Impacts of a catastrophic ice storm on an old-growth, hardwood forest

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"You think (do you not?) that you have
only to state a reasonable case and people must listen and act upon it at once.
It is just this conviction that makes you so unpleasant."

F. M. Cornford,
Microcosmographica Academica:
A Guide for the Young Academic Politician
(Cambridge: Bowes and Bowes, 1908).

General Abstract

I investigated the impacts of a catastrophic ice storm on the old-growth, hardwood forests of Mont St. Hilaire, Quebec. The mass of litter resulting from the ice storm of January 1998 was estimated using equations relating the basal diameter of fallen branches with branch mass for each of the ten major species. The ice storm of January 1998 produced 19.9 metric tonnes or 33.6 m^3 of woody-litter per hectare. These losses of woody biomass are approximately 20 times greater than what is expected in a normal year and correspond to between 7-10% of the total above-ground biomass of the pre-storm forest. This level of litter production positions the ice storm of 1998 as the most severe ice storm on record and amongst the most powerful forms of climatic disturbance experienced in forested ecosystems.

I also investigated differences in the magnitude and nature of the biomass losses sustained by each study species. While the magnitude of biomass lost by the study species was not related to either wood strength or stiffness, the nature of the biomass lost was. All species primarily lost branches less than 5 cm in diameter, but it was the relatively few branches greater than this diameter that accounted for the majority of downed biomass. Smaller branches were lost in relation to differences in species-specific mechanical properties, while larger branches appear to be lost in response to weakening by decay and other age-dependent factors. The ecological and evolutionary implications of these results emphasise the need for an analysis of the interplay between mechanical properties and canopy architecture in determining overall susceptibility to ice damage.

Résumé

J' ai étudié l'impact d'une tempête de verglas catastrophique sur les forêts de bois dur du mont St-Hilaire, Québec. La quantité de litière provenant de la tempête de verglas de janvier 1998 a été évaluée en utilisant des équations reliant le diamètre basal des branches tombées et leur poids pour 10 espèces principales. La tempête de verglas de janvier 1998 a produit 19.9 tonnes métriques ou 33.6 mètres cubiques de litière ligneuse par hectare. Ces pertes de biomasse ligneuse sont environ 20 fois plus élevées que ce qui est attendu pour une année normale. Ceci correspond à 7-10% de la biomasse totale de la forêt avant la tempête. Ce niveau de production de litière situe la tempête de verglas de 1998 dans les records de domage et en fait l'une des plus puissantes formes de perturbations climatiques jamais vu les écosystèmes forestiers.

J'ai aussi étudié les différences entre la qualité et la nature des pertes de biomasse pour chaque espèce étudiée. La nature de la biomasse perdue s'est avérée reliée à la rigidité de l'espèce, contrairement à la quantité. Toutes les espèces étudiés ont d'abord perdu des branches ayant un diamètre inférieur à 5 cm. Cependant, ce fut la relativement petite quantité de branches ayant un diamètre supérieure à 5 cm qui a formée la majorité de la biomasse perdue. Les plus petites branches ont été perdues en relations avec la diffèrence des proprietés méchaniques spécifiques aux espèces. Les plus grosses branches semblent être perdues en réponse à des faiblesses dues à la dégradation de la matière et d'autres facteurs dépendant de l'âge. Les implications écologiques et évolutionnaires de ces résultats soulèvent le besoin d'analyser l'interrelation entre les proprietés méchaniques et l'architecture de la canopé, afin de déterminer la susceptibilité des domages causés par la glace.

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Preface

In accordance with the rules and regulations set out in the "Guidelines for Thesis Preparation", I am obligated to note that the final two chapters of this thesis will form the basis for articles to be submitted to peer-review journals. Chapter 2 will be co-authored with Ken Arii and Martin J. Lechowicz while Chapter 3 will be co-authored with Martin J. Lechowicz alone. The position of Ken Arii and Martin Lechowicz as co-authors reflects the assistance provided by both individuals in the collection of data and editing of manuscripts. Specifically, Ken Arii generously provided access to his permanent forest dynamics plots and assistance in the field while Martin J. Lechowicz exercised a general editorial and supervisory capacity throughout the preparation of the thesis.

Acknowledgments

Although this thesis bears my name alone, it represents the generous intellectual contributions of many people. Foremost, without the wise counsel of Professor Martin Lechowicz this project most certainly would not have come to fruition.

Assistance with data collection and general fieldwork were provided by Pavel Parfenov, Ken Arii, and Christian Marks. Ken Arii also generously provided access to the permanent study plots that he established on Mont St. Hilaire in the summer of 1997. Helpful statistical advice, Maoist indoctrination, and tutelage in the finer points of SAS programming were provided by Wang Zhang Ming. Many thanks go to Karl Niklas of Cornell University, who discussed the ideas in Chapter 3 with me at short notice, and to Benôit Coté, who kindly provided information on primary productivity. Virginie Bachand Lavallée very graciously translated the general abstract into French. My largest debt of gratitude goes to Sylvia Lee, whose companionship provided a welcome and often much needed respite from the field and lab.

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Although their contributions of love and patience warrant a much better product, I dedicate this thesis to my parents and grandparents who instilled in me a love of nature and of learning.

Finally, while many people provided me with assistance during the preparation of this thesis, its inaccuracies and inadequacies are my responsibility alone.

CHAPTER 1

General Introduction

"When I see birches bend to left and right
Across the lines of straighter darker trees,
I like to think some boy's been swinging them.
But swinging doesn't bend them down to stay.
Ice-storms do that."

Robert Frost,
Birches, from Mountain Interval
(New York: Henry Holt, 1916)

I. The influence of ice storms on forested landscapes: An introduction to the phenomenon and a review of the literature

Ice storms are a recurring form of disturbance in most deciduous forests of North America (Abell 1934, Bennett 1959, Lemon 1961). A gradient of increasing storm frequency and intensity extends across the continent from southwest to northeast with most of the Eastern Deciduous Forest Biome falling in a zone of heavy to moderate glaze occurrence (Lemon, 1961). The regions most affected by ice storms are the Northeast and Midwest of the United States and adjacent Canada (Melancon and Lechowicz, 1986).

Ice storms, also referred to as glaze-ice storms, are regional climatic events that vary in severity as well as frequency (Hauer *et. al.*, 1993). The glaze itself is a clear layer of ice formed when supercooled precipitation freezes on the surface of ground-level objects (Haynes, 1947; Lemon, 1961). Glaze accumulation occurs when a relatively warm air mass encounters ground level temperatures below 0° Celsius (Christie and Chartier, 1943). As rain falls from a warm air mass through layers of colder air near ground level it reaches the earth supercooled and forms glaze on impact. The extent of glaze formation depends on the specific heat and thermal conductivity of the objects struck at ground level (Lemon, 1961).

As a result of their unpredictability, our understanding of the effects of ice storms on forests and forest trees has largely been inferred from *post facto* observations of damage to forests of unknown composition and structure (Bruederle and Stearns, 1985). Most information on the effects of ice storms on forested landscapes and on forest trees has either been descriptive or has relied upon observation of open-grown individuals (Bruederle, 1978). The characteristic unpredictability of ice storms combined with difficulties associated with quantifying ice storm damage are in part responsible for ice storms receiving less attention than other forms of forest disturbance (Bruederle, 1978). Fires and wind storms have instead occupied most of the resources of those interested in the ecology of disturbance (Perley, 1891; Loucks, 1970). Nevertheless, over the course of the twentieth century a small but eclectic body of literature on the subject of ice storms has accumulated.

Early work on ice storms suggested that they were a major factor in shaping the forests of the Atlantic coast of America. Ashe (1918, p. 374) proposed that "over certain sections (of the Masanutten and Shenandoah Mountains of Virginia), the general appearance of the forest seems to indicate that practically all of it has been injured by ice during some period of its existence." Early investigators focused on describing the effects of ice storms and considered what role they might play in the development of the forests of the northeastern United States (Harshberger; 1904; Illick, 1916). Although these studies were largely qualitative they had the advantage of drawing on observations taken over wide areas and in many different communities in a period when forest harvesting was less ubiquitous than now (Seischab *et. al.*, 1993).

Beginning in the 1920's, quantitative work was begun by Rogers (1922, 1923, 1924) and was followed by Croxton (1939) and Deuber (1940). These authors focused on the species-specific effects of glaze deposition but did not differentiate between open- and forest-grown individuals. Abell (1934), McKellar (1942), and McCullough (1943) looked not only at the susceptibility of species to damage but also at the nature of the damage that they sustained. Campbell (1937), Sleeth (1938), and Campbell and Davidson (1940) considered the future of damaged forest stands following ice storms by looking at broken branches and the infection of tree wounds. The contribution of Downs (1938), who studied the role of ice storms in forest succession, was of great importance as it marked the beginning of a more ecological interpretation of the role of these events in forested landscapes. Downs (1938) characterised the meteorological and biological aspects of a storm that struck a birch-beech-maple-hemlock forest in Pennsylvania and New York.

Beginning in the 1950's, Bennett (1959) and Lemon (1961) summarised previous studies regarding ice storms and attempted to create a synthesis of past findings. Lemon (1961) focused on the biological aspects of susceptibility to ice damage and collated existing data on species susceptibility while Bennett (1959) dealt primarily with the meteorology of ice storms and provided an overview of glaze formation and occurrence in North America and Europe. Carvell *et. al.* (1959) in turn investigated the effects of glaze on the development of hardwoods in the Appalachians of West Virginia and focused on the management implications of ice storm damage to forests. They found that trees in heavily thinned plots sustained more damage than trees in less thinned plots and that the degree of thinning was proportional to the extent of damage because of the greater exposure of crowns in thinned stands to ice accumulation (Carvell *et. al.*, 1957).

In 1976, Siccama *et. al.* looked at the role that vines of the genus *Vitus* play in determining the susceptibility of trees to ice storm damage and found that trees that were heavily infested sustained more ice storm damage. Around the same time a comprehensive thesis on damage following a Wisconsin ice storm was produced (Bruederle, 1978). In the 1980's Whitney and Johnson (1984) investigated the effects of heavy glaze accumulation on tree mortality and reproductive patterns while Bruederle and Stearns (1985) studied the patterns of damage resulting from an ice storm in a southern Wisconsin mesic forest and summarised the earlier results of Bruederle's thesis work (1978).

The work of Bruederle (1978) and Bruederle and Stearns (1985) was the first to quantify the extent of litter production arising from an ice storm. They found that 19 m^3 ha^{-1} of litter were produced as the result of the accumulation of 10-31 mm of glaze ice in a mesic, hardwood forest in southern Wisconsin (Bruederle, 1978; Bruederle and Stearns, 1985). They also used hemispheric photographs to evaluate changes in canopy openness and were able to determine that topographic and climatic factors were important in influencing the extent of ice storm damage. Slope and aspect as well as wind were found to be of particular importance in determining the extent of ice storm damage to individual trees. Bruederle (1978) also attempted to find correlations between the mechanical attributes of various species and their susceptibility to damage and theorised that certain architectural and form related properties are important in influencing the extent of damage a species sustains.

In the 1980's Whitney and Johnson (1984) documented the effects of an ice storm on damage, mortality, and reproductive patterns of trees in four forests in Virginia two growing seasons after a major ice storm. Damage was categorised into arbitrary classes and was discussed in terms of forest succession. Melancon and Lechowicz (1987) focused on the susceptibility of Sugar Maple and Beech to damage and considered how the greater destructive impact of ice storms on Beech might affect forest replacement at Mont St. Hilaire, Quebec. Boerner *et. al.* (1988) studied the damage sustained by a forest in south central Ohio and found that susceptibility varied amongst tree species and that the degree of damage was positively correlated with tree height, tree diameter, and canopy crown diametre but was not correlated with root crown diametre or slope, aspect, or elevation.

More recently, De Steven *et. al.* (1991) documented changes over a 16-year period following an extreme glaze disturbance in the same southeast Wisconsin Beech-Sugar maple forest that was studied by Bruederle (1978) and Bruederle and Stearns (1986). It was noted that that disturbance accelerated forest succession towards increasing dominance by Sugar maple and that a windward versus leeward dichotomy existed in the extent of damage sustained by individual trees (De Steven *et. al.*, 1991). Rebertus *et. al.* (1997) also investigated the effects of glaze damage. Their study inventoried damage and woody debris input to a Oak-Hickory forest in northern Missouri and revealed that damage levels increased with stem diametre and that trees with more dominant crowns were more heavily damaged. In this case, the deposition of 25 mm of glaze (NOAA, 1944) led to the production of 5.1 m^3 ha^{-1} of coarse woody debris (Rebertus, *et. al.*, 1997).

Nicholas and Zedaker (1989) classified damage into broad categories and recorded mortality following ice storms in the winters of 1986 and 1987 in the Black Mountains of

North Carolina. In these montane Spruce-Fir forests, it was found that the frequency of damage to stems tended to increase with increasing elevation.

While ecologists, foresters, and botanists have expressed interest in ice storms as a force driving forest succession and as a source of environmental stress for forest trees, arboriculturalists have demonstrated a more applied interest in ice storms. As ice accumulation has the potential to damage trees both structurally and aesthetically, arboriculturalists and urban foresters have sought to describe and quantify the effects that ice accumulation has on urban, park-land, and ornamental trees.

Sisinni *et. al.* (1991) inventoried the response of the street trees of Rochester, New York to glaze accumulation. Trees were classified into damage categories and the responses of the 129 species of street trees to glaze accumulation recorded. In Urbana, Illinois, Hauer *et. al.* (1993) conducted surveys of parkway trees to determine the repair and removal needs of trees of 25 species immediately following a severe ice storm. They found that larger trees with broader crowns incurred greater amounts of damage and that fine branching, structural weakness, and higher degrees of lateral branching were associated with greater incidence of damage. Work by Butler and Swanson (1974) also provided recommendations for the selection of urban and park-land trees based on measurements of susceptibility to ice storm damage following a severe winter storm in Colorado.

Managers of plantation forests have also given considerable attention to ice storms, especially with reference to the management of pine plantations in the central and southern United States. For example, Williston (1974) evaluated the role of thinning in protecting stands of Loblolly and Shortleaf pine against ice storm damage and found that trees with higher proportions of biomass in their crowns fared better under ice-loading conditions (Williston, 1974). Shepard (1975) looked at the role of thinning in the protection of plantations against ice storm damage and found that in dense stands damage was focused on taller individuals with higher crowns, while in thinned stands trees of different sizes did not experience differences in the extent of damage. Belanger *et. al.* (1996) continued the work of both Williston (1974) and Shepard (1975) and found that thinned stands of Loblolly pine in Georgia had a higher incidence of stem breakage and storm-related mortality than did unthinned stands. Belanger *et. al.* (1996) also noted that during regrowth following an ice storm, growth related to restoring crown components in damaged trees takes precedence over lower stem growth.

Although the motivations and nature of past work on ice storms are diverse, two related lines of inquiry have emerged in the literature. On the one hand, we have a fairly comprehensive assessment of the susceptibility of individual tree species to glaze damage. This assessment, however, is only semi-quantitative and the causes of susceptibility remain little understood. On the other hand, there has been an emphasis placed on the impacts of ice storms on whole forests. Work in this area has focused on the influence of ice storms on forest succession. This work has also been largely qualitative, with quantitative measurements of woody-litter being made in only a few cases. Overall, ice storms have received less attention than fire and wind as sources of forest disturbance, and less attention than is deserved given their frequency and impact in the forests of eastern North America. The purpose of this thesis is to begin to rectify this imbalance through a comprehensive examination of the magnitude and nature of damage sustained by an old-growth forest in southern Quebec as the result of a catastrophic ice storm.

II. The ice storm of January 1998: An opportunity to assess impacts on an old-growth hardwood forest.

This study was conducted at the Gault Estate of McGill University at Mont St. Hilaire, Quebec (45°32'N, 73°09'W) (Figure 1). Mont St. Hilaire is covered by old-growth deciduous forests and represents the largest undisturbed tract of the original Great Lakes-St. Lawrence forest in this region (Maycock, 1961). The mountain itself is part of a series of plutonic intrusions that are collectively referred to as the monteregian petrographic province (Feininger and Goodacre, 1995). The highest peak rises to an elevation of 297 m above sea-level. Vascular plant diversity on the mountain is high, with in excess of 500 species recorded (Maycock, 1961). Stands of *Acer-Fagus* or *Fagus-Acer* predominate on north- and east-facing slopes, while south- and west-facing slopes tend to support stands of *Quercus-Acer, Acer-Quercus*, and *Quercus-Pinus* (Maycock, 1961; Enright and Lewis, 1985). On the whole, the forests of Mont St. Hilaire can be considered old-growth, with many trees in excess of 150-200 years old and some as old as 450 years or more (Phillips, 1972). For the most part the forests have been unaffected by human intervention, although some sectors sustained modest disturbance due to selective logging and harvesting of maple sap in the nineteenth century. The mountain is protected as a United Nations Biosphere Reserve and provides an important site for long-term monitoring of natural forest dynamics.

