

Influence of a Late Spring Freeze on the Quantity and Quality of Birch Foliage

Martin J. LECHOWICZ and Benoit ST-JACQUES

*Department of Biology, McGill University
1205 Avenue Dr. Penfield,
Montreal, Québec, Canada*

Correspondence to : martin@BIO1.lan.mcgill.ca

Abstract

We compared the foliage of white birch (*Betula papyrifera* Marsh.) trees that were or were not damaged by a late spring freeze. The freeze event occurred after all the trees had burst bud and were unfolding their first leaves, but not all trees showed signs of freeze damage. The foliage of freeze-damaged trees in the spring had higher concentrations of nitrogen and lower concentrations of total phenolics and precipitable tannins. The foliage of damaged trees had higher concentrations of condensed tannins than undamaged trees later in the summer. Damaged trees had proportionately more late-leaves than undamaged trees, and these late-leaves have lower total phenolic content when young and higher condensed tannin content when they are old. We observed significantly more leaf-chewing insects on damaged trees through the growing season, an observation attributable to their relatively high proportion of young leaves. These young leaves, richer in nitrogen and less well-defended by condensed tannins, are more vulnerable to attack by leaf-chewing insects than older leaves.

Key words : *Betula papyrifera*, freeze damage, nitrogen content, total phenolics, precipitable tannins, leaf-chewing insects

Introduction

The timing of foliage production in spring differs substantially among species of deciduous trees in north temperate forests (Lechowicz 1984; Hunter and Lechowicz 1992). Species that leaf earlier in the growing season gain a potentially longer period of photosynthetic productivity, but the freezing resistance associated with overwintering tissues is lost as leaf development and shoot

growth begin (Gansert 1999). Thus earlier-leaving trees risk damage to young foliage by late spring frost, a risk that may be exacerbated by climatic instabilities associated with global change (Lechowicz and Koike 1995; Kramer 1996). Some species, such as those in the genus *Betula*, reduce this risk by only producing part of their foliage in early spring (Caesar and MacDonald 1983, 1984). A few leaves from preformed initials are produced early in spring, and later in the season neofor- med leaves are produced on long shoots with indeterminate growth (MacDonald and Moth-

ersill 1983; Macdonald *et al* 1984). These long shoots are a minority in the tree crown; the majority, referred to as short shoots, have determinate growth. The early- and late-leaves differ in size and shape — birches are heterophyllous (Clausen and Kozlowski 1965). The early-leaves are produced from stored carbon reserves, the late-leaves on long shoots from photosynthates produced by the early-leaves (Clausen and Kozlowski 1965; Kozlowski and Clausen 1966). Thus in species of *Betula* the loss of early-leaves to frost or freeze events involves not only loss of the leaves themselves, but also may impair the production of later leaves and full development of foliage in the tree crown.

In this paper we have taken advantage of a freeze event occurring after shoot growth had begun to investigate the degree of damage and subsequent recovery of trees in a grove of *Betula papyrifera* Marsh. We focus on two aspects of the foliage and crown: 1) the degree to which the growth of short and long shoots differs between undamaged and freeze-damaged trees and 2) the nature of qualitative changes in foliage produced on undamaged and damaged trees. We consider the degree to which quantitative and qualitative changes in the foliage of freeze-damaged birch trees may leave them more susceptible to leaf-feeding herbivores.

Materials and Methods

We studied 13 individual trees of *Betula papyrifera* that grew in an abandoned sand and gravel pit on the south-facing slopes of Mont St. Hilaire, Quebec (45°31'N, 73°08'W). The trees were widely spaced over an area of about a hectare and had open-grown crown form. They were 8-9 m tall, 10-12 cm in diameter at breast height, and about 20 years old. In spring of 1981 90% of the buds had burst and leaves were beginning to unfold on all the trees by April 28; 90% of the early-leaves on all the trees had unfolded by May 5. A light frost (night-time minimum of -0.1°C) on May 1 had little or no apparent effect on the trees, but on May 6-7 some trees were damaged by freezing rain and temperatures

dropping as low as -1.7°C . Based on the appearance of the crown, we classed trees as damaged ($n=5$) or undamaged ($n=8$). Many young shoots were killed on damaged trees, with leaves partly browned and circular in shape rather than light-green and ovoid as on undamaged trees. Damaged and undamaged trees did not differ significantly in height or diameter (St-Jacques 1984). In this paper we compare the characteristics of foliage produced subsequent to the freeze event in damaged versus undamaged trees.

