Carbohydrate reserves in *Acer saccharum* trees damaged during the January 1998 ice storm in northern New York

B.L. Wong, L.J. Staats, A.S. Burfeind, K.L. Baggett, and A.H. Rye

Abstract: To assess the effect of the ice storm of January 1998 on sugar maple (*Acer saccharum* Marsh.) tree health, starch, and soluble sugars in twigs from two damaged sugarbushes (younger: trees 50–100 years old, and older: trees approximately 200 years old) in northern New York were measured throughout the leafless phase (September 1998 – May 1999). Trees severely damaged by the ice storm exhibited signs of recovery during the first growth season (1998), that is, greater numbers of lateral (epicormic) shoots and increased wood production in the current year growth ring of branches at mid-crown, and high concentrations of starch in the twigs at the time of leaf drop. Differences in reserve and soluble sugar profiles between damaged and slightly damaged or undamaged sugar maple trees and between trees of the older sugarbush and those of the younger sugarbush indicate changes in cold season physiology of damaged trees in adapting to or tolerating cold temperature. In damaged trees of the younger and older sugarbushes, the profiles of sucrose, stachyose, raffinose, and xylose were similar to those of corresponding slightly damaged or undamaged trees throughout the cold season, except for late winter sucrose, glucose, and fructose profiles, which exhibited differences in concentration and profile configurations compared with respective slightly damaged or undamaged trees. A lower concentration of sucrose in damaged older tree wood tissue after dehardening in late winter and a lower concentration of "resynthesized" starch just prior to vernal growth were observed. The data indicate that the profiles of individual sugars can provide information on changes in physiological and biochemical processes in damaged trees during the cold season.

Key words: starch, sucrose, glucose, fructose, raffinose, stachyose.

Résumé : Afin d'évaluer l'effet de la tempête de verglas de janvier 1998 sur la santé de l'érable à sucre (*Acer saccharum* Marsh.), les auteurs ont mesuré, tout au long de la période sans feuille (septembre 1998 – mai 1999), les teneurs en amidon et en sucres solubles, dans des rameaux provenant de deux érablières endommagées du nord de l'état de New-York (jeune : arbres de 50 à 100 ans, et plus âgée : arbres d'environ 200 ans). Les arbres sévèrement endommagés par le verglas montraient des signes de recouvrement au cours de la première saison de croissance (1998), c'est-à-dire, un plus grand nombre de pousses latérales (épicormiques) et une production ligneuse accrue, chez les anneaux de croissance de l'année provenant de branches à mi-hauteur du houppier, ainsi que de fortes teneurs en amidon dans les rameaux de l'année, au moment de la chute des feuilles. On a observé des différences dans les patrons de réserves en sucres solubles, entre les érables endommagés et ceux qui l'étaient faiblement ou pas du tout, et entre les arbres de la vieille érablière comparativement à ceux de la forêt plus jeune; ceci indique que des changements sont intervenus, au niveau de la physiologie de la saison froide, chez les arbres endommagés quant à leur adaptation ou leur tolérance à la température froide. Chez les arbres endommagés, de la jeune érablière et de celle plus âgée, les patrons des saccharose, stachyose, raffinose et xylose étaient semblables à ceux des arbres correspondants, faiblement à fortement endommagés, tout au long de la saison froide. Cependant, les patrons des saccharose, glucose et fructose montraient des différences dans leurs teneurs et leurs patrons, comparativement et respectivement aux arbres légèrement ou non endommagés. On a observé une plus faible teneur en saccharose dans les tissus ligneux des vieux arbres endommagés après la reprise d'activité cambiale à la fin de l'hiver, et une plus faible teneur en amidon 'resynthétisé', juste avant la croissance vernale. Ces données indiquent que les patrons des sucres individuels peuvent fournir des informations sur les changements qui surviennent, au cours de la saison froide, dans les processus physiologiques et biochimiques chez les arbres endommagés.

Received 14 October 2004. Published on the NRC Research Press Web site at http://canjbot.nrc.ca on 6 July 2005.

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 doi: 10.1139/B05-041

Mots clés : amidon, saccharose, glucose, fructose, raffinose, stachyose.

[Traduit par la Rédaction]

Introduction

The damage caused by the January 1998 ice storm in the northeastern United States and southeastern Canada was unprecedented in intensity, duration, and the area covered. Damage to trees, including stands of sugar maples (*Acer saccharum* Marsh.), varied greatly with some trees losing only a few branches, to others having their entire crowns destroyed or being uprooted (Irland 1998; Miller-Weeks and Eager 1999). The most visible and useful variable to quantify the impact of the January ice storm on maple stands is the amount of crown loss due to branch breakage (DesRockers and Allen 2001).

Crown loss reduces photosynthetic surface area and reserve carbohydrate storage capacity of the trees. The amount of starch stored in early autumn in the xylem parenchyma has been used as an indicator of tree vitality (Wargo 1971, 1981; Carroll et al. 1983; Gregory et al. 1986; Rasmussen and Henry 1990; Renaud and Mauffette 1991; McLaughlin et al. 1996; Wargo et al. 2002). Winter survival during the leafless period depends on adequate reserves. In sugar maples, starch is the main source of carbon for: (*i*) the development and maintenance of cold tolerance (Yelenosky 1975; Raese et al. 1978; Siminovitch 1981; Gregory et al. 1986), (*ii*) cellular maintenance and respiration (Kramer and Kozlowski 1979), and (*iii*) vernal growth, e.g., flower and shoot development (Wargo 1981; Gregory and Wargo 1986). Low levels of stored starch in autumn have been implicated in tree dieback and mortality (Gregory et al. 1986; Rasmussen and Henry 1990; Renaud and Mauffette 1991). Wong et al. (2001) found that cold season profiles of reserve and soluble carbohydrates were different in sugar maple trees with crown dieback symptoms and healthy sugar maple trees. Changes in cold season starch and soluble sugar profiles could reflect stress-induced changes in tree physiology.