The forests at Mont St. Hilaire were heavily damaged by the most severe ice storm in recorded history, which began on January 5 1998 and struck southwestern Quebec, eastern Ontario, and parts of the northeastern United States (Hydro Quebec, 1998; Kerry *et. al.*, 1999). On the morning of the 5th of January, meteorologists forecast the merging of a large warm air mass from the Gulf of Mexico with a cold air mass moving south from Labrador. Three factors combined to create the conditions leading to the ice storm (Kerry *et. al.*, 1999). First, a shift in the jet stream brought large amounts of moisture from the Gulf of Mexico. Second, a high pressure area over northeastern Canada kept the ground very cold. Finally, a nearly stationary Arctic front extending just south of the

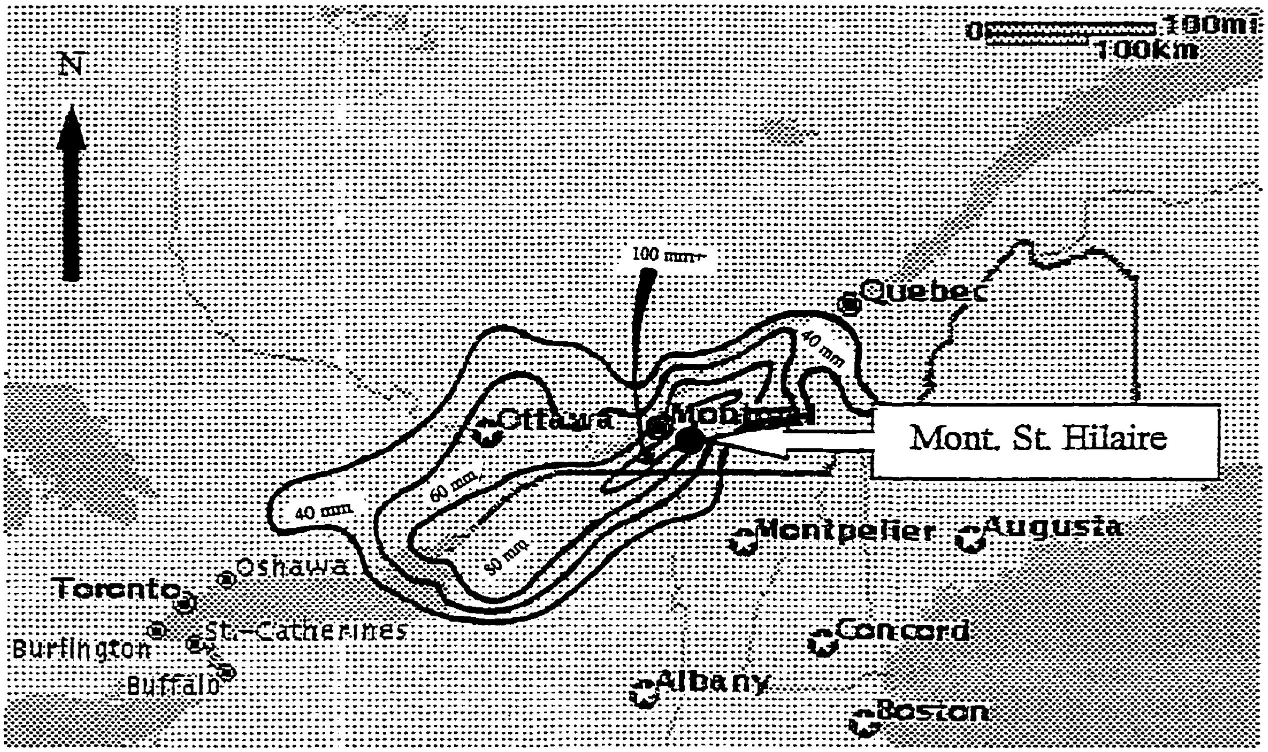

Figure 1. Location of the study site at the Gault Estate of McGill University on Mont St. Hilaire, Quebec (45°32'N, 73°09'W). Map shows contours of maximum ice glaze accumulation associated with the ice storm of January 1998. Accumulation of glaze at the study site was between 78-110 mm (Statistics Canada, 1998)

affected area created a temperature inversion. While the storm affected much of the northeast United States and adjacent Canada, the hardest hit region centered on southwest Quebec where over 1.62 million hectares of forest sustained damaged (Irland, 1998).

By the end of the first day, 19.6 mm of freezing rain had accumulated at St. Hubert, the weather monitoring station nearest to the study site (39 kilometres away) (Hydro Quebec, 1998). Ice continued to accumulate over the next two days with 20 to 30 km/hr winds from the northeast. By January 7, 42 mm of frozen precipitation had been recorded. On January 8, the second wave of the ice storm hit adding an additional 22.7 mm of ice between noon and midnight. Finally on January 9, the third wave of the ice storm struck bringing the amount of ice accumulation measured at St. Hubert to 78.4 mm. According to data from Statistics Canada (1998), the actual amount of frozen precipitation that accumulated at Mont St. Hilaire was between 78-110 mm (Figure 1).

An ice storm such as that of January 1998 provides an exceptional opportunity to design and implement a programme of research that will allow us to answer critical questions about the role of ice storms in the ecology of northern hardwood forests. In this thesis I present the results of a quantitative study of the impacts of the 1998 ice storm on the old-growth, hardwood forests of Mont St. Hilaire, Quebec. I consider the scale of litter production arising from this storm with respect to other ice storms as well as to other forms of climatic disturbance (Chapter 2). As well, I examine the influence of mechanical characters on the magnitude and nature of biomass losses sustained by northern, hardwood species as a result of ice-loading (Chapter 3). These data provide insight into the nature of ice storms as a form of natural disturbance in the forests of northeastern North America and provide a baseline for assessment of recovery in the forests of the region.

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CHAPTER 2

Stand-Level Effects of the January 1998 Ice Storm on the Forests of Mont St. Hilaire, Quebec

Some say the world will end in fire,
Some say in ice.
From what I've tasted of desire
I hold with those who favor fire.
But if it had to perish twice,
I think I know enough of hate
To say that for destruction ice
Is also great
And would suffice.

Robert Frost
Fire and Ice, from New Hampshire
(New York: Henry Holt, 1923)

Abstract

We investigated the effects of the largest ice storm of this century on the standing biomass and wood volume of the forests of Mont St. Hilaire, Quebec. The storm produced 19.9 metric tonnes or 33.6 m^3 of woody-debris per hectare. This amount of litter production is approximately 20 times greater than what is expected in a normal year and represents a loss of between 7.2-10.2% of the total above-ground biomass of the pre-storm forest. Results from studies after other forms of forest disturbance suggest that, because of rapid re-establishment of biotic control over biogeochemical processes, this degree of damage will bring about only limited changes in nutrient cycling and other ecosystem-level processes. The degree of woody-litter production, however, indicates that the storm's impact on forest succession and dynamics will be substantial. The magnitude of biomass losses places the ice storm of 1998 as the most powerful ice storm on record and among the most severe forms of climatic disturbance to have been recorded in forested landscapes anywhere.

Introduction

Ice storms are the most frequent form of major disturbance in the forests of eastern North America, occurring every 20 to 100 years (Lemon, 1961). Catastrophic windstorms and fires, the other primary agents of disturbance in the region, occur less frequently with return times of 100 to 1000 years in northern hardwood forests (Canham and Loucks, 1984). As a recurring source of physical perturbation, ice storms are known to play a role in determining forest succession and are an important factor influencing the history and dynamics of the region's forests (Bruederle and Stearns, 1985; De Steven *et. al.*, 1991; Rebertus *et. al.*, 1997).

Ice storms develop when warm, moist air passes over ground-level air masses at or near freezing temperature (Bennett, 1959). Under these conditions supercooled rain falls and freezes on contact with ground-level objects (Lemon, 1961). In forested landscapes, these conditions lead to accumulations of ice on tree limbs and trunks and result in the loss of branches and twigs from the forest canopy (Whitney and Johnson, 1984; Bruederle and Stearns, 1995). The loss of canopy biomass that characterises ice storm damage results in the redistribution of living and dead biomass, increases organic inputs to the soil surface, reduces canopy height and vertical stratification, and exposes mineral soil. Woody litter produced by ice storms represents a substantial, yet little studied, pool of energy, carbon, and nutrient elements in forest ecosystems (Harmon *et. al.*, 1986). While the scale of these episodic biomass inputs to the forest floor remain unquantified for northeastern forests, it is recognised that such transfers can influence ecosystem-level processes such as nutrient cycling, hydrology, and atmospheric exchange (Sanford, *et. al.*, 1991).

Early studies of ice storms focused on qualitative descriptions of damage (Harshberger, 1904; Illick, 1916; Deuber, 1940). Most of the studies that have been completed since the middle of the century have concentrated their attention on *post-facto* categorizations of tree-level damage according to a number of arbitrarily chosen damage classes (McKellar, 1938; Croxton, 1939; Whitney and Johnson, 1984; Boerner *et. al.*, 1988;

Nicholas and Zedaker, 1989; Hauer *et. al.*, 1993; Seischab *et. al.*, 1993; Sisinni *et. al.*, 1995; Rebertus *et. al.*, 1997). Only a few papers have quantified the number of fallen branches (Melancon and Lechowicz, 1987) and the volume of litter (Bruederle and Stearns, 1985; Rebertus *et. al.*, 1997) arising from major ice storms.

The objective of this paper is to quantify the effects of a catastrophic ice storm on the standing biomass and volume of a northeastern, old-growth, hardwood forest. A need exists for an understanding of how ice storms might affect ecosystem-level processes and primary productivity in forest stands. Since the dynamics of nutrient elements in temperate forests largely depend on the amount and rate of biomass transfer (Khanna and Ulrich, 1991), it is suspected that large ice storms will be capable of initiating considerable changes in nutrient cycling and element dynamics. This study will serve to put the effects of the catastrophic ice storm that struck southwest Quebec in January 1998 (Irland, 1998) into perspective in terms of forest ecology. This storm resulted in the accumulation of between 78-110 mm of glaze ice and damaged up to 1.62 million hectares of Quebec forest (Irland, 1998; Statistics Canada, 1998). The intensity and scale of damage sustained as a result of this storm will be compared to normal changes in primary productivity and to those arising from other forms of disturbance and the implications of this level of damage for nutrient dynamics and other ecosystem-level processes will be considered.

Methods

Seven permanent transects for monitoring forest dynamics had been established on Mont St. Hilaire, Quebec (MSH) in the summer of 1997. Located along these seven transects were 117 randomly stratified circular plots, each with a radius of 6 metres (Figure 2). We used these representative plots to assess damage caused by the ice storm of January 1998.

To quantify biomass losses due to the ice storm it was necessary to accurately and quickly measure the biomass of each piece of fallen debris. This was accomplished by developing a sampling protocol based on the conserved relationship that exists between branch diameter and mass over a wide variety of plant species of many sizes (Whittaker and Woodwell, 1968). Regressions relating fallen branch diameter and branch biomass were created for the major forest tree species of Mont St. Hilaire in May 1998 and were used to estimate the total biomass of fallen material in our study plots (Appendix I).

To create these branch diameter to mass relationships, focal collection sites were established at seven representative locations on Mont St. Hilaire. At these sites branches from the most frequently encountered species were collected. These sites were chosen to provide the greatest number of branches from the most common tree species. For each species, individual branches were gathered from at least three sites to ensure the generality of the resulting equations. For less frequently occurring species, branches were gathered in the course of expeditions over the mountain conducted with the express purpose of gathering enough replicates to satisfy the minimum sample size needed to create useful regressions.

To minimise changes in the moisture content of fallen material during the course of sampling, branches were collected during a three week period from 21 May, 1998 to 10 June, 1998. Because the storm occurred in January, well before sap flow began, the fallen material was essentially air-dry and provided highly repeatable estimates of the diameter-biomass relationship. In all, branches from ten species were sampled: Striped

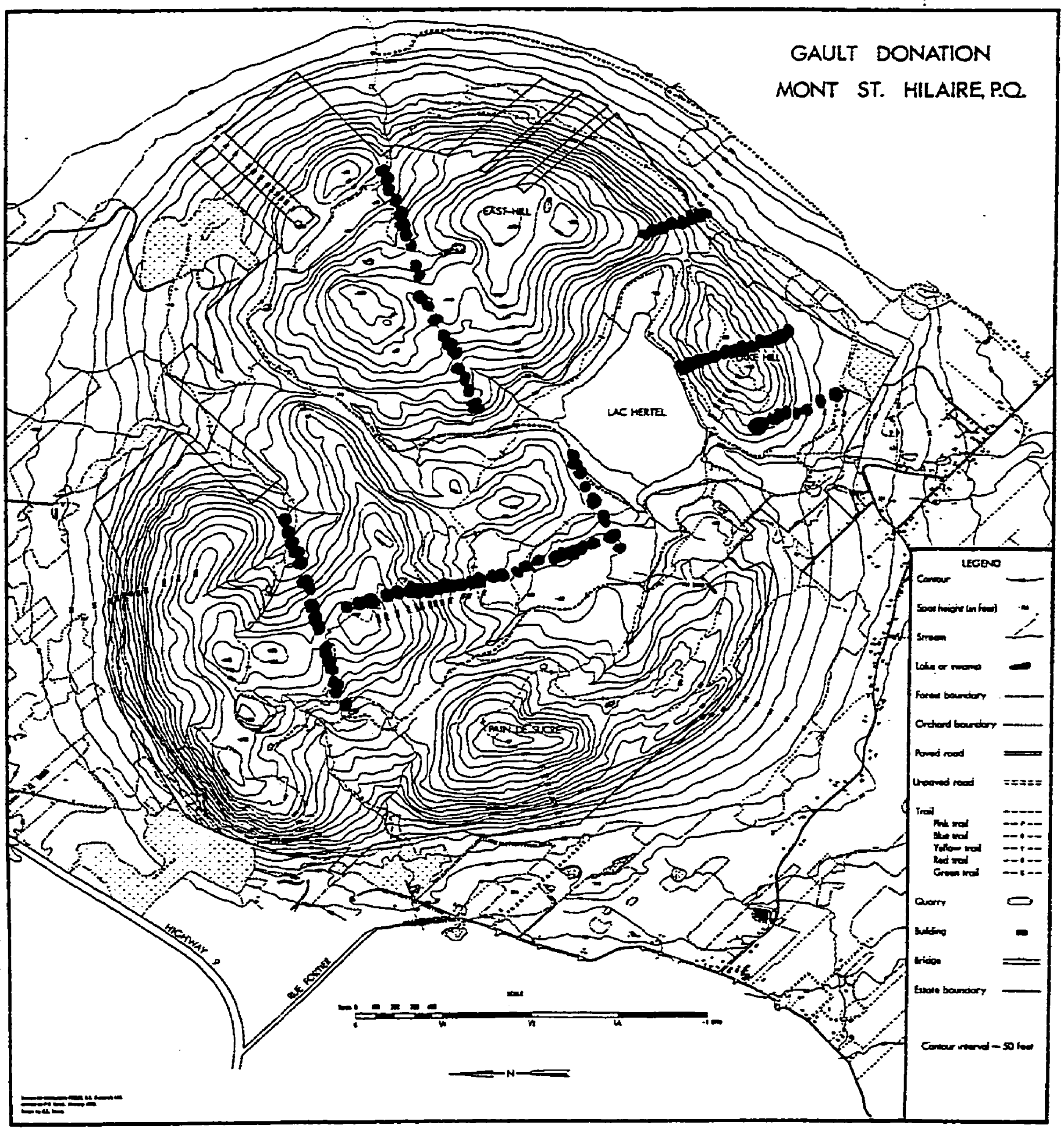

Figure 1. Location of seven permanent transects and 117 forest dynamics study plots on Mont St. Hilaire, Quebec. The plots were established by Ken Arii in the summer of 1997 as part of another study; they are broadly representative of the forests of the mountain.

maple (*Acer pensylvanicum* L.), Sugar maple (*Acer saccharum* Marshall.), Paper birch (*Betula papyrifera* Marshall.), Yellow birch (*Betula alleghaniensis* Britton.), White Ash (*Fraxinus americana* L.)., American beech (*Fagus grandifolia* Ehrh.), Ironwood (*Ostrya virginiana* (Miller) K. Koch.), Large-tooth aspen (*Populus grandidentata* Michx.), Red oak (*Quercus rubra* L.), and Basswood (*Tilia americana* L.).