From May 12 to August 12, 1981 we sampled the foliage of damaged and undamaged trees at regular intervals. We recorded the initiation and development of leaves on both short and long shoots, and estimated the proportion of the crown composed of early-versus late-leaves. We estimated the foliage area lost on damaged trees, and counted insects in chewing, sucking and mining guilds on every tree at each sampling interval. To compare the average foliage of undamaged and freeze-damaged trees, we sampled leaves randomly from the mid-crown. We also randomly sampled early-versus late-leaves at two developmental stages (5-20 days old, 67 days old) from throughout the tree crown to specifically compare differences among leaf types and ages in undamaged and freeze-damaged trees. We assayed the nitrogen content, total phenolics, precipitable tannin, and condensed tannins of all foliage samples. Nitrogen was assayed by colorimetry of nesslerized Kjeldahl digests (Middleton 1960) and expressed as a % dry mass. Leaves for phenolic analyses were freshly collected, dried 48 hours at 40°C in a forced draft oven, and then extracted three times in boiling 50% methanol (Tempel 1982, Martin and Martin 1982). We used a Folin-Denis assay (Swain and Hillis 1959) to estimate total phenolics, a proanthocyanidin assay (Swain and Hillis 1959) to estimate condensed tannins, and precipitation by proteins in isinglass to estimate "precipitable tannins" (St-Jacques 1984) in the methanol extract.

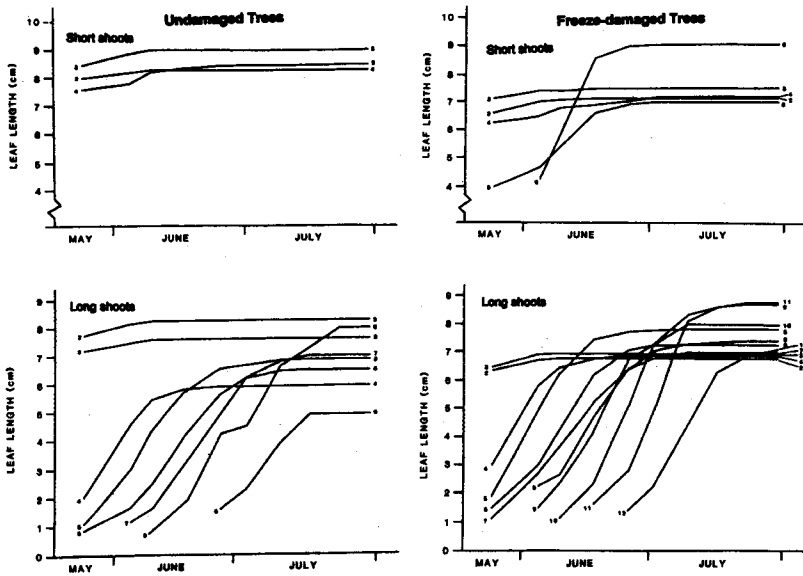


Figure 1 Temporal progression of leaf initiation and expansion on short (A) and long (B) shoots of *Betula papyrifera* trees undamaged by a late spring freeze event. Numbers code the temporal order in which leaves are initiated. Individual trees did not all produce the maximum possible number of leaves; hence sample sizes later in the sequence of leaf initiations diminish.

Table 1 Mean values (\pm standard error) for the 8 undamaged and 5 freeze-damaged birch trees over the course of the 1981 growing season. A light frost occurred on May 1 and freezing rain on May 6-7; 90% of the buds had burst on all the trees by April 28 and 90% of the early-leaves on all the trees had unfolded by May 5.