Little information is available on the impact of ice storm damage on reserve carbohydrate metabolism and cold season physiology of damaged sugar maple trees. In this study, reserve and soluble carbohydrates of damaged and slightly damaged or undamaged trees were quantified from September 1998 to May 1999, in a younger sugarbush (50- to 100-year-old trees) and in an older sugarbush (approx. 200-year-old trees), to assess the impact of the ice storm stress on cold season tree physiology of these two age classes trees. The recovery potential of sugar maple trees was evaluated using the number of lateral (epicormic) shoots, annual ring width, and the amount of starch stored in the twigs in late summer or early autumn.

Materials and methods

Study sites

This study was conducted in two private sugarbushes located in Clinton County, New York. In the older of the two sugarbushes, trees are approximately 200 years old, and have been tapped for syrup production for decades. The sugarbush is a complete monoculture of sugar maple and has no under-story woody plants. In the younger sugarbush, trees are 50–100 years old, and have been tapped for syrup production for several years. The younger sugarbush is a mix of sugar and red maple (*Acer rubrum* L.) with some areas of white pine (*Pinus strobus* L.). Damage was more severe in the older sugarbush with more trees experiencing greater crown loss than in the younger sugarbush. Presumably healthy trees with no large wounds, cankers, or other obvious disease signs or symptoms were identified at each of the sugarbushes in August. Trees flagged in 1998 with slight crown damage (0% to less than 25% crown damage) were designated as "slightly damaged or undamaged", and trees with significant crown damage (greater than 50% crown damage) were designated as "damaged".

Sample collections

To determine the cold season carbohydrate profiles, four twig samples (three to five growth rings) were collected from each of three randomly selected trees of each crown class (<25% and >50% crown loss) from each sugarbush at each collection date. Biweekly twig samples were removed from branches at mid-crown level from mid-September to mid-May and transported at ambient temperature to the Northeastern Forest Research Station in South Burlington, Vermont. To ameliorate differences in position of twigs and for consistency, all twigs were collected from the southeast aspect at mid-crown level. In addition, to ameliorate diurnal influences, all collections were made between 0900 and 1100 hours.

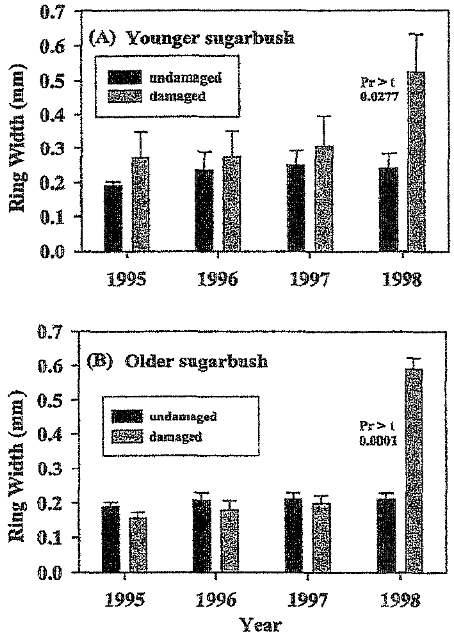
Sample preparation

All twig samples were immediately processed upon arrival at the laboratory (approximately 1 h postharvest). Wood samples were collected from the basal internode of each twig (containing three to five growth rings). After removal of the bark, phloem, cambium, and pith, the xylem tissue samples were submerged into test tubes containing 5 mL of 80% ethanol, and then the tubes were placed in a boiling water bath for 15 min, followed by evacuation at –52 kPa for 15 min. Each wood sample was homogenized with a Brinkman Instruments (Westbury, Massachusetts) Polytron™ in 80% ethanol and centrifuged for 15 min at 3000 r/min, and the macerated samples were extracted twice more with 5 mL of 80% ethanol. For each sample, the supernatants were combined, filtered through a 0.45-μm syringe filter, and used for soluble sugar analysis. The ethanol-insoluble pellets were used to determine the starch content.

Soluble sugar determination

Ethanol-soluble fractions were analyzed for sucrose, glucose, fructose, stachyose, raffinose, and xylose using a HPLC system with a Waters Sugar-pak™ column and solvent (0.1 $mmol \cdot L^{-1}$ Ca EDTA) flow rate of 0.6 $mL \cdot min^{-1}$ at 90 °C (Wong et al. 2001, 2003). Sugars were detected with a Wa-

Fig. 1. Comparison of 1995, 1996, 1997, and 1998 growth ring widths of damaged and slightly damaged or undamaged trees from younger (A) and older (B) sugarbushes.



ters model 410 refractive index detector connected to a Digital Equipment Corp. (Maynard, Massachusetts) personal computer equipped with Water Millenium™ software. The separated soluble sugars were identified and quantified with known standards and converted to milligrams of sugar per gram residue dry weight.

Starch determination

Starch was quantified by the method of Hendrix (1993) with some modification. The starch was gelatinized in each pellet with 0.2 mol·L^{-1} KOH and was hydrolyzed to glucose with amyloglucosidase (No. 10115, Fluka Chemical Co., St. Louis, Missouri). Glucose was quantified colorimetrically using the INT assay (glucose assay kit No. 115-A, Sigma Chemical Co., St. Louis, Missouri) as described by Hendrix (1993). The concentration of starch was calculated from glucose standard curves and expressed as milligrams per gram residue dry weight.

Lateral (epicormic) shoots

In early spring of 1999 prior to bud break, the number of epicormic shoots was counted using 8 × 30 binoculars. The epicormic shoots arose from released suppressed buds on the southeast aspect of trees from each crown-damaged class of the younger and older sugarbushes.