Branches were weighed using a Salter 235-10 Angling Scale from Salter-Weightronix Ltd., of West Bromwich, West Midlands, England (100 pound capacity in 2-ounce increments). The scale was fitted with a net constructed from a 1-m^2 sheet of aluminum mesh and was suspended at each sampling site from a pole lashed between two trees approximately one metre apart. Before each branch was weighed, the diameter of the basal end (the larger broken end that would have been proximal to the trunk) was measured using a vernier caliper. Individual branches were then broken into smaller sections approximately one metre long and were placed inside the net and suspended from the scale. The weight, species, and basal diameter of each piece of debris were recorded.

The primary criteria for selection of branches were (1) that they should be relatively intact and (2) that they should be larger than 1 centimetre in diameter at the base. The first criterion was adopted to ensure that small secondary branches would be accounted for on selected branches. The second was necessary in light of the inability of the scale to measure objects weighing less than 0.057 kg, approximately the mass of branches 1 centimetre in diameter.

Equations relating branch basal diameter to mass were developed for each of the study species. In creating these equations, however, several statistical concerns had to be adressed since some investigators have reported a bias in linear regressions after logarithmic transformation. Satoo (1970), Crow (1971), and Baskerville (1972) have all recorded errors of this nature. Logarithmic transformation introduces a systematic bias into predictive calculations; it is well recognised that a correction factor (CF) is necessary to allow for this bias (Finney, 1941; Baskerville, 1972). Despite the fact that the bias introduced through logarithmic transformation has been explained in detail by several authors (Baskerville, 1972; Whittaker and Marks, 1975), considerable confusion exists concerning the actual formulation of the required correction factor (Sprugel, 1983). Many of the published formulae do not contain the appropriate number of degrees of freedom. The appropriate formula is $CF = \exp(SEE^2/2)$, where SEE is the standard error of estimate with degrees of freedom N-2 for a two variable equation (Sprugel, 1983). Since the standard error of estimate as calculated in this formula depends on the base to which the logarithms are taken, the correct value will only be achieved when the formula is based on the natural logarithm. Although it is recognised that the errors resulting from logarithmic transformation are small (Whittaker and Niering, 1975; Gosz, 1980), they are easily correctable and the appropriate correction should be made (Sprugel, 1983). In this study, correction factors were calculated for each logarithmically transformed equation relating branch basal diameter and biomass. To estimate the biomass of a fallen branch, the ln(biomass) of the branch is estimated from its ln(diameter), the ln(biomass) is back-transformed to kilograms, and the back-transformed value is multiplied by the correction factor.

In the 117 permanent study plots, the basal diameter of all pieces of woody debris greater than 1 centimetre in diameter was recorded. It was possible to differentiate newly fallen material resulting from the ice storm of 1998 from material arising from previous years according to position in the strata of downed material, wood colouration, and fragility. Each branch or branch fragment was identified to species. The biomass of fallen material in the 117 plots was calculated by inputting the diameters of all fallen branches into the appropriate species-specific equations relating branch basal diameter to mass.

To produce a second, independent measure of the amount of damage sustained at the stand level, the volume of downed macro-litter resulting from the ice storm was determined using a modified version of the VanWagner (1965) method (Bruederle, 1978;

Bruederle and Stearns, 1985). Measurements were made along short transects (12 metres) at each of the 117 study plots. Transects were established in random compass directions at each plot to avoid directional bias. The species and diameter of each piece of debris with a diameter greater than 1 centimetre was recorded at each point of intersection with the transect. Sampling guidelines for inclusion of macro-litter in the tally followed Van Wagner (1968).

Litter volume was calculated according to the equation (Van Wagner, 1968; Bruederle and Stearns, 1985):

$$V = (\pi^2 \sum d^2 / 8L) * (10\,000 \text{ m}^2 / \text{ha})$$

Where:

V = volume of macro-litter in cubic metres per hectare

d = diameter of residue at the point of intersection, measured in centimetres

L = length of the sample line in metres

By applying this equation to the diameters of branches found to intersect with the 117 plot-centered line transects it was possible to estimate the total volume of downed woody material in our plots.

In July of 1998, the diameter at breast height (dbh) of all trees with dbh greater than 3 cm in the 117 study plots was recorded. These dbh measurements were then input into species-specific allometric equations for total above-ground biomass from the literature to predict the pre-storm distribution of biomass at the study site (Baskerville, 1965; Bickelhaupt *et. al.*, 1973; Whittaker *et. al.*, 1979; Wiant *et. al.*, 1977; Brenneman *et. al.*, 1978; Ker, 1980; Young *et. al.*, 1980; Schmitt and Grigal, 1981; Freedman *et. al.*, 1982; Ker, 1984; Perala and Alban, 1994). The output from these allometric equations was used to estimate the proportion of standing biomass lost as a result of the ice storm of 1998.

Results

To create species-specific equations relating debris diameter and mass, linear regression analyses were performed on untransformed branch weights and basal diameters and their natural logarithmic transformations. Transformation improved the coefficient of determination (r^2) significantly. Therefore, the relationships between the two variables presented here are based on the transformed data.

Strong relationships were found between branch basal diameter and biomass for each of the ten species under investigation (Table 1, Appendix I). Coefficients of determination were above 0.94 in all cases, with $p < 0.001$.

Table 1. Logarithmically transformed equations relating branch basal diameter (cm) and woody-biomass (kg) for ten deciduous forest tree species at Mont St. Hilaire, Quebec.

Species	N	Slope	CF	R^2	p	Diam. Range (cm)
Acer pensylvanicum	67	ln Mass = 2.660 - 3.017*ln(d)	1.027	0.945	<.0001	1.04 - 5.00
Acer saccharum	39	ln Mass = 2.771 - 2.942*ln(d)	1.024	0.979	<.0001	1.19 - 10.77
Betula alleghaniensis	59	ln Mass = 2.520 - 2.575*ln(d)	1.017	0.986	<.0001	1.00 - 11.11
Betula papyrifera	21	ln Mass = 2.770 - 2.998*ln(d)	1.021	0.972	<.0001	1.52 - 6.61
Fraxinus americana	58	ln Mass = 2.607 - 2.644*ln(d)	1.021	0.972	<.0001	1.05 - 6.64
Fagus grandifolia	66	ln Mass = 2.657 - 2.744*ln(d)	1.023	0.983	<.0001	1.00 - 17.13
Ostrya virginiana	39	ln Mass = 2.709 - 2.799*ln(d)	1.014	0.987	<.0001	1.27 - 8.95
Populus grandidentata	22	ln Mass = 2.921 - 3.325*ln(d)	1.024	0.968	<.0001	1.84 - 7.56
Quercus rubra	63	ln Mass = 2.795 - 3.023*ln(d)	1.019	0.973	<.0001	1.70 - 11.05
Tilia americana	65	ln Mass = 2.928 - 3.768*ln(d)	1.051	0.937	<.0001	1.28 -7.70

The total number of pieces of woody debris of all species recorded in the 117 study plots was 17,534 (Table 2). The ten species under study account for 97% of all of the branches recorded and for 98% of the total basal area of trees in the study site. As a result the values that we produced do provide an excellent approximation of the total values. Table 2 presents the resulting biomass values for the ten study species across all plots and per hectare. The volume of downed woody debris was calculated according to a modified version of the VanWagner line-transect method (VanWagner, 1968) and is also shown in Table 2.

Table 2. Total biomass and volume losses in all 117 plots and per hectare for ten study species.

Species	Biomass of litter in all plots (kg)	Biomass of litter per hectare (kg/ha)	Volume of litter per hectare (m^3/ha)	# of pieces of litter	Basal Area of trees in study plots (m^2)
Acer pensylvanicum	415.1	313.7	0.92	617	0.72
Acer saccharum	10962.7	8284.7	14.26	8747	19.16
Betula alleghaniensis	161.8	122.3	0.05	105	0.63
Betula papyrifera	79.9	60.3	0.26	177	0.88
Fagus grandifolia	781.2	590.4	3.97	3434	2.09
Fraxinus americana	6067.4	4585.2	0.51	1058	7.08
Ostrya virginiana	269.0	203.3	1.40	163	1.18
Populus grandidentata	65.4	49.4	0.01	32	0.07
Quercus Rubra	7429.4	5614.6	11.94	3071	7.92
Tilia americana	128.4	97.0	0.01	133	0.42
Other*	N/A	N/A	0.22	471	0.64
Total	26360.2	19920.9	33.55	17534	40.79

*Other species: *Amelanchier laevis* Wieg. (Serviceberry), *Prunus nigra* Ait. (Black cherry), *Cornus alternifolia* L.f. (Pagoda dogwood), *Prunus virginiana* L. (Choke cherry), *Acer spicatum* L. (Mountain maple), *Prunus serotina* Ehrh. (Pin cherry), *Pinus resinosa* Ait. (Red pine), *Pinus strobus* L. (White pine), *Tsuga canadensis* (L.) Carrière (Eastern hemlock).

The total above-ground biomass (dry mass) per hectare was calculated for all of the study species for which allometric equations exist in the literature. This allowed us to estimate the pre-storm distribution of total above-ground biomass at the study site and to estimate the proportion of biomass lost as a result of the ice storm of 1998 (Table 3, Figure 2). Multiple equations for total above-ground biomass were found in the literature for eight of the ten study species. Since no equations were found for either *Acer pensylvanicum* or *Ostrya virginiana*, the estimate of total biomass lost per hectare by these eight species is slightly less than the 19921 kg ha^{-1} based on all ten study species. The eight species with allometric equations for total above-ground biomass produced 19404 kg ha^{-1} of woody litter as a result of the ice storm. This latter value will only be used to estimate the percent of pre-storm standing biomass lost as a result of the ice storm and will not replace 19921 kg ha^{-1} as our estimate of total woody litter production.

Table 3. Predicted total (woody and foliage) standing biomass (kg ha^{-1}), fallen woody-biomass (kg ha^{-1}), and corresponding percent loss (%) for eight of ten study species.

SPECIES	STUDY	SITE	PREDICTED BIOMASS (KG/HA)	PREDICTED STANDING BIOMASS (KG/HA)	MASS FALLEN KG/HA)	% LOSS
Acer saccharum	Ker, 1980[a]	N.B.	96836.2	96836.2 - 145938.1	8284.7	5.7 - 8.6
	Perala and Alban, 1994	Gr. Lakes	110672.9			
	Freedman *et. al.*, 1982	N. S.	112992.6			
	Bickelhaupt *et. al.*, 1973	N. Y.	120450.0			
	Bickelhaupt *et. al.*, 1973	N. Y.	125266.4			
	Whittaker *et. al.*, 1979	N. H.	133161.8			
	Brenneman *et. al*, 1978	W. Virg.	141718.9			
	Pastor and Bockheim, 1981	Wisc.	145938.1			
Betula alleghaniensis	Young *et. al.*, 1980	Maine	3417.7	3417.7 - 4920.8	122.3	2.5 - 3.6
	Ker, 1980[a]	N.B.	3740.3			
	Baskerville, 1965	N. B.	3825.5			
	Freedman *et. al.*, 1982	N. S.	4003.6			
	Perala and Alban, 1994	Gr. Lakes	4918.0			
	Whittaker *et. al.*, 1979	N. H.	4920.8			
Betula papyrifera	Baskerville, 1965	N.B.	2553.0	2553.0 - 3691.4	60.3	1.6 - 2.4
	Ker, 1984	N.B./N. S.	3086.7			
	Ker, 1980[b]	N.B.	3102.6			
	Freedman *et. al.*, 1982	N. S.	3240.8			
	Perala and Alban, 1994	Gr. Lakes	3355.5			
	Young *et. al.*, 1980	Maine	3453.6			
	Schmitt and Grigal, 1981	Canada-US	3691.4			
Fagus grandifolia	Ker, 1980[a]	N.B.	30907.0	30907.0 - 48825.7	4585.2	9.4 - 14.8
	Young *et. al.*, 1980	Maine	36524.4			
	Brenneman *et. al*, 1978	W. Virg.	38172.9			
	Whittaker *et. al.*, 1979	N. H.	48825.7			
Fraxinus americana	Ker, 1980[a]	N.B.	9404.2	9404.2 - 11262.9	590.4	5.2 - 6.3
	Perala and Alban, 1994	Gr. Lakes	10881.7			
	Brenneman *et. al*, 1978	W. Virg.	11262.9			
Populus grandidentata	Freedman *et. al.*, 1982	N. S.	199.8	199.8 - 227.2	49.4	21.7 - 24.7
	Perala and Alban, 1994	Gr. Lakes	227.2			
Quercus Rubra	Brenneman *et. al*, 1978	W. Virg.	45368.8	45368.8 - 54448.6	5614.6	10.3 - 12.4
	Perala and Alban, 1994	Gr. Lakes	47533.7			
	Wiant *et. al.*, 1977	W. Virg.	54448.6			
Tilia americana	Perala and Alban, 1994	Gr. Lakes	1042.7	1042.7 - 1298.5	97.0	7.5 - 9.3
	Brenneman *et. al*, 1978	W. Virg.	1298.5			
Total	-	-	-	189729.4 - 270613.2	19403.9	7.2 - 10.2

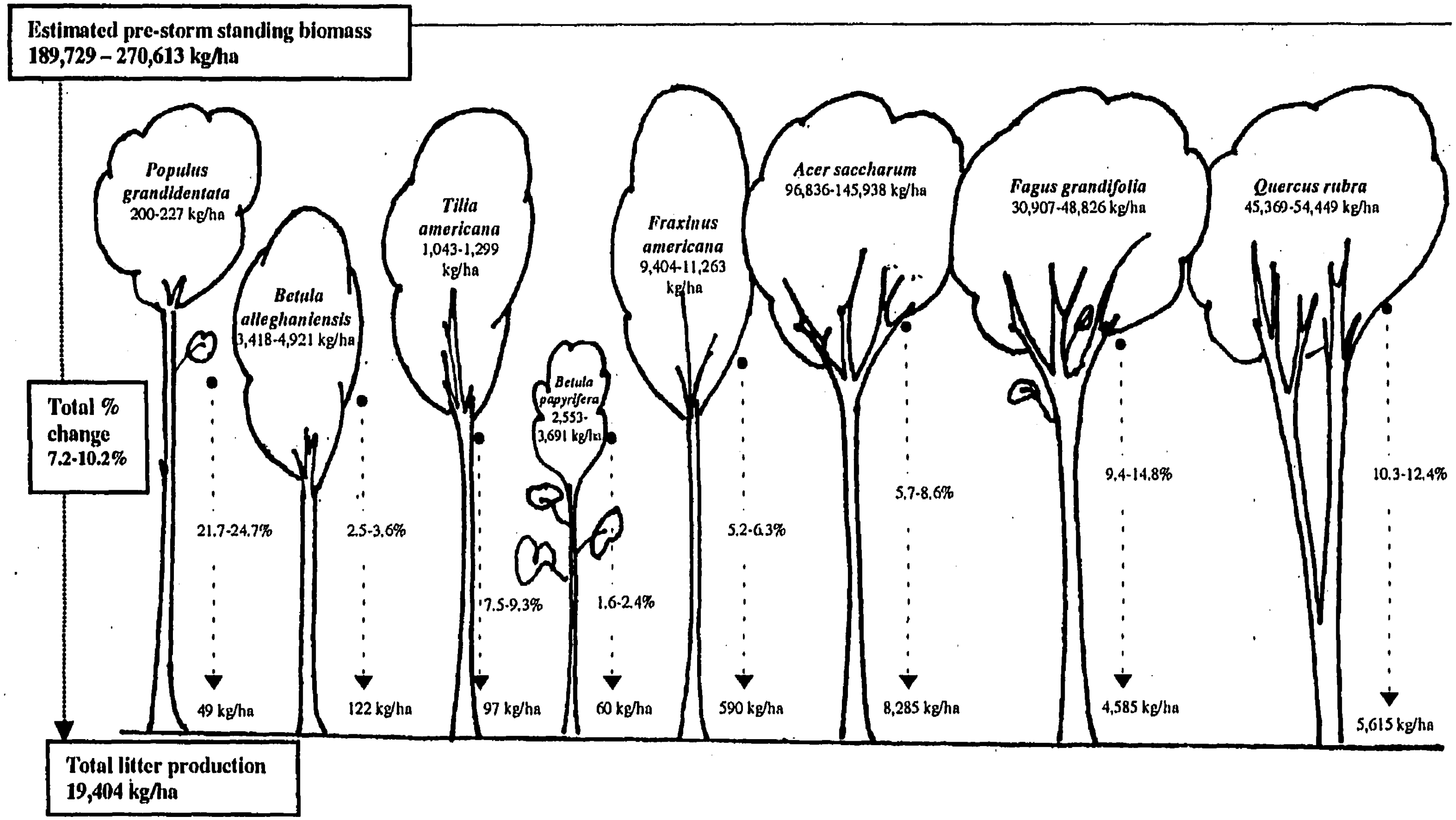

Figure 3. Diagrammatic representation of changes to pre-storm total standing biomass (dry mass, including foliage) as a result of the ice storm of January 1998. Values associated with tree crowns represent the estimated range of pre-storm standing biomass as predicted from a concert of allometric equations taken from the literature (Table 3). Values associated with the forest floor represent the mass of woody-litter (>1cm diameter) produced by each species. Percent-change values for each species correspond to the estimated % loss of pre-storm standing biomass as litter. Values and silhouettes for only eight of the ten study species are shown since allometric equations are not published for *Acer pensylvanicum* (Striped maple) and *Ostrya virginiana* (Ironwood).