Sampling Date	12-May	19-May	26-May	9-Jun	23-Jun	6-Jul	21-Jul	12-Aug
Total nitrogen (% dry mass)								
Undamaged trees	3.99 \pm 0.11	2.82 \pm 0.12	2.70 \pm 0.11	2.19 \pm 0.09	2.25 \pm 0.08	2.19 \pm 0.09	2.12 \pm 0.08	2.17 \pm 0.11
Damaged trees	4.51 \pm 0.12	3.32 \pm 0.12	3.16 \pm 0.04	2.39 \pm 0.12	2.39 \pm 0.09	2.12 \pm 0.07	2.13 \pm 0.14	2.11 \pm 0.09
Condensed tannin (A550)								
Undamaged trees	.110 \pm 0.01	.151 \pm 0.23	.196 \pm 0.26	.233 \pm 0.18	.271 \pm 0.04	.273 \pm 0.03	.300 \pm 0.04	.282 \pm 0.02
Damaged trees	.122 \pm 0.26	.169 \pm 0.04	.232 \pm 0.06	.329 \pm 0.07	.339 \pm 0.08	.445 \pm 0.08	.427 \pm 0.09	.365 \pm 0.07
Precipitable tannin (% dry mass as Tannic Acid Equivalent)								
Undamaged trees	5.67 \pm 0.09	7.42 \pm 1.02	7.98 \pm 1.30	7.68 \pm 0.76	7.58 \pm 0.62	6.93 \pm 0.72	7.23 \pm 0.82	5.67 \pm 0.32
Damaged trees	2.98 \pm 0.55	5.05 \pm 1.05	6.57 \pm 0.83	6.58 \pm 0.76	7.43 \pm 0.60	6.48 \pm 0.72	6.60 \pm 1.32	5.22 \pm 1.03
Total Phenolic (% dry mass as Tannic Acid Equivalent)								
Undamaged trees	13.47 \pm 1.18	15.71 \pm 1.44	15.71 \pm 1.66	14.71 \pm 1.25	14.48 \pm 1.05	14.18 \pm 1.21	14.77 \pm 1.20	15.63 \pm 1.06
Damaged trees	9.15 \pm 0.74	11.82 \pm 1.45	12.01 \pm 1.29	12.79 \pm 1.23	13.81 \pm 0.79	12.84 \pm 1.31	12.76 \pm 1.88	12.92 \pm 1.41

Results

Figure 1 shows the progression of leaf development on short and long shoots of undamaged and freeze-damaged trees, respectively. The new leaves on short

shoots reached full size by mid-June; new leaves on long shoots reached full size between mid-June and late-July. Shoot extension growth had stopped in all trees by early to mid-July, which is normal for trees with indeterminate shoot growth in our region. Undamaged trees produced an average of 2.32 leaves on short shoots (range 2-3)

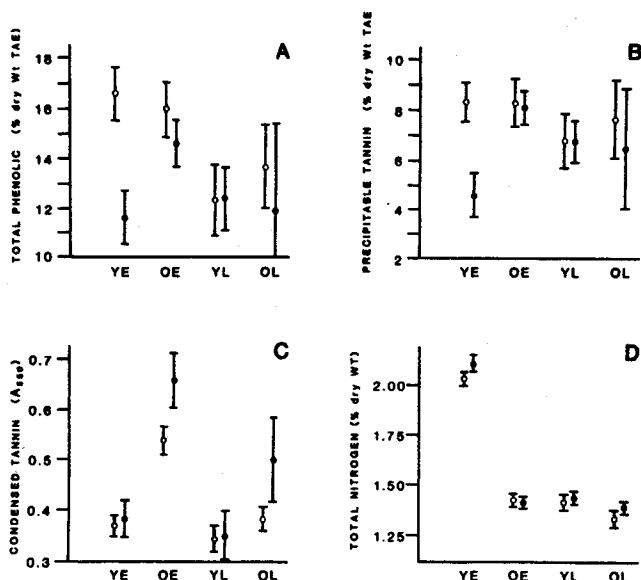


Figure 2 Mean values (\pm standard error) for the foliar characteristics of early- and late-leaves at two developmental stages (young, old) on the 8 undamaged (open circles) and 5 freeze-damaged (closed-circles) birch trees. Young leaves were 5–20 days old, old leaves consistently 67 days old. YE = young, early-leaves; OE = old, early-leaves; YL = young, late-leaves; and OL = old, late-leaves.

Table 2 Comparison of mean insect abundances on undamaged and freeze-damaged birch trees of comparable size and growing in close proximity. Based on summation of 8 censuses from May 12 through August 12, 1981. Differences tested using Wilcoxon's two sample test.

Insect guild		# insects/tree	Probability
Chewing	Damaged	6.80	0.032
	Undamaged	2.13	
Sucking	Damaged	4.80	0.550
	Undamaged	4.25	
Mining	Damaged	2.20	0.867
	Undamaged	1.25	

and 2 on long shoots in early spring, and then an average of 5.35 (range 3–11) on long shoots through mid-July. In the crown of undamaged trees, 15% of the shoots were long and 85% short; only about 5% of the total crown consisted of leaves still growing after the end of June. Freeze-damaged trees also produced 2 or 3 leaves on short shoots and 2 on long shoots in early spring, but after the freeze event produced up to 4 more leaves on short shoots and up to 10 more on long shoots. In freeze-damaged trees the average

number of leaves produced on short shoots was 2.69 and on long shoots 5.93. In the crown of freeze-damaged trees, 20% of the shoots were long and 80% short; about 10% of the total crown consisted of leaves still growing after the end of June. In terms of leaf area, about 10% of the crown of undamaged trees was borne on long shoots compared to 20% on freeze-damaged trees.