Growth rings

The effect of crown loss on radial growth was determined from branches (8–15 years old) of slightly damaged or undamaged (n = 6) and damaged (n = 6) trees in the younger and older sugarbushes, which contained the 1998 growth ring as well as growth rings from previous years. Samples were collected in early March 1999 from the southeast aspect of the trees. The widths of the growth rings formed in 1995, 1996, and 1997 prior to the 1998 ice storm and in 1998 immediately following the growing season were measured. Ring widths were measured microscopically with a calibrated ocular micrometer along two radial axes of each branch cross-sections.

Statistical analyses

After testing for normality using the Shapiro–Wilk test, data were analyzed using the SAS Statistical package (SAS Institute Inc. 1985). Analysis of variance and Duncan's multiple range test were used to test for differences in means of starch, sucrose, glucose, fructose, stachyose, raffinose, and xylose concentrations for each collection date between damaged and slightly damaged or undamaged trees and between two age classes at p <0.05 level of significance. Also, t tests were employed to determine differences in mean ring widths or number of epicormic branches between damaged and slightly damaged or undamaged samples for each year.

Results and discussion

Recovery potential

Sugar maple trees with greater than 50% crown loss caused by the 1998 January ice storm from both the younger and older sugarbushes exhibited evidence of recovery. Crown recovery in damaged trees consisted of shoots from buds formed the previous year and shoots from suppressed buds. The number of released shoots (epicormic) from suppressed buds formed during the 1998 growing period was greater in damaged than slightly damaged or undamaged trees (Table 1). Epicormic shoots in damaged trees increase the amount of shoot structure (Bachelard 1969; Wignall and Browning 1988; Godman et al. 1990; Remphrey and Davidson 1992; Lautenschlager and Winters 2001), but do not compensate for the loss in crown density. Crown maintenance of slightly damaged or undamaged trees occurs mainly with increases in crown density by the rapid elongation of short and heterophyllous shoots from buds formed during the previous summer (see Zimmermann and Brown 1971; Kramer and Kozlowski 1979).

The ring width in branches (8–15 years old) from the southeast aspect at mid-crown level of damaged trees for 1998 was about twice the radial growth in each of the previous 3 years (Fig. 1). In contrast, the 1998 ring width in slightly damaged or undamaged trees was similar to previous years (Fig. 1). The increase in branch radial growth in damaged trees is another indicator of recovery after ice glazing and may be attributed to increased photosynthetic capacity since a greater proportion of the lower leaves are in full sunlight with crown thinning (Lamson and Smith 1989; McJannett and Vertessy 2001).

The increases in shoot sprouting (Table 1) and radial growth (Fig. 1) in branches, observed in this study, demonstrate greater growth activity in the crown region of damaged trees than in slightly damaged or undamaged trees during the growing season (1998) immediately following the January ice storm. The presently observed rapid growth activities in the crown region following damage may be most reflective of an increase in photosynthetic capacity with greater light penetration in damaged crowns. Such high growth activity in damaged crowns may occur at the expense of other areas of the tree, such as for example, the reduction

Table 1. Incidence of epicormic branching.

Age and damage class	No. of trees	No. of epicormic branches*	Pr > t
YD	51	12.8±1.26	0.0001
YU	44	2.0±0.57	
OD	44	10.8±1.26	0.0715
OU	9	5.4±1.87	

Note: Y, younger sugarbush; O, older sugarbush; U, slightly damaged or undamaged; D, damaged.
*Data are means ± SE.

Table 2. Concentrations of starch ($mg \cdot g^{-1}$ residue dry weight) at each collection date.

A. Autumn transition period.					
	Collection dates				
Sugarbush age and damage class	18 Sept. 1998	1 Oct. 1998	12 Nov. 1998	24 Nov. 1998	3 Dec. 1998
YD	24.28±0.78b	30.22±3.07b	13.12±1.18b	7.60±0.71b	6.18±0.56c
YU	25.88±1.36ab	23.98±1.75b	12.58±0.58b	10.35±0.61a	10.08±0.42c
OD	29.34±1.36a	38.68±4.12a	14.21±1.37b	7.17±0.15b	5.07±0.34c
OU	24.74±1.41b	22.89±1.26b	17.98±1.10a	10.79±1.09a	14.66±1.19a
Pr > F	0.0283	0.0008	0.0190	0.0014	0.0001
B. Late winter transition period.					
	Collection dates				
	3 Feb. 1999	3 Mar. 1999	25 Mar. 1999	6 Apr. 1999	21 Apr. 1999
YD	6.53±0.56a	11.78±1.25ab	22.09±1.10a	18.35±1.15a	19.40±1.74b
YU	8.12±0.76a	10.14±0.88b	17.26±0.49b	18.48±1.08a	18.85±1.17b
OD	4.89±0.39b	6.95±0.70c	13.96±1.15c	16.36±0.82ab	16.94±0.88b
OU	3.99±0.38b	14.63±0.80a	22.43±0.40a	14.59±0.74b	26.65±0.55a
Pr > F	0.0001	0.0001	0.0001	0.0383	0.0003

Note: Y, younger sugarbush; O, older sugarbush; U, slightly damaged or undamaged; D, damaged. Data are means ± SE (n = 12); numbers within a column that do not share a letter are significantly different.

in trunk radial ring growth in sugar maple trees damaged by the January 1998 ice storm as reported by Smith and Shortle (2003).