Discussion

The importance of natural disturbances in shaping landscapes and influencing ecosystems is gaining wide recognition (Pickett and White, 1985). However, while small, frequent disturbances have become better understood, natural perturbations that affect large areas and occur infrequently remain poorly understood. This study, in an attempt to amend the paucity of data that exists on ice damage in the forests of northeastern North America, found that the ice storm of January 1998 produced 19921 kg or 33.6 m^3 of woody-litter per hectare.

In temperate deciduous forests total annual litterfall includes a woody-litter component as well as fine-litter elements such as leaves, bud scales, flowers, and fruit (Gosz *et. al.*, 1972). For this reason, estimates of total litterfall exceed those for woody-litter alone. In northern deciduous forests unaffected by catastrophic disturbance, the largest inputs of litter are associated with the autumnal shedding of leaves (Bray and Gorham, 1964). That is, non-woody litter accounts for the major part of total litterfall. For example, it is reported that the autumn leaf-fall in the forests of New Hampshire accounts for up to 70-80% of total litter fall (Anon, 1932; Bray and Gorham, 1964; Gosz *et. al.*, 1972). Since ice storms are a winter phenomenon, lost biomass from damaged forests is unlike litter produced over the course of a normal year in that it does not include leaf-matter and is principally composed of woody-debris, primarily branches and occasional tree stems (Bjorkbom and Larson, 1977).

The production of 19921 kg ha^{-1} of woody-litter (>1 cm diameter) at Mont St. Hilaire is substantially greater than the annual production of woody-litter found in similar non-disturbed forests. Gosz *et. al.* (1972) determined that the northern deciduous forests of New Hampshire produce 2072 kg ha^{-1} of woody litter annually (Table 4). In addition, two reviews of the literature give average values for the worldwide production of woody litter. From Bray and Gorham (1964) it is possible to determine that that the average production of woody litter in cool, temperate, deciduous forests is 1325 kg ha^{-1}. In a more comprehensive survey, Vogt *et. al.* (1986) found that the average annual woody litterfall in cool, temperate, broadleaved forests is 1046 kg ha^{-1} (Table 4). This corresponds to a loss of between 0.28 and 0.40 percent of the total above-ground biomass pool at the study site. Given the loss of 19921 kg ha^{-1} of woody-litter - approximately 7.2-10.2% of total above-ground biomass - it is possible to determine that woody-biomass losses resulting from the 1998 ice storm are about 20 times greater than would be expected under non-ice storm conditions (Table 3).

At the Hubbard-Brook forest in New Hampshire, the annual above-ground overstory litterfall (woody- and foliage-litter) for a Beech-Maple forest generally similar to those at Mont St. Hilaire was 5702 kg ha^{-1} (Gosz *et. al.*, 1972; Whittaker *et. al.*, 1979). This falls within the range of values reported by Rodin and Bazilevich (1967) in their summary of world litter production where it is estimated that the annual litterfall in temperate deciduous forests is 4000 to 7000 kg ha^{-1}. The loss of 19921 kg ha^{-1} of woody-litter observed at Mont St. Hilaire as a result of the ice storm of 1998 is 65-80 % greater than the average total litter loss for similar forests around the world as reported by Rodin and Bazilevich (1967). Not only does the amount of woody litter associated with the ice storm of 1998 exceed annual levels of woody-litter production in similar forests, it also exceeds levels of total litterfall, including both woody- and foliage-litter elements, for these forests.

The losses of biomass resulting from this ice storm exceed non-disturbance litterfall values for all of the major forest types of the tropics as recorded by Vitousek (1984) and Bray and Gorham (1964), and the major forest types of the temperate world, as recorded by Harmon *et. al.* (1986). The greatest recorded non-disturbance litterfall value in the tropics is for a mixed deciduous forest in Belize, with an annual total litter input of 12600 kg ha^{-1} (Lambert *et. al.*, 1980). In temperate regions, the greatest input values are for the production of woody debris (> 2.5 cm in diameter) in *Pseudotsuga* forests in Oregon, where annual inputs of 7000 kg ha^{-1} were recorded (Grier and Logan, 1977). The total amount of lost biomass in the form of branches > 2.5 cm in diameter at Mont St. Hilaire was 17970.1 kg ha^{-1}. This is 2.5 times greater than the largest recorded

Table 4. Comparison of biomass losses resulting from the ice storm of January 1998 at Mont St. Hilaire with normal biomass losses and those resulting from other disturbances.

STUDY	FOREST TYPE - LOCATION	REFERENCE	DEBRIS SIZE LIMIT	BIOMASS OR VOLUME LOST	COMPARABLE LOSSES AT MSH
This Study	Old-Growth, northern, hardwood - Mont St. Hilaire	Hooper *et. al.*, 1999	> 1 cm	19920.9 kg ha^{-1}	-
Woody Litterfall Following Ice Storm	Old-growth Oak-Hickory Forest, Missouri	Rebertus *et. al.*, 1997	Woody-litter > 1 cm	5.1 m^3 ha^{-1}	33.55 m^3 ha^{-1}
Woody Litterfall Following Ice Storm	Wisconsin Mesic Acer-Fraxinus Forest	Bruederle and Stearns, 1985	Woody-litter > 1.3 cm	19.35 m^3 ha^{-1}	32.61 m^3 ha^{-1}
Generalised Woody Litterfall Inputs	Cool Temperate Forests	Bray and Gorham, 1964	Woody-litter > 1cm	1325 kg ha^{-1} yr^{-1}	19920.9 kg ha^{-1}
Generalised Woody Litter Inputs	Hardwood Forests of New Hampshire	Gosz *et. al.*, 1972	Woody-litter > 1 cm	2072 kg ha^{-1} yr^{-1}	19920.9 kg ha^{-1}
Generalised Woody Litterfall Inputs	Cold Temperate Broadleaf Deciduous Forests in General	Vogt *et. al.*, 1986	Woody - litter > 1 cm	1046 kg ha^{-1} yr^{-1}	19920.9 kg ha^{-1}
Woody Litterfall Following Hurricane Gilbert	Tropical Dry to Very Dry Forest, Yucatan Pen., Mexico	Whigham *et. al.*, 1991	Coarse Woody Debris > 10 cm	16000 kg ha^{-1}	8867.9 kg ha^{-1}
Macro-litter Associated With Hurricane Hugo	Tropical broad-leaved - Mt. Luquillo, Puerto Rico	Frangi and Lugo, 1991	> 1 cm	18100 kg ha^{-1}	19920.9 kg ha^{-1}
Woody Litterfall Following Hurricane Iniki	Tropical Acacia kao forests Kauai Isl., Hawaii	Harrington *et. al.*, 1997	Woody-litter > 1 cm	1200 - 4400 kg ha^{-1}	19920.9 kg ha^{-1}
Woody Litterfall Following Major Wind Storm	Great Britain	Kirby *et. al.*, 1998	Woody - litter > 1 cm	13.00 m^3 ha^{-1}	33.55 m^3 ha^{-1}
CWD Associated With Beetle Damaged Forest	Temperate, moist, Pseudotsuga forest Washington & Oregon States	Wright and Lauterbach, 1958	> 2.5 cm	30000 kg ha^{-1} 69.8 m^3 ha^{-1}	17970.1 kg ha^{-1} 33.55 m^3 ha^{-1}

temperate non-disturbance coarse woody debris input value and 1.4 times greater than the largest recorded tropical value.

Relatively few studies have looked at the effects of catastrophic climatic disturbances on forest ecosystems in a quantitative way. In one of the few studies that has broached the subject, it was found that, in 1989, Hurricane Hugo brought about the transfer of 18100 kg ha^{-1} of biomass to the forest floor in the tropical, broadleaved forests of the Luquillo Mountains of Puerto Rico - a value only slightly less than that generated at Mont St. Hilaire (Frangi and Lugo, 1991) (Table 4). Biomass losses resulting from Hurricane Hugo in Puerto Rico, while accounting for a marginally smaller transfer of biomass, accounted for the loss of a similar proportion of the original standing biomass of the forest. It was found that the above-ground live-tree biomass was reduced by 10 percent as a result of Hurricane Hugo (Frangi and Lugo, 1991), as compared with a loss of 7.2-10.2% of total above-ground biomass resulting from the ice storm of 1998. A critical difference, however, between the impacts of the two storms is the fact that a large portion of the litter produced as a result of Hurricane Hugo, as a summer disturbance, consisted of non-woody material while all of the debris resulting from the ice storm was woody in nature.

The largest natural woody debris input values on record are from mature, insect-disturbed forests in Oregon and Washington states (Wright and Lauterbach, 1958). There, *Pseudotsuga* stands generated 30,000 kilograms of litter during the peak year of a 10 year extreme bark beetle epidemic (with an average annual input of 17,000 kg ha^{-1} over the course of the entire outbreak) (Wright and Lauterbach, 1958) (Table 4). Considering that coniferous forests generally provide greater inputs of coarse woody debris than deciduous forests (Vogt *et. al.*, 1986) and that these extreme values were the product of highly disturbed coniferous forests, the similarly large values found at Mont St. Hilaire are truly impressive. As well, the fact that the storm at Mont St. Hilaire produced a greater amount of woody debris than well-documented Hurricane Hugo, when tropical broad-leaved forests such as those in Puerto Rico are considered to produce the greatest amounts of litter of all forest types (Vogt *et. al.*, 1986), has great implications for the role of ice storms in influencing the dynamics and structure of forests.

The most powerful climatic disturbance on record was documented by Whigham *et. al.* (1991). Following Hurricane Gilbert it was found that the annual input of coarse woody debris (> 10 cm in diameter) in the dry, tropical forests of the Yucatan Peninsula of Mexico was 16000 kg ha^{-1} (Whigham *et. al.*, 1991) (Table 4). At Mont St. Hilaire, it was found that 8867.9 kg ha^{-1} of coarse woody debris of this size range was produced. In these terms, Hurricane Gilbert produced almost twice as much downed coarse woody debris in this size range as the ice storm of 1998. This makes Hurricane Gilbert the most damaging climatic disturbance documented to date. It also provides some perspective as to the amount of damage caused as a result of the ice storm. The ice storm of 1998, while not the most severe climatic disturbance on record, is in the upper ranks of recorded disturbances (Table 4).

Although widely considered in forestry literature, volume is less frequently employed as a variable in ecological studies. A close relationship exists between the volume and biomass of downed material due to the limited variability in wood density between different tree species (Harmon *et. al.*, 1986). Volume losses of coarse woody debris vary considerably between forests of different types (Bray and Gorham, 1964). The greatest recorded volume loss recorded is 69.8 m^3 per hectare per year, again in association with a beetle outbreak in Washington and Oregon states (Wright and Lauterbach, 1958) (Table 4). As a result of the storm under study, 33.6 m^3 ha^{-1} of woody-litter were generated. This value is approximately half that of the highest recorded annual volume loss and slightly lower than the average annual volume loss sustained as a result of that same insect outbreak (39.2 m^3 per hectare) (Wright and Lauterbach, 1958). Apart from these extreme volume losses generated in distressed *Pseudotsuga* forests with extremely high standing biomass, the volume losses observed as a result of the ice storm of January 1998 are greater than for any other documented non-fire disturbance.

Large volume losses associated with climatic disturbances have been documented in three other sources, two of which record the effects of ice storm damage in deciduous forests. In the first of these studies, Bruederle and Stearns (1985) recorded the production of a large volume of woody-litter in association with an ice storm in Wisconsin. It was found that 19 $m^3 ha^{-1}$ of woody litter greater than 1.3 cm in diameter were produced (Bruederle and Stearns, 1985) (Table 4). In the second study, it was found that 5.1 $m^3 ha^{-1}$ of litter were produced following an ice storm in a Missouri oak-hickory forest in 1994 (Rebertus *et. al.*, 1997). In a third study, it was found that when massive wind-storms swept England in 1987 the volume of litter on the forest floor rose by 13 $m^3 ha^{-1}$ (Kirby *et. al.*, 1998) (Table 4). The production of woody litter in the same size ranges at Mont St. Hilaire is 1.7 fold greater than that produced following the Wisconsin ice storm, 6.6 fold greater than that recorded for the 1994 Missouri ice storm, and 2.6 fold greater than that recorded following the 1987 wind storms in England.

Of the possible effects of natural disturbances, changes in ecosystem energetics and primary productivity have been the focus of comparatively little study (Sprugel, 1985). However, while measurements of net primary productivity are difficult to obtain, it is possible to estimate the annual increment of biomass accumulation. The annual increment of primary productivity in a Quebec *Fagus-Acer* forest similar to those at the study site was found to be between 900 and 1300 kg ha^{-1} (Coté *et. al.*, 1999 pers. comm.). Using this value as a baseline, the total amount of biomass lost at Mont St. Hilaire as a result of the ice storm represents between 15 and 22 years of growth by an intact canopy. However, this time window provides only a conservative estimate of how long it will take for the forest at Mont St. Hilaire to return to its pre-storm condition because it does not take into account the fact that the canopy is far from intact and that a large proportion of buds were lost as a result of the ice storm. The actual amount of time needed for recovery of the canopy at Mont St. Hilaire could be considerably longer than 22 years. This is especially apparent when it is considered that it took 16 years for the canopy to recover from the ice storm of 1983, which deposited only one-sixth to one-fourth as much ice as the ice storm of 1998 (Melancon and Lechowicz, 1987).

While it is recognised that catastrophic disturbances have important implications for ecosystem-level processes, studies of nutrient cycling following natural disturbances other than fire are uncommon, due in part to the unpredictability of such events (Vitousek, 1984). It is known, however, that the dynamics of nutrient elements in temperate forests largely depend upon the amount and rate of transfer of biomass (Khanna and Ulrich, 1991). For this reason, large-scale disturbances of the type evidenced at Mont St. Hilaire should play an important role in forest nutrient dynamics, due in large part to their ability to initiate movements of biomass from the canopy to forest floor.

In mature deciduous forests, 8 to 10 percent of the above ground nutrient pool is returned to the soil through annual litter fall (Rodin and Bazilevich, 1967). However, it is not possible to determine the percent of the total above ground nutrient pool lost as a result of this storm by simple extrapolation from the mass of litter lost. This is because the composition of litter generated over the course of a normal year and that resulting from an ice storm differ substantially in nutrient composition.

Of all tree components, leaves have the greatest nutrient content (Whittaker *et. al.*, 1979). Under non-disturbance conditions, the largest component of the litter generated in cool, temperate, broad-leaved forests over the course of a year consists of leaves shed in the autumn (Bray and Gorham, 1964; O'Neill and DeAngelis, 1981). This leaf-litter has a higher nutrient content than the branches and twigs which account for most of the litter generated by ice storms (Bray and Gorham, 1964). The material lost due to the ice storm will have a lower proportional nutrient content than would a similar mass derived over the course of a normal year's growth. The type of litter that is lost will influence the extent to which nutrient cycling is affected by a disturbance. Disturbances that occur predominantly during the winter season, as ice storms do, will return proportionally less nutrients than biomass to the soil than if they were to occur during a season when trees were bearing leaves.

Of all woody parts of a tree, branches and twigs have the greatest concentrations of nutrients. This is partially because bark contains more nutrients than wood (Khanna and Ulrich, 1991). Since the bark to wood ratio is highest in branches and twigs, the relative nutrient composition of these components is also high. As well, the branches and twigs of the canopy are subjected more than other parts of the tree to atmospheric conditions and its branches and twigs receive nutrients from the atmosphere through wet and dry deposition (Khanna and Ulrich, 1991). Twigs and buds also tend to have high concentrations of nutrients (Duvigneaud and Denaeyer-de Smet, 1970). Because of a combination of these effects, canopy components tend to possess higher concentrations of nutrients than bole components.

