Differences in the damage caused by glaze ice on codominant Acer saccharum and Fagus grandifolia

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A severe glaze ice storm had greater destructive impact on Fagus grandifolia than on codominant Acer saccharum trees in a mature southern Quebec forest. Both the numbers and total biomass of major branches lost by beech were significantly greater than by sugar maple compared with the contribution of each species to the canopy composition. This greater ice damage to beech suggests that reciprocal replacement processes involving beech and maple seedlings cannot completely account for the maintenance of beech—maple codominance in northern forests subject to relatively frequent ice storms. We hypothesize that the ability of beech to root sprout is important in compensating for its greater susceptibility to ice damage and contributes to the maintenance of beech—maple codominance in northern forests.


Les dommages subis par Fagus grandifolia suite à une importante tempête de verglas se sont avérés relativement plus sérieux que ceux de l’espèce codominante Acer saccharum dans une forêt mature du Québec méridional. Par rapport à la contribution de chaque espèce dans la strate arborescente, le nombre et la biomasse totale des branches perdues par le hêtre furent significativement plus élevés que ceux de l’ébèbe à sucre. L’effet relativement plus destructeur du verglas sur le hêtre suggère que le principe du remplacement réciproque ne peut tenir compte de façon exclusive du maintien de la codominance hêtre—ébèbe dans les forêts méridionales sujettes aux fréquentes tempêtes de verglas. Nous formulons l’hypothèse que la capacité de reproduction végétative (par grimpement) du hêtre devient un élément compensatoire important à la perte plus lourde en branches causée par les tempêtes et qu’il contribue au maintien de la codominance hêtre—ébèbe dans les forêts méridionales.

Introduction

Ice storms are a frequent disturbance in the hardwood forests of north central and northeastern United States and adjacent Canada. Ice storms develop when a warm, moist air mass passes over ground level air with temperatures below freezing; under these conditions supercooled rain can fall that freezes on contact with surfaces to form glaze ice (Lemon 1961). Such storms can increase the canopy weight up to 100-fold (Rogers 1922) with consequent widespread breaking of branches (Downs 1938; Siccama et al. 1976; Whitney and Johnson 1984; Bruederle and Stearns 1985). Branch losses directly disrupt canopy form, can initiate debilitating fungal infections, and in the case of severe damage can kill trees outright (Spaulding and Bratton 1946; Carvell et al. 1957). Major ice storms, with a return time on the order of 20–100 years (Lemon 1961), are considerably more frequent than comparably destructive events like major windstorms and fire, which have return times on the order of 100–1000 years in northern hardwood forests (Henry and Swan 1974; Lorimer 1977; Bormann and Likens 1979; Canham and Loucks 1984).

Although past surveys have established that hardwood tree species differ in their susceptibility to glaze damage, there is conflicting evidence on the susceptibility of the two species most frequently codominant in northern hardwood forests: beech (Fagus grandifolia Ehrh.) and sugar maple (Acer saccharum Marsh). Both species are traditionally recognized as of intermediate susceptibility compared with other hardwood species (Lemon 1961). Siccama et al. (1976) reported sugar maple to be slightly more susceptible to ice damage than beech, Downs (1938) found beech slightly more susceptible than sugar maple, and Bruederle and Stearns (1985) found both species to be essentially equally susceptible. These studies involved all canopy species and did not focus on ice damage to beech and maple in forests where the two species were codominant and had comparable size-class distributions. We therefore studied the cumulative impact of two consecutive ice storms on codominant beech and maple trees in a mature forest at Mont St. Hilaire, Quebec, near the northern limit of deciduous forest in eastern North America. Our goal was to assess any differences in ice damage to beech versus maple that might influence the mechanisms underlying the maintenance of beech—maple codominance in this northern forest.

Materials and methods

On December 13 and 14, 1983, a severe ice storm struck the Montreal region, with glaze accumulation of 15 mm accompanied by winds up to 18 km/h (Hydro-Quebec, unpublished data). A second storm of lesser magnitude occurred in February 1984, but most damage was caused by the first storm. These storms stripped even large branches from trees in exposed forests on the slopes of Mont St. Hilaire. In many localities, including our study site, only bare trunks were left standing on some trees. The two previous ice storms of comparable magnitude in the region had occurred in February 1961 and December 1942 (Powe 1969; Environment Canada 1983).

We measured damage to beech and maple at an approximately 1-ha site on the north base of Lake Hill at Mont St. Hilaire immediately adjacent to the shore of Lac Hertel (Maycock 1961; Rouse and Wilson 1969). The site is dominated by a mature canopy of codominant beech and sugar maple growing on glacial till and is similar to forests that have occupied the site since soon after the retreat of the Wisconsin ice (Terasmae and Lasalle 1968). Similar forests on the opposite shore of Lac Hertel have been described in detail (Holland 1971a, 1971b) and studied with regard to the reciprocal replacement model of beech—maple codominance (Cyrpher and Boucher 1982).