High starch concentration in the twig wood of damaged trees at the time of leaf drop is another indicator of recovery. In the present study, the amount of starch stored in the woody twigs in damaged trees of the older sugarbush in early autumn (early October) was significantly higher (41%) than in slightly damaged or undamaged older trees (Table 2). In contrast, the amount of starch stored in twigs of damaged trees in the younger sugarbush was similar to that of both slightly damaged or undamaged trees of the younger and older sugarbushes (Table 2). Branch thinning caused by ice glazing allows greater light penetration to the leaves in the interior and lower crown, thus increasing the photosynthetic surface for light interception (Wignall and Browning 1988; Remphrey and Davidson 1992) and hence results in increased photosynthetic capacity. The differences in amount of early autumn starch stored in the two age classes of damaged sugar maple trees may be attributed to differences in crown architecture between older and younger trees or greater translocation of fixed carbon in younger damaged trees to other distant sinks, such as the roots. In slightly damaged or undamaged trees, the photosynthetic capacity of the canopy is normally modified by the mutual shading of the leaves. Ellsworth and Reich (1993) documented that leaves of the upper crown have a higher photosynthetic flux than that of the shaded leaves located in the interior and lower crown.

Cold season carbohydrate patterns

In this study, the reserve carbohydrate profiles in slightly damaged or undamaged sugar maple trees exhibit predictable patterns, which correspond with cold season physiological activities (Table 3) and are similar to those observed in previous studies of healthy sugar maple trees (Gregory et al. 1986; Wong et al. 2001, 2003). The reserve carbohydrate stored in the wood tissue in early autumn is used for various biochemical and physiological activities associated with cold acclimation (hardening), freeze tolerance, cellular maintenance and respiration, dehardening, and vernal growth. These are the main roles played by carbohydrate reserves in perennial plants under cold climate (Wargo 1981; Gregory et al. 1986; Rasmussen and Henry 1990; Renaud and Mauffette 1991). In addition, in this study as observed in other studies, the seasonal patterns of reserve and soluble carbohydrates in the twigs from relatively slightly damaged or undamaged mature sugar maple trees were independent of age (Wong et al. 2001, 2003) and similar to seasonal patterns observed in samples from the main stem and roots (Gregory et al. 1986). Changes in reserve and soluble carbohydrate profiles from healthy (slightly damaged or undamaged) sugar maple trees during the leafless phase may indicate alterations in cold season adaptation due to ice storm damage.

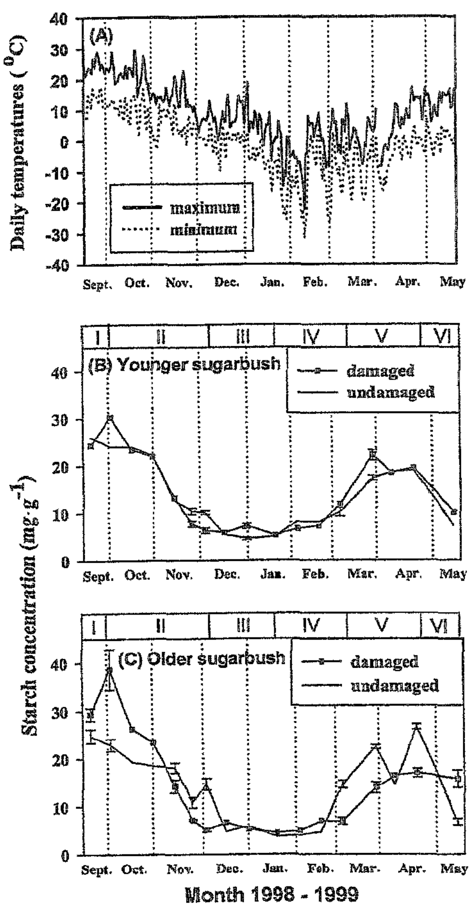
Starch

Starch stored in wood tissue is the main source of carbon during the leafless phase. The starch profiles of sugar maple trees (Figs. 2B and 2C) are closely related to temperature

Table 3. Phenological and physiological events in sugar maple trees throughout the leafless phase based on observed and reported results.

Period	Season	Month	Physiological process
I	Late summer	Late September	Near completion of secondary growth. Reduced photosynthate to sinks. Accumulation of reserve carbohydrate
II	Autumn	October to mid-December	Leaf senesces. Leaf drop. Beginning of dormancy. Development of cold tolerance
III	Early winter	Mid-December to early January	Low cellular activity. Dormancy
IV	Late winter	Mid-January to mid-March	Cessation of dormancy. Increase in cellular activity. Dehardening
V	Early spring	Mid-March to mid-April	Xylem sap flow. Starch resynthesis
VI	Spring	Mid-April to mid-May	Vernal growth. Active period of primary growth

Fig. 2. Daily maximum and minimum temperatures (A) in relation to changes in cold season starch reserves in twigs of slightly damaged or undamaged (<25% crown loss) and damaged (>50% crown loss) sugar maple trees from the younger (50- to 100-year-old trees) sugarbush (B) and the older (approx. 200-year-old trees) sugarbush (C). Temperature data were compiled from the Northeast Regional Climate Center at Cornell University, Cornell, New York. Mean starch values are shown and standard error bars are given for points with significant differences ($p < 0.05$) at each collection date (n = 12). Roman numerals refer to the physiological and phenological events presented in Table 2.



(Fig. 2A) during the leafless period. The profiles exhibited rapid declines from high concentrations stored during late summer and early autumn (periods I and II) through autumn (October and November) to winter low concentrations (period III) in trees from both younger (Fig. 2B) and older (Fig. 2C) sugarbushes. Starch concentrations remained low (period III) in the wood tissue until starch resynthesis by mid-February (period IV). Resynthesized starch (spring starch) reached a peak by late March (period V) before declining with vernal growth (Figs. 2B and 2C, period VI).