The different types of debris produced in response to catastrophic disturbances will influence the degree to which nutrient cycling and other ecosystem-level processes are affected. Since the most common response of forest trees to ice accumulation is the shedding of branches and twigs, the material lost as a result of the ice storm is heavily weighted towards these components. This predominance of branches and twigs in the litter means that the amount of nutrients lost will be relatively higher than would be expected for a similar mass of bole-material. While the influence of the resulting debris on nutrient cycling will be mitigated to some extent by the fact that the material contains no nutrient-rich leaves, the predominance of branches and twigs will mean that more nutrients are returned to the forest floor than if bole-material instead made up the major portion.

The same factor by which annual woody litterfall was found to have increased as a result of the ice storm at Mont St. Hilaire could be reasonably applied to the reported values for nitrogen and phosphorus composition of woody litterfall in temperate, broad-leaved deciduous forests. However, since most of the nutrient content of the litter is locked in relatively non-labile pools, little of it will be immediately available to the disturbed forest (Vitousek *et. al.*, 1982). After a disturbance a risk exists that nitrogen will be lost due to interrupted plant uptake, increases in decomposition and nitrogen mineralization, and increases in leaching and runoff (Vitousek *et. al.*, 1982). Since the mineralization of phosphorus, unlike nitrogen, is coupled with demand and not decomposition, phosphorus availability may not change substantially following a major disturbance (Vitousek *et. al.*, 1982). Although it is known that large transfers of litter to the forest floor, like those initiated by ice storms, influence nutrient dynamics and cycling, too little is known about the processes of nutrient mobilization and decomposition to predict the exact nature of these changes.

The effects of ice storm damage on ecosystem-level processes have never been studied previously. Work has focused instead on documenting the types of physical changes that occur in affected forests with relatively little attention paid to longer-term and larger-scale ramifications. In the case if the ice storm of 1998, major impacts include: vertical redistribution of living and dead biomass, subsequent reduction of foliage in the canopy, increase in organic inputs to the forest floor, reduction in canopy height, and exposure of mineral soil. The careful characterization of ice storm impacts that has dominated the study of ice storms in the past has laid the groundwork for further more rigorous study of the ecosystem-level effects of ice storms. This is because it is acknowledged that these direct changes initiated by ice storms all have the potential to alter characteristics of the soil and microenvironment that control ecosystem-level processes (Foster and Boose, 1995).

While data on the nutrient dynamics of ice storm damaged forests are non-existent, data from temperate and tropical sites affected by other forms of climatic disturbance indicate that nutrient retention in soils and biomass is high, nutrient losses are slight, and recovery of ecosystem processes is more rapid than following logging (Steudler *et. al.*, 1991; Lodge and McDowell, 1991; Bowden *et. al.*, 1993). In an experimental disturbance, in which 36 % of hardwood trees were uprooted and 32% snapped or bent, emissions of important trace gases at the soil surface were remarkably similar to control values (Bowden *et. al.*, 1993). Emissions of carbon dioxide and methane did not differ from those in the adjacent intact forest, whereas existing emissions of nitrous oxide were lowered by 78%, but only for one year. Net nitrification was low and quite similar in control and experimental areas. A major conclusion from this experiment is that nutrient-poor temperate forests, like those of Mont St. Hilaire, are resistant to changes in fluxes of carbon and nitrogen gases and are capable of establishing rapid control of ecosystem processes following extensive climatic disturbance (Foster and Boose, 1995). Despite catastrophic impact on forest structure this experimental disturbance exerted little impact on nutrient cycling (Bowden *et. al.*, 1993).

The apparently limited effect of catastrophic forest damage on nutrient cycling is the product of numerous biotic mechanisms that mitigate nutrient losses and restore pre-disturbance biogeochemical processes in forests (Vitousek *et. al.*, 1979). Following a major loss of woody-litter to the forest floor, most of the organic matter stays on-site and rates of vegetation survival and resprouting are high. In disturbance experiments in New England, initial survival of over 70% of uprooted trees during the first year after damage created an extensive canopy 1-3 metres above the ground (Foster and Boose, 1995). As observed at Mont St. Hilaire, the sprouting of damaged trees, coupled with the rapid expansion of fern, seedling and shrub layers, produces dense shade (Arii, 1999 pers. comm.). As a result, soil temperatures are elevated only slightly and little change is detected in soil moisture (Bowden *et. al.*, 1993). Rapid establishment of biotic control of the soil environment, temperature, and nutrient cycling results from plant survival, expansion and regrowth (Bowden et. al., 1993; Carlton, 1993). As well, microbes may immobilise and retain nutrients in the mineral soil and organic horizons (Lodge and McDowell, 1991).

As nutrient losses are often closely linked to changes in hydrology, information on water balances and nutrient concentrations would be especially helpful in understanding the effects of ice storm damage at the ecosystem-level (Gosz *et. al.*, 1972). In the only examination of post disturbance changes in hydrology, Patric (1974) showed that watersheds damaged by a 1938 hurricane in New England exhibited increased out-flows over a 5 year period in comparison with undamaged watersheds. Increases peaked the first year and then declined consistently (Patric, 1974). These results indicate a capacity of forested systems for recovery and normalization of flow regimes with flows gradually returning to pre-disturbance levels. This capacity may be even greater than appears from these results for heavy cutting in areas damaged by the 1938 hurricane may have been responsible for much of the observed increases in stream-flow (NETSA, 1943; Foster and Boose, 1995).

Results from studies of hurricanes and from experimental disturbances indicate that the effects of large-scale climatic disturbances on nutrient cycling and other ecosystem-level processes are generally slight and of short duration (Foster and Boose, 1995). Survival and recovery of the vegetation results in a rapid re-establishment of leaf area that mitigates soil and microenvironmental changes and promotes nutrient uptake. The result is biotic control over biogeochemical processes despite a long legacy of ensuing vegetation dynamics (Foster and Boose, 1995).

While it is well recognised that hurricane-induced wind damage is largely responsible for the structural patterning and dynamics of the forests of central New England (Foster, 1988; Henry and Swan, 1974), the role of ice storms is generally not considered in studies of forest dynamics. In this study it has been shown that the ice storm of 1998 had effects comparable to those of Hurricane Hugo in Puerto Rico (Frangi and Lugo, 1991) and roughly half those of Hurricane Gilbert (Whigham *et. al.*, 1991). Since catastrophic ice storms have been shown to occur more frequently in the forests of northeastern North America than either catastrophic wind storms or fires (Lemon, 1961), there is great potential that ice storms play a fundamental role in the dynamics and history of the forests that fall within their sphere of influence. Since the impacts of a disturbance are known to be largely related to its extent and magnitude, the effects of the ice storm of 1998, shown to be one of the most powerful disturbances on record, are likely to be substantial (De Steven *et. al.*, 1991).

A lack of knowledge concerning the effects of large scale, infrequent disturbances in forested ecosystems must be rectified if the ecological importance of these events is to be fully understood. This study reveals that ice storms are an extremely powerful form of disturbance capable of causing as much damage as other major forms of catastrophic climatic disturbance. The storm of January 1998 at Mont St. Hilaire was found to have effects greater than almost all other forms of recorded climatic disturbance, including catastrophic wind and hurricanes. Despite this, the role of ice storms in the dynamics, history, and structure of the forests of the northeast United States and adjacent Canada remains largely unknown. While preliminary results from studies of other disturbance types and from experimental disturbances indicate that the effects of ice storms on nutrient cycling and hydrology may be limited, the role of ice storms in structuring forests and driving forest succession, as indicated by the scale of biomass lost to the forest floor, appears substantial. Given that forest fires, through improved methods of suppression, are becoming less of a threat to forested lands, the importance of ice storms in structuring forest ecosystems could become more important. As well, changes in the disturbance regime of ice storms - for example, as a result of global climate change - could have important implications for the forests of the region. The substantial ecological implications of ice storms and their effects merit special attention in future work.

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CHAPTER 3

The Influence of Mechanical Properties on the Magnitude and Nature of Biomass Losses Sustained by Northern, Hardwood Tree Species Under Ice-Loading

"Trees are large heavy plants that
can kill you if they fall on you."

Alex L. Shigo,
A New Tree Biology: Facts, Photos, and Philosophies
on Trees and Their Problems and Proper Care
(Durham, NH: Shigo and Trees, 1989).

Abstract

We investigated the influence of species-specific mechanical properties on the magnitude and nature of biomass losses sustained by ten northern, hardwood tree species following a major ice storm at Mont St. Hilaire, Quebec. Differences in the magnitude of damage sustained by different species were interpreted via a susceptibility index that referenced the total biomass of litter produced against a surrogate of the pre-storm standing biomass of each species. Differences in the magnitude of damage that the study species sustained were uncorrelated with wood strength and stiffness. The nature of the biomass lost by the study species was examined in terms of the size distribution of branches in the resulting litter. The size range of lost branches indicates that the most common type of failure experienced by all species under ice-loading is associated with the smallest branch sizes measured (approximately 1.0-5.5 cm in diameter). Less than 9% of the branches lost by any of the species are greater than 5.5 cm in diameter. The median size of fallen branches decreases with the strength and stiffness of a species' wood. The proportions of branches lost from large size-classes, that account for the largest proportion of the mass lost by each species, are not predictable by mechanical properties and are more likely lost as a result of rot, disease, and other age-dependent factors. The restricted range of branch sizes from which the vast majority of branches were lost across all the study species is consistent with the range proposed to have the lowest safety-factors in the branching superstructure of forest tree species. The results of this study suggest that the distribution of factors of safety is important in determining the nature of biomass lost under ice-loading and indicate that this distribution may be generalisable across species. Building a model of this distribution would be a first step towards understanding how mechanical and architectural traits define how a canopy design copes with glaze accumulation. This study reveals that species-specific mechanical properties are not significantly related to the magnitude of biomass losses sustained by forest tree species as a result of ice storm damage, but are significantly related to the nature of the biomass lost.

Introduction

The structure and species composition of forests are influenced by the unique responses of different tree species to disturbance (Lemon, 1961; Grubb, 1977; Zimmerman *et. al.*, 1994). As a result, forests can be thought of as spatial-temporal mosaics of patches of land in different stages of recovery following disturbance (Watt, 1947; Whitmore, 1978; Putz *et. al.*, 1983). Research over the past 100 years has shown that ice storms, like other forms of climatic disturbance, influence the structure, development, and succession of forest communities (Whitney and Johnson, 1984). However, the exact nature of the influence exerted by ice storms on forested landscapes is poorly understood. This is due in part to an underlying lack of knowledge of what factors are important in determining how tree species respond to ice glaze accumulation.

Branches are shed by forest trees as a means of coping with the biomechanical stress generated by ice-glaze accumulation (Lemon, 1961; Hauer *et. al.*, 1993). When accumulations of ice reach 0.5-1.3 cm in thickness there is conspicuous breakage in smaller branches of shrubs and trees (Lemon, 1961). Branch failure occurs when loading exceeds wood resistance or when ice loading further exacerbates an already weakened area in a branch (Shigo, 1989; Hauer *et. al.*, 1993). At first only faulty limbs are lost, but as ice loads increase healthy branches are increasingly likely to be shed (Lemon, 1961). The major response of forests to the deposition of glaze is the creation of a layer of fallen woody-debris, the magnitude of which provides a quantitative measure of storm intensity.

Most ice storm studies have examined ice damage by assigning individuals to a number of arbitrary qualitative damage-classes. Only four studies have evaluated the susceptibility of species to damage in terms of the amount or type of litter produced (Bruederle, 1978; Melancon and Lechowicz, 1987; Rebertus *et. al.*, 1997; Kirby *et. al.*, 1998). The litter produced by a disturbance is particularly informative since it can provide information on not only the magnitude but also the nature of damage sustained by different species. The distribution of branch diameters provides an indication of the different modes of failure experienced by the species under ice-loading and the mass of litter can provide a highly quantitative measure of the susceptibility of species to the loss of biomass.

Species respond differently to ice glaze accumulation and some seem inherently more susceptible to ice damage than others (Abell, 1934; McCullough, 1943; Bennett, 1959; Bruederle, 1978; Whitney and Johnson, 1984). The inherent susceptibility of a species is in some part a product of species-specific properties (Bruederle, 1978). While many aspects of tree structure and morphology play a role in the mechanical response of forests to large-scale natural disturbances, some are considered to be of exceptional importance (Asner and Goldstein, 1997). Specifically, species-specific mechanical traits are considered to be among the most important factors involved in determining the susceptibility of a species to damage (Sisinni *et. al.*, 1995).

Numerous attempts have been made to correlate the mechanical properties of species with susceptibility, albeit with relatively little success (Miller, 1991). Attempts have variously been made to correlate susceptibility with wood density (Vorreiter, 1937), modulus of elasticity, modulus of rupture (Lemon, 1961; Bruederle and Stearns, 1985), and with all three of these properties (Hauer *et. al.*, 1993). In all cases, statistical relationships have not been established, although trends have been noted between the magnitude of damage sustained by a species and specific gravity and modulus of elasticity.

The nature of the biomass lost by forest tree species has received less attention than the magnitude of biomass lost. The sizes of branches lost as a result of ice-loading has only been addressed in four studies (Bruederle, 1978; Melancon and Lechowicz, 1987; Seischab *et. al.*, 1993; Rebertus *et. al.*, 1997). However, studies of the range of branch sizes lost as a result of other types of disturbance have been addressed in more detail (Putz *et. al.*, 1983). These studies indicate that species-specific mechanical properties, specifically specific gravity and modulus of elasticity, and safety-factors may be important in the determining patterns of breakage associated with climatic disturbance (Asner and Goldstein, 1997). Results from these studies indicate that tree trunks and intermediate-sized branches tend to fail when subjected to large external loads, even though the youngest branches they support remain mechanically intact (Putz *et. al.*, 1983; Mattheck, 1992; Coutts and Grace, 1995). These results indicate that the factor of safety against catastrophic mechanical failure may not be large for branches of intermediate size and may vary as a function of branch age and position (Niklas, 1999).

The concept of safety-factors is well known in the engineering and biological sciences. In these disciplines it has been recognised that any load-bearing structure may have to cope with unprecedented loads, but can not do so at the expense of an uneconomical investment in materials that is liable bring about increases in self-loading (Volk, 1958; McMahon, 1973; King, 1981; Niklas, 1999). Factors of safety provide a useful expression of the balance between the probability that a structure will fail under loading and the construction costs required to prevent that failure. The factor of safety quantifies the extent to which the mechanical and architectural attributes of a given stem or branch are able to provide a buffer against failure under loading. Niklas (1999) showed that the factor of safety varies significantly within the superstructure of *Robinia pseudoacacia* trees and adheres to a well established distribution across individuals. Evidence from the same and similar studies indicates that trends in the factor of safety may apply across species (King, 1981; Putz *et. al.*, 1983; King, 1986; Sterck and Bongers, 1998).

Two factors are expected to be important in determining the size of branches lost under ice-loading. The first of these factors is the distribution of safety factors within the superstructure of forest trees -- a distribution that it is suspected could be generalisable across species (Niklas, 1999). This distribution should mean that branches of intermediate size will be shed in greatest abundance by all species under constant loading. The second factor is the strength of the different species. Strength is often used in a general sense to refer to all mechanical properties of wood. However, wood exhibits many different types of mechanical and elastic properties. Modulus of elasticity represents a major component of the stiffness of the wood of a given species (USFPL, 1987; Niklas, 1999). Specific gravity, on the other hand, provides an approximation of wood strength and of the overall mechanical properties of a wood (USFPL, 1987). Both specific gravity and modulus of elasticity have been linked to tree failure under high wind conditions (King, 1986; Mosbrugger, 1990) and are the most important determinants of the type of structural failure experienced by a species (Putz *et. al.*, 1983). It is expected that they may influence the types of failure resulting from ice-loading conditions as well.

This paper examines the response of ten northern, hardwood tree species to a major ice storm that struck the northeastern United States, eastern Ontario, and western Quebec in January 1998. The storm resulted in the deposition of 74-110 mm of ice glaze and ranks as the most powerful ice storm on record (Hydro Quebec, 1998; Kerry *et. al.*, 1999). Our study looks at the magnitude and nature of biomass losses caused by this storm. We investigate whether mechanical properties -specifically wood strength and stiffness - are related to differences in the magnitude of biomass losses sustained by different forest tree species as a result of this storm. We also examine whether mechanical properties and the generalised distribution of factors of safety are important in determining the nature of biomass lost by the same species. By gaining a more complete understanding of how tree species respond to ice storm damage it will be possible to more fully appreciate the role that ice storms play in the ecology and dynamics of northern, hardwood forests as well as to gain insights into the evolution of alternative canopy designs in forest trees.

