,962)	3,875 (1,645)

Table 2. Regression equation of the relationship between the DCA axis scores in 2005 and those in 1997 for canopy trees ($DBH \geq 10$ cm) and understory trees ($1 \leq DBH < 10$ cm). Values in parenthesis indicate the 95% of the confidence intervals. Reduced major axis regression was used for the calculation. All regressions are significant at the level of 1%.

Size class	y	x	Slope	Intercept	R^2	n
Canopy	A1 ₀₅	A1 ₉₇	1.026 (0.885 ~ 1.167)	1.1 (-22.1 ~ 19.9)	0.77	87
Canopy	A2 ₀₅	A2 ₉₇	0.971 (0.762 ~ 1.181)	6.2 (-32.6 ~ 45.0)	0.43	87
Understory	A1 ₀₅	A1 ₉₇	1.025 (0.963 ~ 1.087)	-4.1 (-14.4 ~ 6.3)	0.96	87
Understory	A2 ₀₅	A2 ₉₇	1.101 (0.970 ~ 1.233)	-11.6 (-26.7 ~ 3.6)	0.83	87

A1₀₅: axis-1 score in 2005, A1₉₇: axis-1 score in 1997, A2₀₅: axis-2 score in 2005, A2₉₇: axis-2 score.

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