The reserve starch profiles of slightly damaged or undamaged and damaged trees of the younger sugarbush (Figs. 2B and 2C) were generally similar during the cold season. Differences in the reserve starch profiles of slightly damaged or undamaged and damaged trees were most evident during both the autumn transition period (mid-September to mid-December) with the development of dormancy and cold tolerance, and the late winter transition period from late winter to spring (February–mid-April), with cessation of dormancy, increased cellular activity, and dehardening (Table 2). In damaged trees, autumn starch concentrations declined to winter low levels (late period II) about approximately 2 weeks earlier (period III) than in slightly damaged or undamaged trees, and starch resynthesis, in the late winter (period V), occurred in early March about 2 weeks later than in slightly damaged or undamaged trees. After the period of dehardening (period IV) but prior to vernal growth (period VI), the difference in the amount of resynthesized starch was especially apparent in damaged older trees, i.e., approximately 25% lower than in slightly damaged or undamaged trees (Fig. 2C). We do not know the cause for the lower level of spring starch in the wood tissue after the dehardening (period V) in the older damaged trees. It may be attributed to increased metabolism and respiration due to changes in cold season physiology, or to greater utilization of soluble carbohydrates for freeze development and maintenance, and (or) it may be the result of greater translocation of sucrose, for example toward the trunk, in early spring during xylem sap flow because of a greater gradient in the damaged trees than in more healthy trees. At the time of growth resumption, low starch reserves could affect the allocation of carbohydrates to various sinks, e.g., flowering, bud break, shoot growth, leaf emergence and enlargement, and primary root growth, etc. (Gregory 1980; Wargo 1981; Gregory and Wargo 1986).

Soluble sugars

The profiles of the ethanol-soluble sugars of damaged sugar maples, i.e., sucrose (Fig. 3), glucose (Fig. 4), fructose (Fig. 5), stachyose (Fig. 6), raffinose (Fig. 7), and xylose (Fig. 8) of the younger and older sugarbushes varied in relation to different cold season physiological processes (Ta-

Fig. 3. Profiles of sucrose concentrations in twigs of slightly damaged or undamaged (<25% crown loss) and damaged (>50% crown loss) sugar maple trees from the younger (50- to 100-year-old trees) sugarbush (A) and the older (approx. 200-year-old trees) sugarbush (B). Mean values are shown and standard error bars are given for points with significant differences ($p < 0.05$) at each collection date ($n = 12$). Roman numerals refer to the physiological and phenological events presented in Table 2.

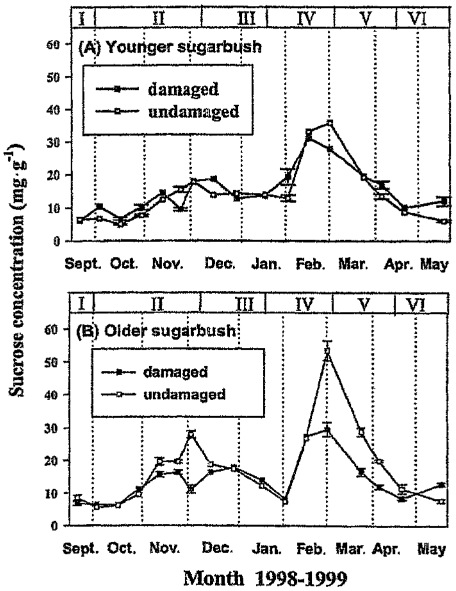


Fig. 5. Profiles of fructose concentrations in twigs of slightly damaged or undamaged (<25% crown loss) and damaged (>50% crown loss) sugar maple trees from (A) the younger (50- to 100-year-old trees) sugarbush, and (B) the older (approx. 200-year-old trees) sugarbush. Mean values are shown and standard error bars are given for points with significant differences ($p < 0.05$) at each collection date ($n = 12$). Roman numerals refer to the physiological and phenological events presented in Table 2.

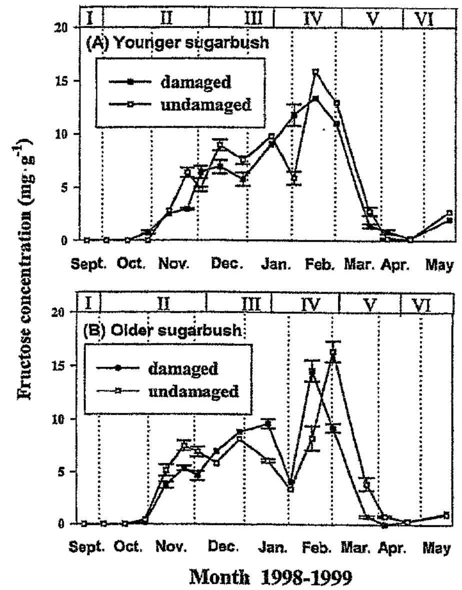


Fig. 4. Profiles of glucose concentrations in twigs of slightly damaged or undamaged (<25% crown loss) and damaged (>50% crown loss) sugar maple trees from the younger (50- to 100-year-old trees) sugarbush (A) and the older (approx. 200-year-old trees) sugarbush (B). Mean values are shown and standard error bars are given for points with significant differences ($p < 0.05$) at each collection date ($n = 12$). Roman numerals refer to the physiological and phenological events presented in Table 2.