Methods

Seven permanent transects for monitoring forest dynamics were established on Mont St. Hilaire, in southwestern Quebec, during the summer of 1997. Located along these seven transects were 117 randomly stratified circular plots, each with a radius of 6 metres (Chapter 1, Figure 1). We used these representative plots to assess damage caused by the ice storm of January 1998 and to determine the composition of the overall forest.

To quantify the mass of litter in our study plots it was necessary to develop a sampling technique that could quickly and accurately measure the biomass of each piece of fallen debris. This was done by creating a protocol based on the conserved relationship that exists between branch diameter and mass over a wide variety of plant species of many sizes (Whittaker, 1968). Regressions relating downed branch basal diameter (>1 cm in diameter) and biomass were created for the major forest tree species of Mont St. Hilaire in May of 1998 and were used to estimate the total biomass of fallen material in our study plots (As discussed in Chapter 2, Methods).

Equations for estimating litter biomass were created for ten species, including: Striped maple (AP, *Acer pensylvanicum* L.), Sugar maple (AS, *Acer saccharum* Marshall.), Paper birch (BP, *Betula papyrifera* Marshall.), Yellow birch (BA, *Betula alleghaniensis* Britton.), White Ash (FA, *Fraxinus americana* L.)., American beech (FG, *Fagus grandifolia* Ehrh.), Ironwood (OV, *Ostrya virginiana* (Miller) K. Koch.), Large-tooth aspen (PG, *Populus grandidentata* Michx.), Red oak (QR, *Quercus rubra* L.), and Basswood (TA, *Tilia americana* L.) (Chapter 1, Table 1).

Differences in the magnitude of biomass lost by the study species were measured via a susceptibility index that normalised the biomass lost by the species by their pre-storm standing biomass. This was necessary since the absolute amount of biomass lost by the species is expected to be highly correlated with their relative dominance at the study site (Bruederle, 1978). The susceptibility index divided the total biomass of litter produced by each species against a surrogate of each species' pre-storm standing biomass. The cumulative diameter-at-breast-height (dbh) of each species in the study plots was used as a surrogate of the pre-storm standing biomass of each species. As the plots were censused for downed branches, the dbh was recorded for all trees in the study plots with dbh greater than 3 cm.

Correlational analyses were performed to determine if the median and mean size of lost branches were related to specific gravity or modulus of elasticity. Correlational analyses were also conducted to determine whether species-specific mechanical properties - specifically, wood strength and stiffness - are related to the magnitude of damage sustained by forest tree species. Specific gravity was used as a measure of overall wood strength and the static bending modulus of elasticity was chosen as a measure of wood stiffness – a higher modulus of elasticity is indicative of greater wood stiffness (USFPL, 1987; Haygreen and Bowyer, 1996). The values for the mechanical properties were taken from a compilation of data on the strengths and related properties of Canadian woods (Jessome, 1977). Green properties were used in the analysis of mechanical characters since a large literature indicates that the strength of wood, as well as the elastic modulus and proportional limit, are significantly lower for green than air-dried wood (USFPL, 1987). Thus, the mechanical behaviour of a living tree is likely to differ significantly from estimates based on the mechanical properties of air-dried wood (Niklas, 1997[b]).

Results

Linear regression analyses were performed on untransformed branch weights and basal diameters and their natural logarithmic transformations (As discussed in Chapter 2, Methods). Transformation improved the coefficient of determination (r^2) significantly over the fit provided by the simple linear model. Therefore, the predictive relationships used were based on the transformed data. Strong relationships were found between branch basal diameter and biomass for each of the ten species under investigation (Appendix I). The coefficients of determination were above 0.94 in all cases, with $p < 0.001$.

The ten major tree species of the forests of Mont St. Hilaire differed in their contributions to the mass of litter (Table 1). Litter from the three most prolific species -- Sugar maple (*Acer saccharum*), Red oak (*Quercus rubra*), and American beech (*Fagus grandifolia*) -- accounted for 93% of the total estimate. Together, the other seven major species at the study site accounted for the remaining 7% of the estimated mass of litter.

Table 1. Mass of woody-litter produced as a result of the ice storm of January 1998, % of total litter mass accounted for by each of the study species, number of pieces of litter from each species, and cumulative dbh and basal area of trees of all species in 177 permanent plots.

Species	Litter Mass ($kg\ ha^{-1}$)	% of Total Litter Mass of Study Spp.	# of Pieces of Litter	Cumulative dbh of Trees per Hectare (cm)
Acer pensylvanicum	313.7	1.6	617	1145.6
Acer saccharum	8284.7	41.6	8747	8817.7
Betula alleghaniensis	122.3	0.6	105	202.2
Betula papyrifera	60.3	0.3	177	637.0
Fraxinus americana	590.4	3.0	1058	895.7
Fagus grandifolia	4585.2	23.0	3434	3400.7
Ostrya virginiana	203.3	1.0	163	1350.0
Populus grandidentata	49.4	0.3	32	31.1
Quercus rubra	5614.6	28.2	3071	2326.7
Tilia americana	97.0	0.5	133	2326.7
Other*	-	-	176	766.5
Total	19920.9	100.0	17713	19816.8

*Other species: *Amelanchier laevis* Wieg. (Serviceberry), *Prunus nigra* Ait. (Black cherry), *Cornus alternifolia* L.f. (Pagoda dogwood), *Prunus virginiana* L. (Choke cherry), *Acer spicatum* L. (Mountain maple), *Prunus serotina* Ehrh. (Pin cherry), *Pinus resinosa* Ait. (Red pine), *Pinus strobus* L. (White pine), *Tsuga canadensis* (L.) Carrière (Eastern hemlock).

Differences in the contributions from the individual species are to a large part a product of differences in the abundance of each species. As determined in previous studies, the litter contributions from different species show a strong positive correlation with the cumulative dbh of each at the study site ($r= 0.91$, $p<0.0005$). For this reason, a susceptibility index was employed that would allow us to assess differences in the susceptibility of the species to loss of biomass irrespective of their individual contributions to the pre-storm biomass of the stand.

When the susceptibility index (S.I.) using the cumulative dbh of each species was calculated, it was revealed that the major tree species of Mont St. Hilaire exhibit variation in susceptibility to ice storm damage (Table 2). A larger susceptibility value indicates greater susceptibility to the loss of biomass.

Table 2. Susceptibility of the study species to loss of biomass as a result of glaze accumulation listed in order of decreasing susceptibility to the loss of biomass.

Species	Susceptibility Index
Quercus rubra (Red oak)	2.413
Populus grandidentata (Large-tooth aspen)	1.587
Fagus grandifolia (American beech)	1.349
Acer saccharum (Sugar maple)	0.940
Fraxinus americana (White ash)	0.660
Betula alleghaniensis (Yellow birch)	0.605
Tilia americana (Basswood)	0.400
Acer pensylvanicum (Striped maple)	0.274
Ostrya virginiana (Ironwood)	0.151
Betula papyrifera (White birch)	0.095

Correlational analysis revealed that neither specific gravity ($r=0.39$, $p=0.29$), as representative of wood strength, nor modulus of elasticity ($r=0.50$, $p=0.15$), as representative of wood stiffness, were significantly correlated with the susceptibility of the species to loss of biomass.

The species show a common trend in the distribution of lost branches over the range of size-classes for all species pooled together (Figure 1). The largest 5% of lost branches account for 75% of the lost biomass. When the lost branches are ranked according to size there is a sudden increase in the cumulative biomass of litter that each additional branch accounts for beyond the 95th percentile. 95% of all branches lost were less than 5.5 cm in diameter but accounted for 25% of the biomass of litter produced.

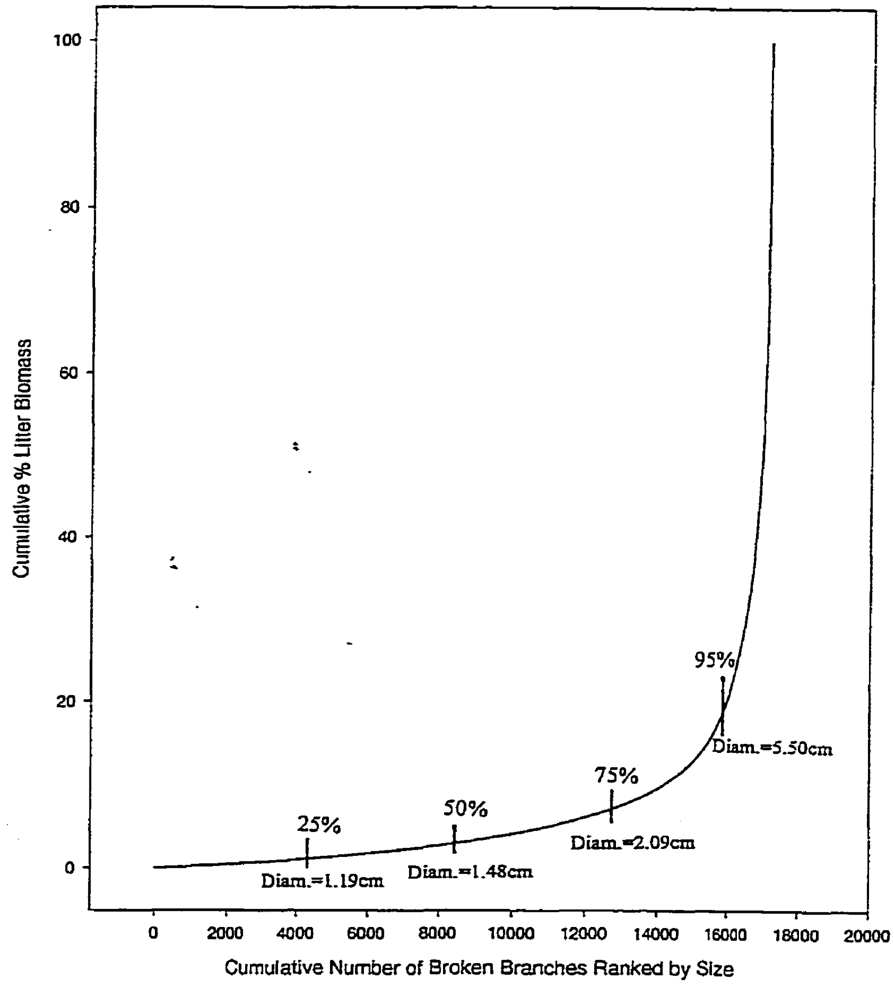

Figure 1. Relationship between the cumulative number of branches ranked by size and the cumulative % of litter biomass accounted for. Slashes denote quartiles, median, and 95th percentile with respect to ranked branch diameter. Diameter values are branch diameters associated with the above percentile.

To discover whether the species in the study plots differ in the size range of branches they shed, the size-distribution of the litter produced by each species was plotted. Figures 2 depicts the frequency of branches in the litter produced by the study species in 0.5 cm diameter size-classes. The diameter recorded was the basal diameter of the fallen branches. The y-axis represents the proportion of the total number of branches and total branch mass in any size-class for a given species.

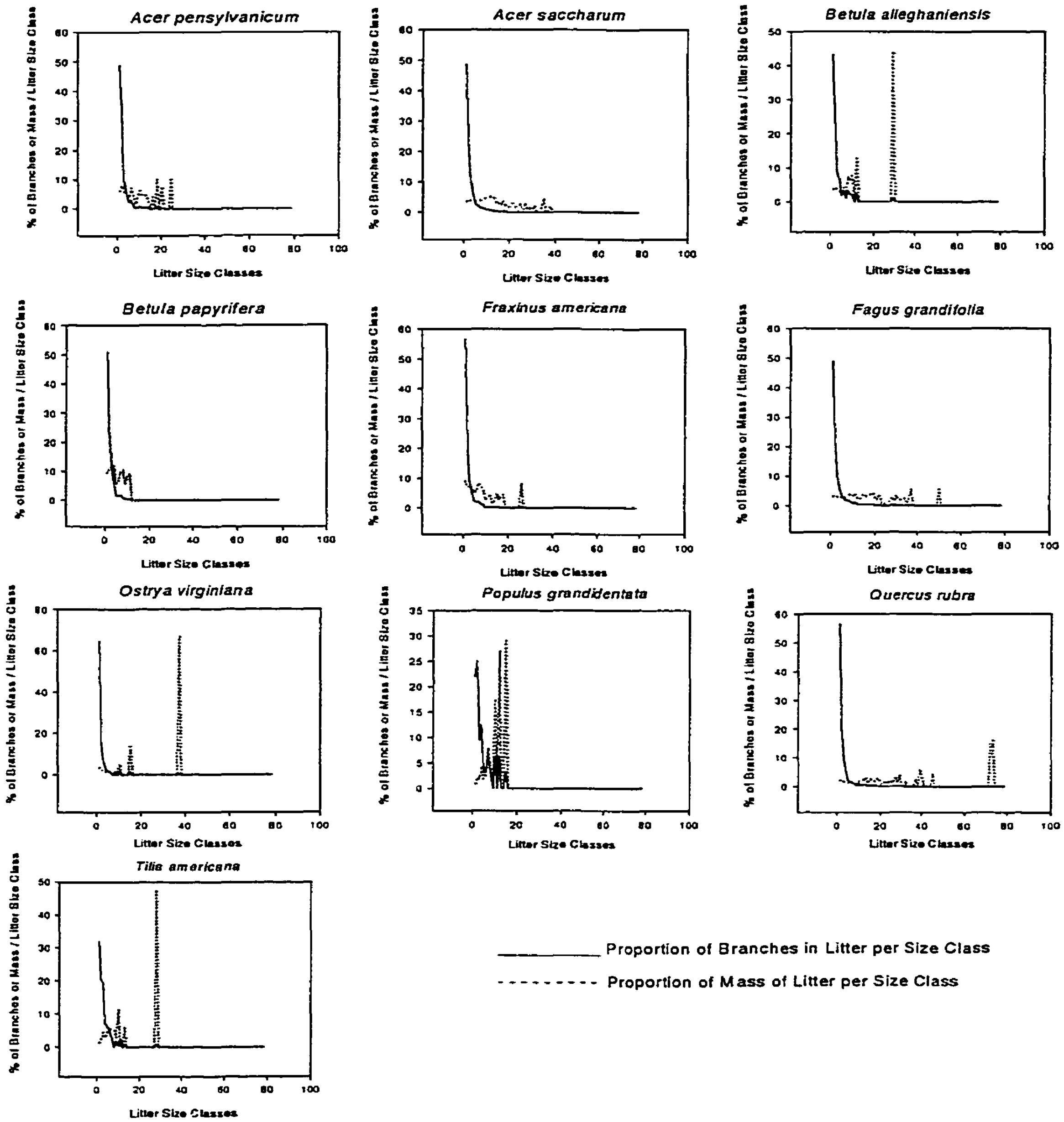

Figure 2. Number and mass of branches in 0.5 cm diameter-classes. The first interval is 1.0-1.5 cm in diameter. Solid-lines indicate proportion of branches in each 0.5 cm size interval (%). Dashed-lines indicate proportion of total litter mass in each size-class (%).

While a trend towards a common dominant mode of failure is shared by all species, the species do also exhibit differences in the size of branches lost. The median diameters of the litter produced by each species were found to be negatively and significantly correlated with both overall wood strength, as represented by specific gravity, and wood stiffness, as represented by the modulus of elasticity. Median diameter was found to be significantly and negatively correlated with specific gravity ($r=-0.88$, $p<0.005$) and modulus of elasticity ($r=-0.87$, $p<0.005$) (Figure 3). Species with stronger, stiffer wood have a smaller median size of lost branches.