The average quality of foliage on undamaged and freeze-damaged trees differed (Table 1). Early in the season, the nitrogen

concentration of leaves on freeze-damaged trees was higher but this difference disappeared as foliar nitrogen declined through the summer. Leaves of freeze-damaged trees had consistently lower total phenolics throughout the season, and lower precipitable tannins early in spring. In early spring, the leaves of undamaged and freeze-damaged trees did not differ in condensed tannin concentrations but by mid-summer the freeze-damaged trees had significantly higher foliar concentrations of condensed tannins. These average foliar characteristics are based on random samples that pool early- and late-leaves in proportion to their relative abundances in the crowns of undamaged and freeze-damaged trees. Random sampling of early- and late-leaves at different, selected developmental stages complements these average foliar values (Figure 2). Compared to freeze-damaged trees, the young, early-leaves of undamaged trees had significantly higher total phenolics and precipitable tannins; this difference disappeared as the early-leaves matured. Older leaves on freeze-damaged trees had higher concentrations of condensed tannins. Except for a slightly higher nitrogen concentration in young, early-leaves, the undamaged and freeze-damaged trees did not differ in their foliar nitrogen profiles.

Freeze-damaged trees were attacked by more leaf-chewing insects on average through the season than undamaged trees (Table 2). Damaged and undamaged trees did not differ in the numbers of sucking and mining insects found on them through the season. It should be noted that there were no insect outbreaks at this site in 1981; these numbers reflect susceptibility to attack by phytophagous insects during non-outbreak periods.

Discussion

The diverse differences in foliage quality and shoot growth between undamaged and freeze-damaged trees of *Betula papyrifera* are unlikely to have arisen from microclimatic differences in exposure to freezing tempera-

tures and freezing rain. All the trees grew together in a small area of uniform exposure and aspect, and there was no spatial pattern segregating undamaged and damaged-trees. It is most reasonable to infer that these trees of very similar age and size differed in characteristics that left them more or less vulnerable to a freeze event occurring after seasonal shoot growth had begun. This vulnerability might arise either from intrinsic differences in phenological responses to spring warming or intrinsic differences in foliage quality and shoot-growth characteristics, or to a combination of these factors. Kudo (1995) has reported such within-population differences in shoot growth of *Betula platyphylla* var. *japonica*. Whatever the cause of these differences among individual trees in the vulnerability of young shoots and foliage to freeze-damage, it is clear that trees more vulnerable to freeze-damage also are more prone to attack by insect herbivores. We observed significantly more leaf-chewing insects on the freeze-damaged trees through the growing season, although the numbers of herbivores and the apparent levels of defoliation were not high.

The quality of foliage drawn randomly from the tree crown (cf. Table 1) cannot account for this difference in herbivore attack between undamaged and freeze-damaged trees. The foliage of damaged trees is consistently higher in condensed tannins. Condensed tannins in *Betula papyrifera* confer significant protection against leaf-feeding beetles (Ayres et al 1997) and against leaf-chewing caterpillars in closely related birch species (Ayres et al 1997; Mutikainen et al 2000). We therefore might expect freeze-damaged birch trees to have lower levels of attack by leaf-chewing insects. The opposite is true, a fact that best can be explained by considering the quantity and quality of different types of leaves within the crowns of undamaged versus freeze-damaged trees.

The association between attack by leaf-chewing insects and freeze-damage to *Betula papyrifera* is founded on the greater relative abundance of young foliage on the damaged trees. Freeze-damaged trees have more young foliage later in the season than do

undamaged trees, a difference that appears to have two causes. First, more buds are released on the short shoots of freeze-damaged trees, which we can assume is some compensation for early-leaves killed or developmentally stunted by the freeze event. Second, the twofold greater abundance of young leaves in mid-season on freeze-damaged trees is attributable to their intrinsically greater proportion of long shoots. About 20% of the shoots on freeze-damaged trees are long, compared to 15% on undamaged trees—a difference that cannot have been caused by the freeze event itself. Freeze-damaged trees appear to have an intrinsic commitment to greater numbers of rapidly growing shoots in their crown. This combined with the growth of additional leaves on short shoots to replace early-leaves damaged by the freeze event yields a tree crown richer in young foliage throughout the growing season.