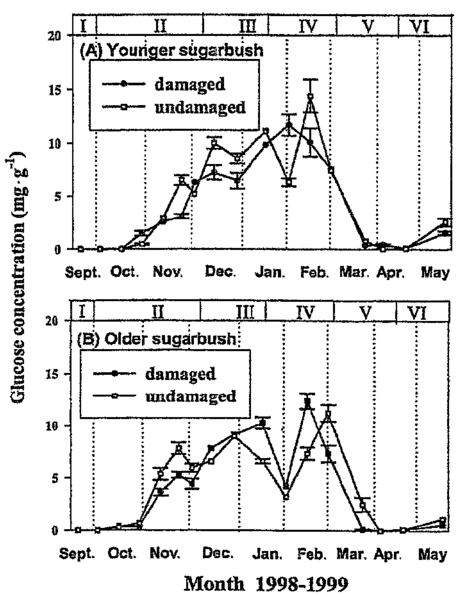


Fig. 6. Profiles of stachyose concentrations in twigs of slightly damaged or undamaged (<25% crown loss) and damaged (>50% crown loss) sugar maple trees from the younger (50- to 100-year-old trees) sugarbush (A) and the older (approx. 200-year-old trees) sugarbush (B). Mean values are shown and standard error bars are given for points with significant differences ($p < 0.05$) at each collection date ($n = 12$). Roman numerals refer to the physiological and phenological events presented in Table 2.

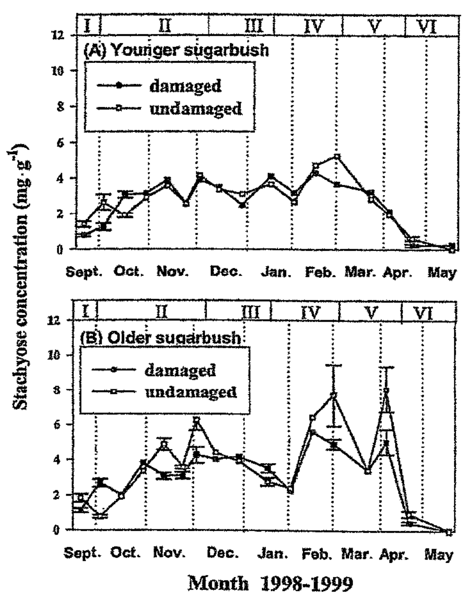


Fig. 7. Profiles of raffinose concentrations in twigs of slightly damaged or undamaged (<25% crown loss) and damaged (>50% crown loss) sugar maple trees from the younger (50- to 100-year-old trees) sugarbush (A) and the older (approx. 200-year-old trees) sugarbush (B). Mean values are shown and standard error bars are given for points with significant differences ($p < 0.05$) at each collection date ($n = 12$). Roman numerals refer to the physiological and phenological events presented in Table 2.

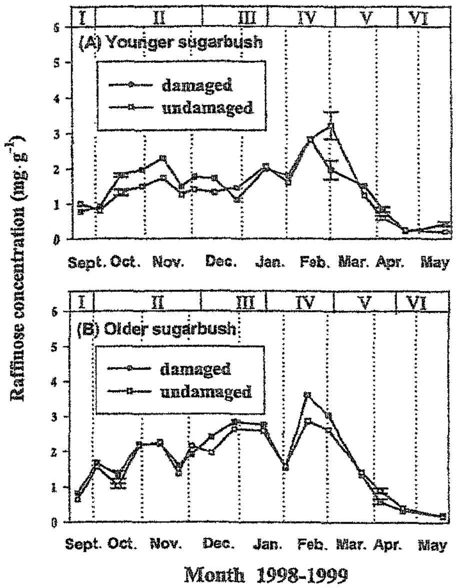
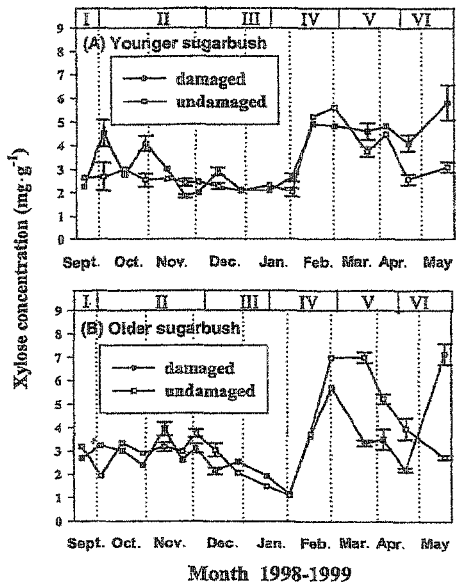


Fig. 8. Profiles of xylose concentrations in twigs of slightly damaged or undamaged (<25% crown loss) and damaged (>50% crown loss) sugar maple trees from the younger (50- to 100-year-old trees) sugarbush (A) and the older (approx. 200-year-old trees) sugarbush (B). Mean values are shown and standard error bars are given for points with significant differences ($p < 0.05$) at each collection date ($n = 12$). Roman numerals refer to the physiological and phenological events presented in Table 2.



ble 2). Quantitative and qualitative differences were observed in sugar profiles between slightly damaged or undamaged and damaged trees of younger and older sugarbushes.

Sucrose is the most abundant soluble sugar in sugar maples during the cold season (Gregory et al. 1986; Wong et al. 2001, 2003). Seasonal profiles of sucrose concentration were inversely related to starch concentration (compare Figs. 2 and 3). The cold season sucrose profiles were similar between damaged and slightly damaged or undamaged trees of the younger and older sugarbushes (Figs. 3A and 3B, Table 4). In damaged older trees, however, the concentration of sucrose was significantly lower during late autumn (period II) and late winter (period IV) compared with that of slightly damaged or undamaged trees (Fig. 3B, Table 4). Differences between damaged and slightly damaged or undamaged older sugar maple trees during the period of cold hardening (period II) may be indicative of alterations in biochemical and physiological processes promoted by low temperature (Alberdi and Corcuera 1991). The presence of a large pool of stored starch at the beginning of the leafless phase (Fig. 2B, period II) and the lower level of sucrose in the wood tissue in late autumn (Fig. 3B, period II) indicate that damaged older trees differ from damaged younger trees in method of compensating for stress caused by the ice storm damage. The reduced sucrose level during late autumn (period II) could be due to conversion of sucrose to other substances during the cold season, such as, glucose, fructose, stachyose, and raffinose (Levitt 1980), and (or) to increased metabolic activities during the acquisition of cold acclimation (Levitt 1980) and during the development and maintenance of cold tolerance (Sakai 1960; Levitt 1980; Siminovitch 1981; Carroll et al. 1983; Gregory et al. 1986).