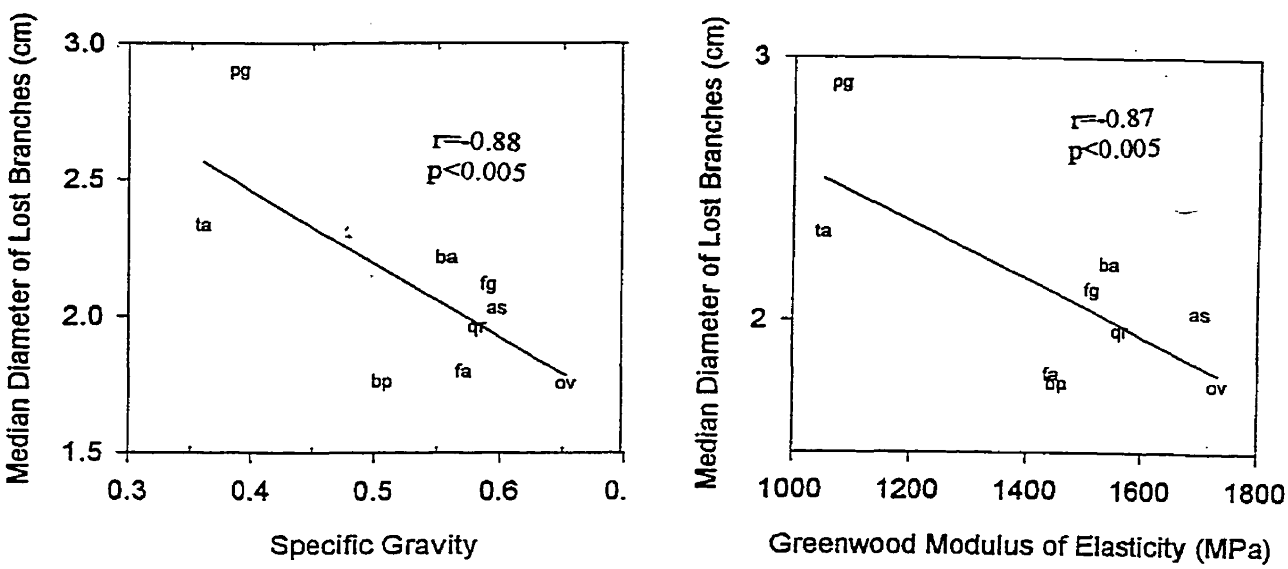

Figure 3. Correlation of the median diameter of branches lost by the study species with greenwood specific gravity ($r=-0.88$, $p<0.005$) and modulus of elasticity ($r=-0.87$, $p<0.005$).

The relationship between median branch diameter and species-specific mechanical properties is driven by differences in the proportion of branches falling in size-classes at the small end of the size scale. Differences in the proportion of branches in each of the three smallest measured size-classes are significantly and positively correlated ($r>0.60$, $p<0.05$) with the wood strength and stiffness, while the proportions of branches in larger size-classes fail to demonstrate significant correlations with these properties.

Discussion

Species-specific mechanical properties are not consistently related to differences in the magnitude of biomass lost as a result of ice-loading, but are related to the nature of that lost biomass. While the first of these results is not different from the findings of most other ice storm studies (Lemon, 1961; Bruederle, 1978; Bruederle and Stearns, 1985; Miller, 1991; Hauer *et. al.*, 1993), the second is novel and will be important in allowing us to better understand how forest tree species respond to glaze accumulation and loading in general.

All of the study species shed a large majority of small branches and a minority of large branches, with the few large branches accounting for the largest proportion of lost biomass. This result focuses attention on the possibility that different factors may be important in determining which relatively large and which relatively small branches are shed under ice-loading. While the size of small branches lost by each species is related to interspecific differences in wood strength and stiffness, large branches may be lost for a wider variety of reasons. This possibility is reinforced by the presence of strong correlations between the proportion of branches in the three smallest measured size classes and differences in the strength and stiffness of the species and by the lack of correlations between these properties and the proportions of branches lost from larger size-classes. Since the effects of rot, disease, and infestation by insects, animals, and micro-organisms accrue over time (Haygreen and Bowyer, 1996), the probability that a branch is lost as a result of these factors is roughly proportional to its age (Bruederle and Stearns, 1985; Sisinni *et. al.*, 1993). Large branches are more likely to be lost as a result of these secondary factors than small branches that have had less exposure to pathogenic elements and previous disturbance. It has been found that the majority of large branches lost as a result of ice storm damage are rotten, while the majority of small branches lost are alive and sound (Rebertus *et. al.*, 1997). The loss of large branches under ice loading parallels the process of natural pruning, while the loss of smaller branches shows a dependence on the mechanical properties of the species that may be indicative of differing evolutionary strategies for coping with glaze accumulation.

Small branches were most commonly shed by the study species in response to ice-loading. The size-range of the branches most commonly encountered in the litter extends up to 5.5 cm in diameter with 95% of all branches having a diameter less than this size. When branches in the litter are ranked by diameter, there is a large increase in the cumulative biomass of litter accounted for by each additional branch greater than 5.5 cm in diameter. This conservative pattern of branch loss is consistent with the expectations of the distribution of factors of safety quantified by Niklas (1999) for *Robinia pseudoacacia*. According to this distribution, branches of intermediate size have the lowest factors of safety in the branching superstructure of this tree species (Niklas, 1999). The margin of error against failure under loading provided by the mechanical and architectural traits of intermediate sized branches is lower than for any other size range of branches because they are less able to accumulate woody tissues in proportion to their rate of extension growth. Despite their high rate of extension growth, the most terminal twigs are expected to have larger factors of safety as a result of their high flexibility (Vogel, 1995). Larger branches more proximal to the trunk have high factors of safety because of their ability to accumulate woody tissue at a rate greater than extension growth (Niklas, 1999). That all the study species responded to glaze accumulation by predominantly losing branches in the size-range expected to have the lowest safety-factors indicates that the distribution of safety-factors may be generalisable across species. Such a general model for the distribution of safety factors is not unrealistic when the conservative nature of primary and secondary stem growth and development across dicot species is considered (Esau, 1965; Gifford and Foster, 1988). Such a model would be especially important since these results indicate that the distribution of safety-factors may be of fundamental importance in influencing how tree species respond to glaze accumulation and to loading in general.

Since the pattern of branch breakage observed in this study suggests that the possibility exists for a model of safety-factors that is generalisable across species, the exact nature of this distribution as it is now known merits some consideration with respect to the damage observed in this study. Two points of greatest weakness under loading are described in Niklas' (1999) quantification of the distribution of safety-factors in forest trees. The lowest factors of safety are associated with the base of the tree and the second lowest are associated with branches of intermediate size, ranging from approximately 1.0-5.0 cm in diameter (Niklas, 1999, pers. comm.). While branches of intermediate size were found to be most abundant in the litter produced by the ice storm, many fewer whole trees were lost as a result of collapse at the base of the trunk. Trunk collapse occurs less commonly than might be expected from the very low associated safety-factors since the force of ice accumulation is directed vertically and, without the added effects of wind, lacks a horizontal component. The extremely low safety-factors associated with the base of trees will be of greater concern in windstorms or in the case of individuals that are either highly flexible or have asymmetric form. For example, in this study Striped maple was found to suffer from a high rate of stem-buckling. Stem-buckling occurred because this species' high flexibility allowed it to accumulate ice along its bent trunk and generate bending strain at the tree base. For most species, however, damage in this storm was focused on branches and the lowest safety-factors of concern in the overall distribution are those associated with branches of intermediate size.

Knowing how and why species respond as they do to ice-loading is important for several reasons. Understanding the nature of the response of species to glaze accumulation can help us to understand the evolution of the mechanical and architectural traits of tree species. As well, an ability to predict the magnitude and nature of the biomass lost by different species under ice loading could be useful for forestry planning (McKellar, 1938; Williston, 1974; Sisinni *et. al.*, 1995). The results of this study indicate that mechanical factors are important in determining how many small branches of different size classes are lost by a species, but are not fundamental in determining how many large branches of different size classes are lost. Most of the biomass lost by a species will be accounted for by the few large branches, which are likely to be lost as a result of disease, rot, or other non-mechanical factors, and not by the many small branches whose size-distribution is predictable. Tree mortality, presumably the impact of greatest concern to foresters, will be most influenced by the somewhat stochastic loss of larger branches. From an applied perspective, it will be important to select trees for planting in ice storm prone areas that are relatively resistant to rot and disease and of lesser concern that species do not have a high proportion of branches that fall within the range most susceptible to loss. While the ability to predict the median size of branches lost by the study species based on mechanical properties will be of limited use in forest planning and management, this ability could represent an advance in the study of the evolution of canopy design.

From an evolutionary perspective, the size-range of lost branches can provide a window into interspecific differences in the evolution of canopy and branch design. Evolutionary questions relating canopy design to the influence of ice storms are especially applicable since ice storms are the most frequent form of disturbance affecting the forests of northeastern North America (Melancon and Lechowicz, 1987) and as such are likely to have played a role in the evolution of specific characters of tree species in the region. In this case, strong interspecific differences in the response of the study species to glaze accumulation were observed. The median size of branches lost by different species showed a strong negative correlation with both wood strength and stiffness. Why should species with weaker and less stiff wood lose larger median size branches? A possible explanation is that these species lose larger branches because their increased flexibility leads to a moment-arm of increased length. Many other possible explanations for the loss of larger or smaller median size branches can be conceived of if the branching traits of the individual species are considered in combination with their mechanical characters. Although we have quantified how mechanical attributes affect the size of lost branches, it is still difficult if not impossible to assess exactly how variation in these traits affects the size of lost branches without a similar quantification of how the species differ with respect to architecture. For instance, differing taper-ratios will have a profound effect on the size of lost branches since this ratio together with the diameter of breakage will dictate the critical moment-arm length. Since each species has a unique taper-ratio, the exact strategic implications of losing different sizes of branches can not be fully explained without both pieces of information. A more complete picture of why species have adopted their unique canopy architectures in glaze-prone regions will only emerge once the second aspect of this equation has been quantified and we are able to put mechanical and architectural attributes together to completely quantify the design parameters of forest tree canopies. Our results show that the mechanical aspect of this equation is of quantifiable importance in the strategy of a species to withstand glaze accumulation and should serve as a call to quantify the architectural aspect in an attempt to fully understand the strategic implications of canopy design for dealing with glaze accumulation. Modelling the distribution of safety factors against failure under loading within and across species would be a first step towards accomplishing this goal.

In this study we established that species-specific mechanical attributes are related to the sizes of small branches shed as a result of ice-loading, but are not related to the sizes of larger lost branches. We also established that the dominant mode of failure under ice-loading is generally consistent across species and occurs in association with branches of intermediate size. This mode of failure coincides with the location of the lowest branch safety-factors in the whole-tree distribution of factors of safety (Niklas, 1999). These results lend credence and support to the idea that there is a consistent distribution of safety-factors in the branch and trunk elements of forest trees and indicate that tree mechanics play an important part in determining the exact types of damage that result from glaze accumulation. The results suggest that it is time for a generalized cross-species model of the complete distribution of safety-factors in forest trees. By allowing us to gain an understanding of how forest trees respond to glaze accumulation, such a model would allow us to understand the influence of ice storms on the ecology and dynamics of the forests of northeastern North America.

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SUMMARY

This study reports the impacts of a catastrophic ice storm on the old-growth hardwood forests of Mont St. Hilaire, Quebec. The total biomass of litter was estimated for ten of the major species at the study site and was compared with losses reported in the literature for other ice storm, windstorms, and insect outbreaks. The influence of mechanical properties on the magnitude and nature of biomass lost by each of the study species formed the basis for a second avenue of investigation.

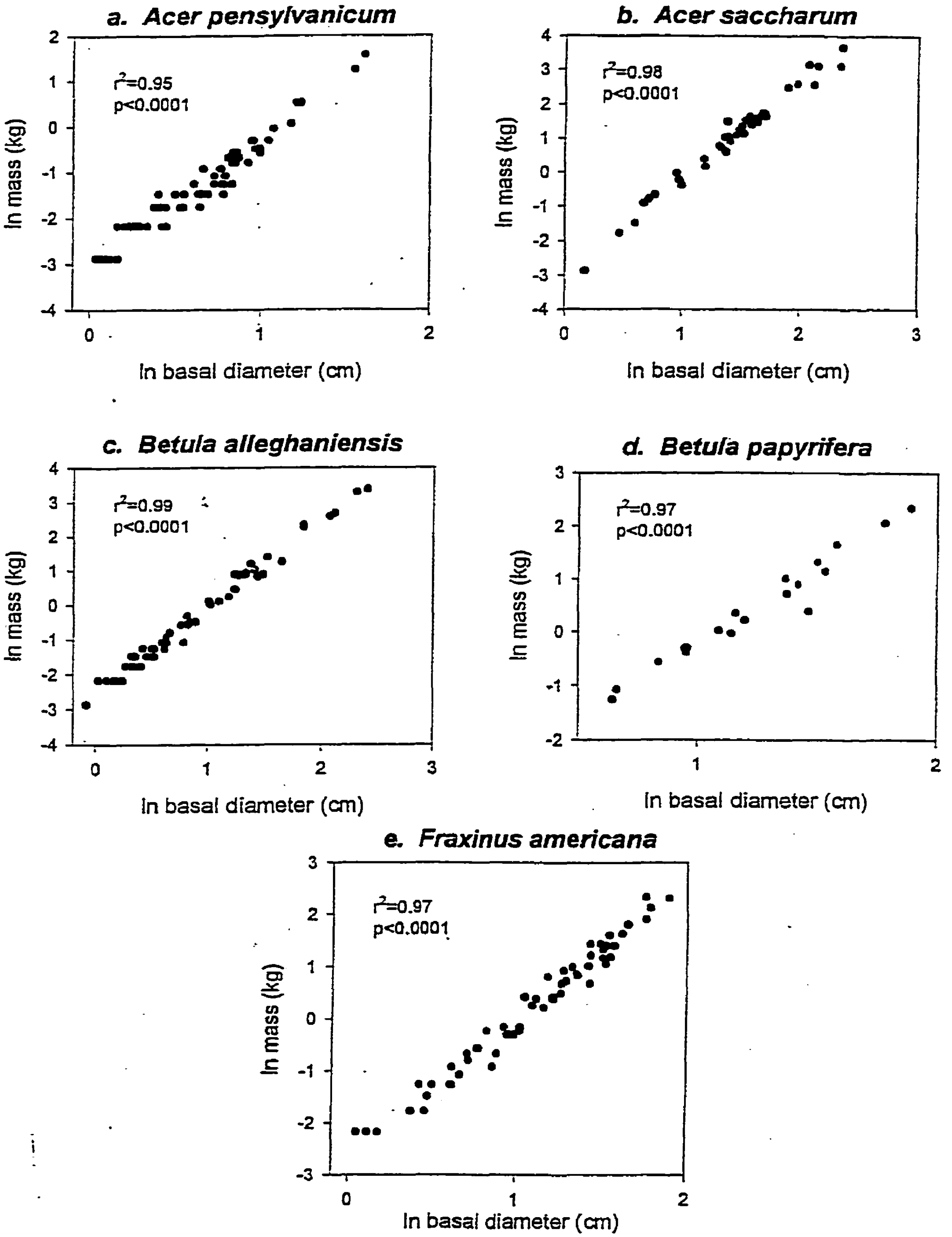
The magnitude of biomass loss sustained at the study site indicates that ice storms of this scale have the potential to play an important role in the ecology and dynamics of northeastern North American forests. The ice storm of January 1998 brought about large changes in the distribution of forest biomass at the study site. We estimate that the ice storm of January 1998 produced 19.9 metric tonnes or 33.6 m^3 of woody litter per hectare. This level of litter production is approximately 20 times greater than is expected in the course of a normal year and corresponds to a loss of between 7-10% of the total pre-storm standing biomass of the stand. In terms of litter production, the ice storm of 1998 ranks as the most powerful ice storm on record and amongst the most powerful forms of climatic disturbance experienced in forested ecosystems. Results from other studies of disturbance in forest ecosystems indicate that the impact on nutrient cycling and other ecosystem-level processes of a disturbance even as large as this ice storm will be mitigated to a large extent by the rapid re-establishment of biotic control over biogeochemical processes. The storm will, however, have a long-lasting influence on vegetation dynamics at the site.