We censused the numbers of trunks and fallen branches of beech and sugar maple along a series of 38 five metre wide belt transects running at approximately 10-m intervals from the lakeshore to the beginning of the steep slope of Lake Hill. The identification and

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diameter at breast height were tallied for all live trunks greater than 8 cm diameter. We recorded the species and diameter at the broken end of all newly fallen branches that were at least 5 cm in diameter and had their broken end within the belt transect.

If beech and sugar maple are equally susceptible to ice damage, we expect the amount of branch material found on the forest floor to be proportional to the amount of each species in the previously intact canopy. We have two measures of the amount of fallen material: the numbers of branches and the sum of their basal diameters. Because there was little evidence that branches broke into pieces with 5 cm or greater diameter on impact, we have a good index of the actual numbers of major branches lost in the storm. The summed diameters of these fallen branches provide a complementary index which allows for the possibility that the two species might differ in the size as well as the numbers of branches lost. The basal diameter of a branch segment is allometrically proportional to the photosynthetic tissues it supported (Whittaker et al. 1974).

We predicted available branch material in the previously intact canopy in two ways: from the sum of diameters at breast height for each species and from a species-specific estimate of branch surface area as a function of diameter at breast height (Whittaker et al. 1974). Diameter at breast height has traditionally been used as an index of canopy composition and dominance, and branch surface area is directly related to the potential to intercept and accumulate glaze. These observed and predicted values were used in a series of chi-square tests to evaluate whether or not beech and maple differ in their susceptibility to glaze damage. All analyses were done with version 6.2 of SAS (SAS Institute 1985) on an IBM XT-type microcomputer.

Results and discussion

Beech and maple are codominant at our study site with *Quercus rubra* L., *Betula alleghaniensis* Britt., *Fraxinus americana* L., and *Tilia americana* L. the other important canopy trees. We encountered 114 maples and 117 beeches in our transects. The median diameter at breast height (DBH) of sugar maple was 30.8 cm, with the largest tree 80 cm. The median DBH of beech was 28.9 cm with the largest tree 66 cm. The frequency distribution of DBH was similar for both species, although beech has somewhat more small individuals (Fig. 1). Cook (1971) has shown that the beech and maple trees in this forest also have comparable age distributions.

Within our belt transects beech lost 253 branches compared with 216 for sugar maple. The basal diameters of fallen branches of beech averaged 8.4 compared with 7.5 cm for sugar maple. The largest beech branch lost had a basal diameter of 43.5 compared with 23.4 cm for the largest sugar maple branch. The frequency distributions of basal diameters for the fallen branches are similar for both species (Fig. 2).

The proportionate numbers of individual branches lost by beech was significantly greater than by sugar maple compared with expectations based on either summed trunk diameters (chi-square = 4.90, p = 0.027) or the estimated total of branch surface area (chi-square = 4.44, p = 0.035). Similarly, the proportionate sum of branch diameters lost by beech was greater than by sugar maple compared with expectations based on either trunk diameters (chi-square = 96.0, p < 0.001) or branch surface area (chi-square = 90.2, p < 0.001). By any available measure the negative impact of glaze ice was thus significantly greater on beech than on sugar maple.

In northern forests where ice storms are relatively frequent, this greater susceptibility of beech to ice damage suggests that more canopy gaps will be created by loss of beech trees than maple trees. The reciprocal replacement model (Woods 1979) currently used to account for the maintenance of codominance in beech–maple forests cannot explain the maintenance of codominance in a disturbance regime characterized by such relatively frequent and differential impacts on the codominant species. The reciprocal replacement model postulates that sugar maple seedlings survive better in the shade of beech and vice versa; thus, there is a high likelihood that the death of a canopy tree will release saplings of the opposite species to occupy the newly opened gap (Woods 1979, 1984; Cypher and Boucher 1982; Runkle 1981, 1984). If reciprocal replacement through saplings originating from seed was the only mechanism by which juvenile beech or maple could capture a canopy gap, we would expect beech to lose codominance in northern forests subject to repeated ice damage during the typical life-span of beech and maple trees.

The root sprouts that occur in beech (Held 1983; Jones and Raynal 1986) but not in maple (Fayle 1964) may compensate for the greater susceptibility to ice damage in beech and provide a supplemental mechanism underlying the maintenance of beech–maple codominance in northern forests. Root sprouts can potentially draw on resources in the surviving tissues of their parent tree to accelerate growth after an ice storm opens the canopy. We hypothesize that in the aftermath of an ice storm, sugar maple seedlings established under a beech canopy will not grow as quickly as beech sprouts and will therefore be less likely to occupy gaps created by ice damage. This hypothesis is in accord with Held's (1983) observation that the proportion of beech reproduction from root sprouts increases in more severe climatic regimes. The relative contribution of maple seedlings, beech seedlings, and beech sprouts to capture of canopy gaps created by ice damage in northern beech—
maple forests merits investigation to test this compensation hypothesis.

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