In the early winter (period III), sucrose remained at elevated levels except for a slight drop in mid-December that corresponded with increases in glucose (Fig. 4) and fructose (Fig. 5). During the late winter transition (period IV), the level of sucrose rapidly declined to a seasonal low in older trees (Fig. 3B, early period IV), and may be associated with the cessation of dormancy with increased cellular metabolism and respiration. While such decline in sucrose was less evident in younger trees (Fig. 3A), the elevated concentrations of glucose (Fig. 4A) and fructose (Fig. 5A) during cessation of dormancy indicate changes in cold season physiology in these trees.

The concentration of sucrose then increased to seasonal high levels (February – early March, late period IV) that coincided with dehardening. The higher concentration of sucrose observed in the wood tissue in early March could be attributed to conversion of cytoplasmic material and membranes, formed during frost hardening, to sugar during the dehardening process (Sakai and Larcher 1987; Guy 1990; Alberdi and Corcuera 1991). In addition to the differences in sucrose profiles, significant differences were observed in the concentrations of sucrose between damaged and slightly damaged or undamaged trees of the older sugarbush just prior to the reappearance of starch in late winter (Fig. 3A, period IV); the sucrose concentration in damaged trees was 55% of that of slightly damaged or undamaged trees. The lower concentration of sucrose in the woody twigs of damaged older trees compared with slightly damaged or undamaged trees prior to starch resynthesis (Fig. 3B, period V)

Table 4. Concentrations of sucrose (mg·g^{-1} residue dry weight) at each collection date.

A. Autumn transition period.					
Sugarbush age and damage class	Collection dates				
	18 Sept. 1998	1 Oct. 1998	12 Nov. 1998	24 Nov. 1998	3 Dec. 1998
YD	5.97±0.32b	10.43±2.04a	14.53±0.26bc	9.58±0.43c	17.95±1.26b
YU	6.34±0.61b	6.62±0.75a	12.47±0.44c	15.48±0.78b	17.72±1.09b
OD	6.83±0.56b	6.49±1.67a	15.72±0.82b	16.39±0.67b	11.17±1.27c
OU	8.62±0.77a	5.62±0.73a	19.63±1.17a	19.61±0.49a	27.96±1.07a
Pr > *F*	0.0129	0.1069	0.0001	0.0001	0.0001
B. Late winter transition period.					
	Collection dates				
	3 Feb. 1999	3 Mar. 1999	25 Mar. 1999	6 Apr. 1999	21 Apr. 1999
YD	19.34±2.34a	27.87±2.82b	19.56±1.44b	17.01±1.10b	10.24±0.70ab
YU	12.94±0.98b	35.83±2.96b	19.23±1.61b	13.62±0.81c	8.79±0.47b
OD	8.17±0.49bc	29.58±2.07b	16.60±1.21b	12.06±0.69c	8.47±0.34b
OU	7.49±0.96c	53.44±2.98a	28.84±1.23a	19.88±0.31a	11.42±1.51a
Pr > *F*	0.0001	0.0001	0.0001	0.0001	0.0496

Note: Y, younger sugarbush; O, older sugarbush; U, slightly damaged or undamaged; D, damaged. Data are means ± SE (n = 12); numbers within a column that do not share a letter are significantly different.

could be due to changes in cold season physiology resulting in greater carbon metabolism, fewer components formed during frost hardening and (or) greater translocation of sucrose during xylem sap flow in damaged older trees. In contrast, little differences were observed in the concentrations of sucrose between slightly damaged or undamaged and damaged trees of the younger sugarbush (Fig. 3A) throughout the cold season (Table 4).

The cold season profiles of glucose and fructose of slightly damaged or undamaged sugar maple trees generally paralleled that of sucrose from late autumn throughout the leafless phase (late period II to early period V) in trees of the younger and older sugarbushes. In early autumn, however, neither glucose nor fructose was detectable in the wood tissue of damaged and slightly damaged or undamaged trees of the younger and older sugarbushes. Moreover, differences were observed in the profiles of glucose (Fig. 5) and fructose (Fig. 6) between damaged and slightly damaged or undamaged trees of younger and older sugarbushes (Table 5). Such differences were most evident during the late winter transition at the time of dormancy termination and dehardening (period IV). In the younger sugarbush, the levels of glucose (Fig. 4A) and fructose (Fig. 5) of damaged trees remained high during the time of dormancy termination (period IV), declining during dehardening with little detectable glucose and fructose after dehardening (period V) compared with slightly damaged or undamaged younger trees. In contrast, the profiles of glucose (Fig. 4) and fructose (Fig. 5B) of damaged older sugar maple trees were relatively similar compared with slightly damaged or undamaged older trees, except for shifts in profile configurations of damaged trees, where the concentrations of glucose and fructose in the wood tissue remained elevated 2 weeks longer during late winter (period IV) before these sugars declined with cessation of dormancy and before increasing to high levels 2 weeks earlier during dehardening (period IV). The high concentrations of glucose and fructose in the cell sap of damaged trees during the late winter transition and shifts in glucose and fructose profile configurations suggest that these sugars are indicative of alterations in adapting to or tolerating low temperatures. Glucose and fructose in damaged trees could act as osmoregulating substances in the cell sap for freeze protection (to preserve membrane fluidity, membrane function, and cell compartmentation) by lowering the freezing point of the tissues (Sakai 1960, 1962, 1966; Raese et al. 1978; Levitt 1980).