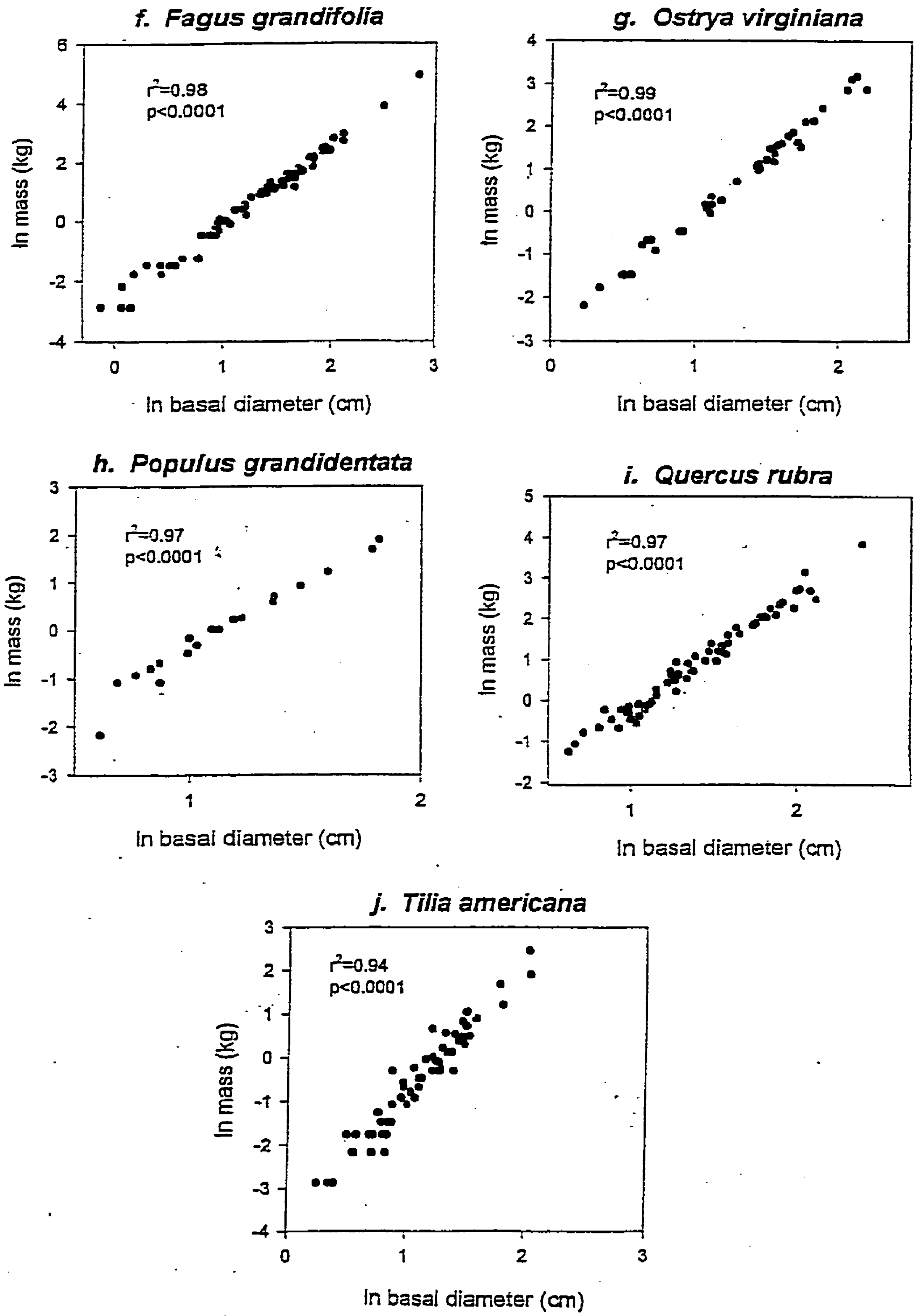
The results of this study also indicate that the nature of the biomass losses brought about by ice storms in northern, hardwood forests are extensive and, to some extent, predictable. Small branches are shed in relation to species-specific mechanical properties, while larger branches are shed primarily in response to other factors. The median size of the biomass lost by these species was negatively correlated with the specific gravity and modulus of elasticity of the study species. The median size of fallen branches decreased with a species' wood strength and stiffness. Species-specific mechanical properties were not correlated with differences in the magnitude of biomass lost by the study species. The study species exhibited some similarity in their response to glaze accumulation. The majority of branches lost were of small size (<5.5cm in diameter), but the majority of biomass lost was accounted for by a relatively small number of large branches. The species responded to glaze accumulation with by predominantly losing branches of a size range associated with the expected position of the lowest factors of safety in the superstructure of forest tree species. The fact that all of the study species demonstrated this common response indicates that the distribution of safety-factors may be generalisable across species. Attempting to model the distribution of safety-factors for different tree species would be a first step in trying to build a better picture of how different canopy designs respond to glaze accumulation and loading in general.

APPENDIX I

Relationship between basal diameter and mass of branches in litter produced by study species

Appendix I. This appendix contains individual graphs of the relationship of ln mass (kg) versus ln basal diameter (cm) for the ten study species. These relationships form the basis for the equations used to estimate the total biomass of litter resulting from the 1998 ice storm at Mont St. Hilaire, Quebec.


a. Acer pensylvanicum
r²=0.95
p<0.0001
ln mass (kg)
ln basal diameter (cm)
b. Acer saccharum
r²=0.98
p<0.0001
ln mass (kg)
ln basal diameter (cm)
c. Betula alleghaniensis
r²=0.99
p<0.0001
ln mass (kg)
ln basal diameter (cm)
d. Betula papyrifera
r²=0.97
p<0.0001
ln mass (kg)
ln basal diameter (cm)
e. Fraxinus americana
r²=0.97
p<0.0001
ln mass (kg)
ln basal diameter (cm)


f. Fagus grandifolia
r²=0.98
p<0.0001
ln mass (kg)
ln basal diameter (cm)
g. Ostrya virginiana
r²=0.99
p<0.0001
ln mass (kg)
ln basal diameter (cm)
h. Populus grandidentata
r²=0.97
p<0.0001
ln mass (kg)
ln basal diameter (cm)
i. Quercus rubra
r²=0.97
p<0.0001
ln mass (kg)
ln basal diameter (cm)
j. Tilia americana
r²=0.94
p<0.0001
ln mass (kg)
ln basal diameter (cm)

Appendix II

Notes on Quantitative Versus Qualitative Assessments of Susceptibility to Damage

Appendix II. This appendix contains a comparison of methods for assessing the susceptibility of forest tree species to ice storm damage. Susceptibility values from the quantitative method pioneered in this thesis for estimating litter-mass are compared with the average damage scores from a qualitative survey method similar to that used in most other post-disturbance damage studies.

Since virtually all post-disturbance studies of forest damage have relied on qualitative surveys to produce estimates of damage, a similar method was carried out in association with this study for comparative purposes. Initially, the dbh of all trees greater than 3 cm in diameter in our 117 study plots was recorded. The degree to which each of these individual trees sustained damage was then tallied according to a five-rank scale (Figure 1). This scale is similar to those used in most other studies of ice storm, and of disturbances in general. A score of 1 corresponds to none to very little damage with canopy loss in the range of 0-5%. A score of 2 corresponds to minimal damage or loss of between 5-25% of the canopy. A score of 3 represents moderate damage and the loss of between 25-50% of the pre-storm canopy, while a score of 4 represents heavy damage and canopy loss exceeding 50%. The highest score, 5, corresponds to complete loss of the canopy and breakage of the stem; a score of 5 represents catastrophic or fatal damage.

To determine how or if the study species differed with respect to their overall response to glaze accumulation the average damage score was computed for each species. This value is simply the average damage rank sustained by a species. According to their average damage scores, the study species differed in their susceptibility to the loss of biomass and in their response to glaze accumulation (Table 1).

Table 1. Average qualitative damage scores for major tree species of Mont St. Hilaire and susceptibility values as determined by estimation of lost biomass per species.

Species	Average damage scores	Susceptibility Values
Acer pensylvanicum	4.18	0.274
Acer saccharum	3.08	0.940
Betula alleghaniensis	2.60	0.605
Betula papyrifera	2.00	0.095
Fraxinus americana	3.28	0.660
Fagus grandifolia	3.35	1.349
Ostrya virginiana	2.14	0.151
Populus grandidentata	4.00	1.587
Quercus rubra	3.44	2.413
Tilia americana	3.00	0.400
All	3.10	-

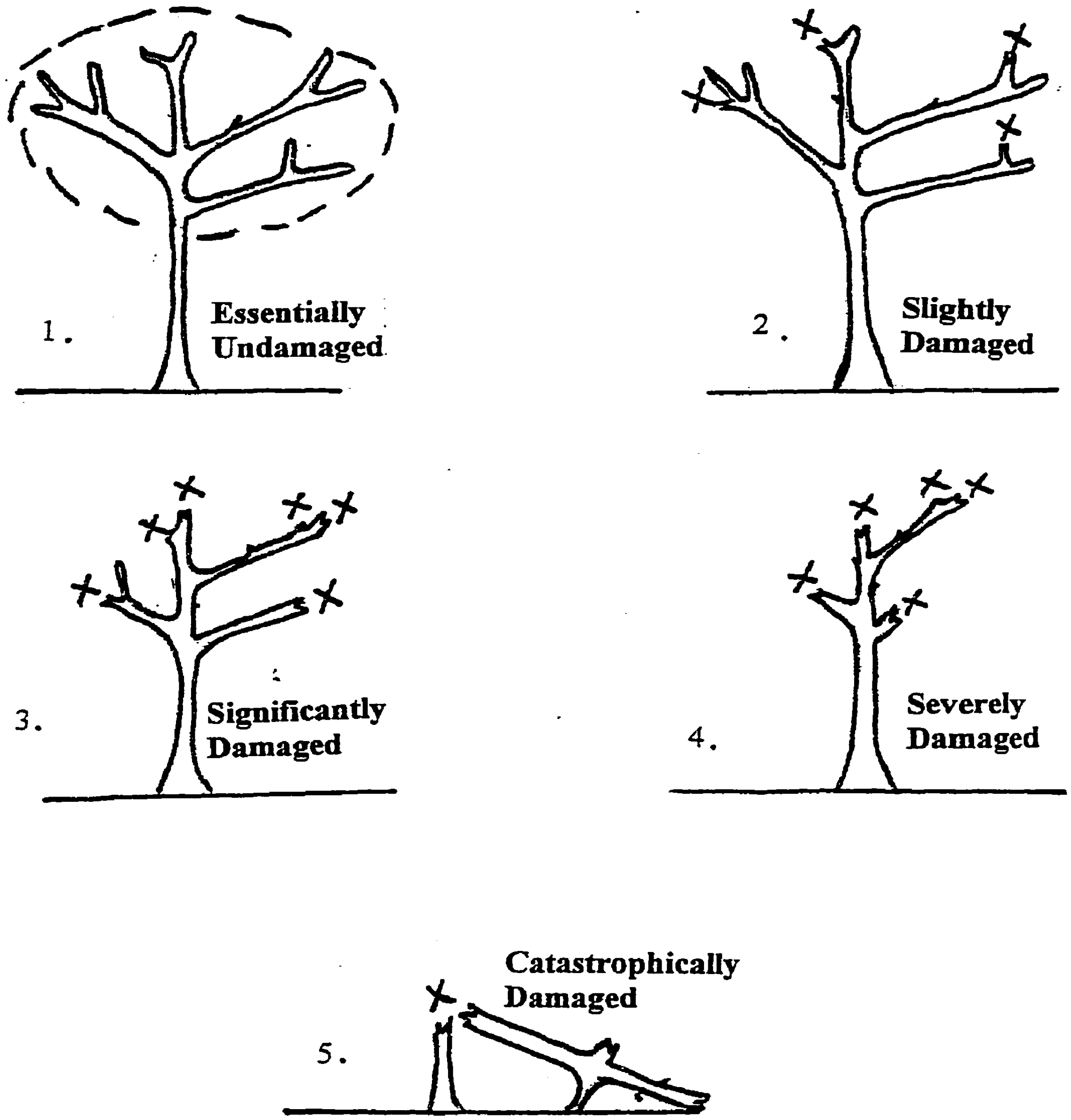


Figure 1. 5-class system for estimating extent of ice storm damage to forest trees. A score of 1 represents loss of 0-5% of branches in canopy. 2 represents loss of 5-25% of branches. A score of 3 corresponds to between 25-50% branch loss. A score of 4 represents greater than 50% damage, while 5 refers to complete stem-collapse and total crown loss.

The average damage scores from the qualitative survey provide a measure of the extent to which different species suffered damage under glaze conditions much in the same way that the values calculated for the susceptibility of each species to the loss of biomass do (Chapter 3). The primary advantage of the qualitative damage survey is the relatively rapid speed with which it can be conducted. Each plot took approximately 1 man hour to census when the qualitative survey was conducted. The quantitative method, on the other hand, required 3-8 man hours per plot.

Susceptibility to loss of biomass, as calculated according to our susceptibility index also provides a measure of the average damage sustained by species as a result of glaze accumulation but is the product of a more careful and quantitative effort. Since the quantitative survey method requires much greater investments of time and labour, it is desirable to see if the results from the two methods are correlated. If a significant correlation exists between the two, a considerable savings of time and labour could be realized by adopting the more rapid and less labour-intensive qualitative survey method.

No significant correlation was found between our susceptibility values and the results of the qualitative survey ($r=0.49$, $p=0.15$). The fact that these two measures of average damage are not significantly related indicates that if one wants to find the susceptibility of a species to loss of biomass, a qualitative survey will not be sufficient. Instead, a method such as the regression technique for estimating downed branch biomass employed in this study will have to be used. To fully understand the ecosystem-level effects of large scale disturbances such as an ice storms one will need to employ a method that is able to quantify damage in terms of the biomass of litter produced.

APPENDIX III:

Archived field and computer files

Appendix III. This appendix names, locations, and other pertinent details on field data and computer files used in this project. All computer files are compressed onto a number of archive diskettes. All files are PC format; the file extensions indicate the programme used to create them.

Archived Field Data and Computer Files Associated with M.Sc. Thesis

These files are compressed into several archived diskettes. Both Professor Lechowicz and myself have copies. All files are PC format; the extensions indicate the programme used to create the files and with which they may be accessed.

.doc - Word for windows 6/98
.sas - SAS code
.txt - text file, for importing data to SAS
.jnb - sigma plot workbook
.xls - Excel file (6/98)

1) **Hard copy of field data:**

All field data collected during the summer of 1998 is recorded in two binders. One copy of the original data is kept by me and the other by Professor Lechowicz.

2) **Spreadsheets of original data:**

a) Qualitative survey of ice storm damage for 117 permanent plots: **MHIcestorm(Archive).doc**

b) Diameters (all plots) and lengths (subset of plots) of pieces of fallen litter > 1cm in diameter for 117 plots: **(Archive)HooperPlotData.doc**

c) Diameters of all litter encountered on plot-centered transects at 64 of the 117 permanent plots (for volumetric estimation): **HoopTrans'98(Arhive).doc**

e) Species, mass, and diameter of all branches collected to produce species-specific regressions relating branch diameter to mass: **Buttdiamregress.jnb**

f) Spreadsheet of mechanical parameters for study species: **Mechsprd.xls**

3) Archived text of thesis:

The entire thesis is archived in hard-copy in the Blacker-Wood Biology Library of McGill University, with Professor Lechowicz, and with myself. The thesis is also stored on the archive diskettes as **Hooperthesis.doc**.

4) SAS codes for manipulation and analysis of data:

All code written in the course of learning to use and actually using SAS is recorded in my lab book. This book has been photocopied and a copy left with Professor Lechowicz. All SAS code is also stored on the archive diskette. Details on critical SAS files are listed below:

a) Dimensional information on litter measured in 117 permanent plots was stored in three smaller files for import to SAS:

Plot_a.txt
Plot_b.txt
Plot_c.txt

b) Three small files created for import to SAS were merged into a single file containing all dimensional information on litter lost in our study plots: **Merge.sas**

c) The mass of fallen litter in each plot was determined by applying the species-specific branch diameter-mass relationship and appropriate correction factors: **Corrfactplot.sas**

d) Mass of litter produced by each species across all plots was determined by applying the species-specific branch diameter-mass relationships and appropriate correction factors: **Corrfactspp.sas**

e) To determine the dbh of each species across all plots the dbh measured for all trees was imported into SAS in spreadsheet form and saved as: **Dbh.txt**

f) To determine the cumulative dbh of each species in all of our study plots: **Dbh.sas**

g) To determine the basal area for each species in the 117 permanent plots: **Basal.sas**

h) To determine the basal area of all trees for each species in all 117 plots: **Baplot.sas**

i) Text file of diameters of downed litter along plot-centered transects for volumetric estimation: **Hooptran.txt**

j) To input diameters measured along plot-centered transects into SAS: **Tran.sas**

k) To produce output of diameters of squared diameters of branches along plot centered transects: **Trandiam.sas**

l) Saved text copy of output of squared diameters for use in volume-estimation equation: **Trandiam.txt**

m) To calculate volume of woody-debris produced by ice storm of 1998: **Volumesp.sas**

n) Saved data on damage classifications for all trees > 3 cm in diameter in our study plots: **Icestorm.txt**

m) To produce mean damage values from qualitative survey of damage: **Icestorm.sas**

n) To estimate total pre-storm standing biomass from different predictive equations for eight of the ten study species: **Treemass.sas**

o) To get frequency and proportion of lost branch mass accounted for by size classes of 0.5 cm, beginning at 1.0 cm: **Classes2.sas**