It is this preponderance of young foliage in their crown that leaves freeze-damaged *Betula papyrifera* more prone to attack by leaf-chewing insects. Young foliage is less well-defended against leaf-chewing herbivores than old foliage. Condensed tannin concentrations in young leaves are low, whether the leaves are produced early or late in the season. Condensed tannin content is greater in older foliage, especially on freeze-damaged trees. Older leaves poor in nitrogen and heavily defended by condensed tannins are unattractive to leaf-chewing insects, while young leaves rich in nitrogen and poorly defended by condensed tannins are more attractive. Thus the relatively high abundance of young leaves on freeze-damaged trees can account for their greater attack by leaf-chewing herbivores through the season.

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References

- Ayres, M. P., T. P. Clausen, S. F. Maclean Jr., A. M. Redman and P. B. Reichardt. 1997. Diversity of structure and antierbivore activity in condensed tannins. *Ecology* 78: 1696-1712.
- Caesar, J. C. and A. D. MacDonald. 1983. Shoot development in *Betula papyrifera*. II. Comparison of vegetative and reproductive short shoot growth. *Canadian Journal of Botany* 61: 3066-3071.
- Caesar, J. C. and A. D. MacDonald. 1984. Shoot development in *Betula papyrifera*. IV. Comparisons between growth characteristics and expression of vegetative long and short shoots. *Canadian Journal of Botany* 62: 446-453.
- Clausen, J. J. and T. T. Kozłowski. 1965. Heterophyllous shoots in *Betula papyrifera*. *Nature* 205: 1030-1031.
- Gansert, D., K. Backes and Y. Kakubari. 1999. Altitudinal and seasonal variation of frost resistance of *Fagus crenata* and *Betula ermanii* along the Pacific slope of Mt. Fuji, Japan. *Journal of Ecology* 87: 382-390.
- Hunter, A. F. and M. J. Lechowicz. 1992. Foliage quality changes during canopy development of some northern hardwood trees. *Oecologia* 89: 316-323.
- Kozłowski, T. T. and J. J. Clausen. 1966. Shoot growth characteristics of heterophyllous woody plants. *Canadian Journal of Botany* 4: 827-843.
- Kramer, K. 1996. Phenology and growth of European trees in relation to climate change. Thesis Landbouw Universiteit Wageningen, CIP-Data Koninklijke Bibliotheek, Den Haag, Netherlands.
- Kudo, G. 1995. Altitudinal effects on leaf traits and shoot growth of *Betula platyphylla* var *japonica*. *Canadian Journal of Forest Research* 25: 1881-1885.
- Lechowicz, M. J. 1984. Why do temperate

- deciduous trees leaf out at different times? Adaptation and the ecology of forest communities. *American Naturalist* 124: 821-842.
- Lechowicz, M. J. and T. Koike. 1995. Phenology and seasonality of woody plants: an unappreciated element in global change research? *Canadian Journal of Botany* 73: 147-148.
- MacDonald, A. D. and D. H. Mothersill. 1983. Shoot development in *Betula papyrifera*. I. Short shoot organogenesis. *Canadian Journal of Botany* 61: 3049-3065.
- MacDonald, A. D., D. H. Mothersill and J. C. Caesar. 1984. Shoot development in *Betula papyrifera*. III. Long shoot organogenesis. *Canadian Journal of Botany* 62: 437-445.
- Martin, J. S. and M. M. Martin. 1982. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. *Oecologia* 54: 205-211.
- Middleton, K. R. 1960. New Nessler Reagent and its use in the direct nesslerization of Kjeldahl digests. *Journal of Applied Chemistry* 10: 281-286.
- Mutikainen, P., M. Walls, J. Ovaska, M. Keinänen, R. Julkunen-Tiitto and E. Vapaavuori. 2000. Herbivore resistance in *Betula pendula*: effect of fertilization, defoliation, and plant genotype. *Ecology* 81: 49-65.
- St-Jacques, B. 1984. The quality of *Betula papyrifera* foliage as a resource for herbivores: seasonal and stress-induced changes. Unpublished M.Sc. thesis, McGill University, Montréal, Québec, Canada.
- Swain, T. and W. E. Hillis. 1959. The phenolic constituents of *Prunus domestica*. I. The quantitative analysis of phenolic constituents. *Journal of the Science of Food and Agriculture* 10: 63-68.
- Temple, A. 1982. Tannin measuring techniques: a review. *Journal of Chemical Ecology* 8: 1289-1298.