The presence of stachyose and raffinose in the cell sap has been positively related to frost hardiness (Sakai 1966; Levitt 1980). In slightly damaged or undamaged sugar maple trees, the profiles of stachyose (Fig. 6) and raffinose (Fig. 7) were generally similar to that of sucrose, i.e., present in the wood during early autumn (period II), maintaining relatively high concentrations during the coldest months (period III), declining with cessation of dormancy, and increasing to peak levels with dehardening (period IV) before declining with starch resynthesis (period V). The level of stachyose was higher in early autumn in damaged older trees compared with slightly damaged or undamaged trees of both age classes (Fig. 6B, period II), while the concentration of raffinose was higher in early autumn in damaged trees of the younger sugarbush compared with slightly damaged or undamaged trees (Fig. 7A, period II) of both age classes.

In damaged trees of the younger sugarbush, the concentration of xylose (Fig. 8A) in the wood tissue was higher in early autumn in damaged trees compared with slightly damaged or undamaged trees (period II) i.e., coinciding with changes in cell wall properties with cold hardening. In older trees, little differences were observed between damaged and slightly damaged or undamaged trees in early autumn. An increase in the concentration of xylose to peak level in late winter (period IV) occurred during dehardening, while a high concentration in early spring in damaged younger and older sugar maple trees coincided with the sprouting phase (period and VI). The role free xylose plays in cold season biochemical and physiological processes in woody plants including sugar maples is not well understood. Xylose has been found to be associated with the hemicellulose component of the cell wall (Fry 1989; Figuciredo-Ribeieo et al.

Table 5. Concentrations of glucose and fructose (mg·g^{-1} residue dry weight) at each collection date.

	Collection dates*					
Sugarbush age and damage class	16 Dec. 1998 (III)	31 Dec. 1998 (III)	19 Jan. 1999 (IV)	17 Feb. 1999 (IV)	3 Mar. 1999 (IV)	25 Mar. 1999 (V)
Glucose						
YD	7.21±0.68b	6.44±0.74b	9.81±0.65a	10.08±1.29bc	7.56±1.23b	0.37±0.08b
YU	9.98±0.54a	8.53±0.47a	11.08±0.22a	14.42±1.52a	7.42±0.92b	0.79±0.20b
OD	7.85±0.58b	9.18±1.04a	10.27±0.52a	12.42±0.78ab	7.36±0.82b	0.15±0.04b
OU	6.55±0.53b	9.01±0.49a	6.61±0.21b	7.39±0.61c	11.23±0.78a	2.53±0.68a
Pr > *F*	0.0011	0.0372	0.0001	0.0024	0.0320	0.0001
Fructose						
YD	6.91±0.63b	5.76±0.62b	9.04±0.60a	13.37±1.09a	11.00±1.37b	1.39±0.19c
YU	8.96±0.50a	7.53±0.39a	9.78±0.20a	15.88±1.19a	12.92±1.79ab	2.79±0.43b
OD	6.97±0.49b	8.81±0.91a	9.59±0.44a	14.58±0.98a	9.22±0.40b	0.77±0.12c
OU	5.81±0.45b	8.16±0.43a	6.04±0.13b	8.22±1.18b	16.35±0.95a	3.89±0.64a
Pr > *F*	0.0015	0.0079	0.0002	0.0004	0.0088	0.0001

Note: Y, younger sugarbush; O, older sugarbush; U, slightly damaged or undamaged; D, damaged. Roman numerals refer to physiological events discussed in Table 2. Data are means ± SE (n = 12); numbers within a column that do not share a letter are significantly different.

1992). Increases in xylose concentrations could be due to activities associated with increased cell wall formation, rearrangement of structural elements within the cell wall, and (or) de novo synthesis and insertion of new cell wall polymers (Fry 1989; Figuciredo-Ribeieo et al. 1992). In addition, it has been reported that free xylose may be converted to hexose in the oxidative pentose phosphate cycle (Meier and Reid 1982).

Conclusion

In ice storm damaged trees with apparent recovery during the growing season, the carbohydrate profiles of reserve and soluble sugars exhibit changes from the predictable profiles of healthy sugar maple trees, which indicate alterations in cold season biochemical and physiological processes during the leafless period. The differences in the concentrations of starch stored in damaged trees of the older sugarbush in early autumn (41% higher) and in early spring (36% lower) suggest greater utilization of reserve carbohydrate in damaged older trees during the leafless period for cold tolerance development and maintenance and (or) reallocation of carbohydrates. The lower concentrations of sucrose in damaged older trees in late winter (lower by 45%) compared with slightly damaged or undamaged trees suggest greater export of sucrose in damaged older trees with warmer temperature during sap flow and (or) conversion to other sugars such as, glucose, fructose, stachyose, and raffinose. In contrast with the difference observed in the concentration of starch stored in the two classes of older trees, the concentration of starch stored in damaged young trees in early autumn was similar to the concentration observed in slightly damaged or undamaged younger trees. Differences in the glucose and fructose profiles between damaged and slightly damaged or undamaged trees were evident and indicate changes in the mode of development in cold tolerance. Moreover, these differences in profile configurations suggest that adaptation and tolerance to cold temperature differ between age classes. High concentrations of glucose and fructose during and following the cessation of dormancy suggest that these sugars may function as substances for cell sap and membrane stability, in increasing osmotic potential, and as sources of materials for assimilation and increased cellular respiration and metabolic activity. The changes in cold season carbohydrate metabolism and physiological processes caused by the damage of the January 1998 ice storm may be only short-term survival mechanisms, thus allowing damaged trees to survive cold temperatures until full recovery.

Acknowledgements

Funding for this study was, in part, from the USDA Forest Service Northeastern Area State and Private Forestry, and the New York State Department of Environmental Conservation Division of Lands and Forests. The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the US Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

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