

Photosynthetic and morphological responses of white birch, balsam poplar, and trembling aspen to freezing and artificial defoliation

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Abstract: Comparative stress resistance of 1-year-old white birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsamifera* L.), and trembling aspen (*Populus tremuloides* Michx.) seedlings was evaluated after exposure to freezing or defoliation. Photosynthesis in leaves surviving freezing (-5°C) declined immediately after treatment, but nearly fully recovered within 3 weeks. Defoliation did not significantly increase photosynthesis in the remaining leaves. Refoliation occurred after freezing that killed terminal shoots and released current buds from apical dominance, while new leaves of larger size were produced through continuous growth of terminal shoots in 50% or 100% defoliation. Freezing and complete defoliation significantly reduced diameter and height growth in all species, whereas 50% defoliation did not affect growth. These results indicate some of the physiological and morphological responses to foliage loss in broadleaved boreal species that can help to maintain growth and productivity under a warming climate, which may result in more frequent damaging spring frosts and insect defoliation.

Key words: frost damage, refoliation, leaf morphology.

Résumé : Les auteurs ont comparé la résistance au stress chez des plantules âgées d'une année, de bouleau à papier (*Betula papyrifera* Michx.), de peuplier baumier (*Populus balsamifera* L.) et de peuplier faux-tremble (*Populus tremuloides* Michx.) après exposition au gel et à la défoliation. Chez les feuilles ayant survécu au gel (-5°C), la photosynthèse a immédiatement décliné après le traitement, mais s'est rétablie complètement en moins de 3 semaines. La défoliation n'augmenta pas significativement la photosynthèse dans les autres feuilles. La refoliation survient après un gel ayant tué les tiges terminales et supprime l'effet de la dominance apicale sur les bourgeons actifs, alors que de nouvelles feuilles plus grandes se forment par croissance continue des tiges terminales, après 50 % et 100 % de défoliation. Le gel et la défoliation totale réduisent la croissance en diamètre et en hauteurs chez toutes les espèces, alors qu'une défoliation à 50 % n'affecte pas la croissance. Ces résultats illustrent certaines réactions physiologiques et morphologiques en réaction de la perte de feuillage chez des espèces boréales à larges feuilles pouvant aider à maintenir la croissance et la productivité sous un climat en réchauffement, lequel pourra conduire à des gels printaniers et des défoliations par les insectes plus fréquents. [Traduit par la Rédaction]

Mots-clés : dommage par le froid, refoliation, morphologie foliaire.

Introduction

Although most studies of North American boreal forests have focused on the more economically important conifer species, broadleaved trees are nevertheless important ecologically and as potential sources of fibre. White birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsamifera* L.), and trembling aspen (*Populus tremuloides* Michx.) are the most common broadleaved trees in Canadian boreal forests (Rowe 1972). They occupy a range of climatic and site conditions and often grow in mixed stands with conifers or other broadleaved trees (Perala 1990; Safford et al. 1990; Zasada and Phipps 1990), contributing to stand and landscape diversity. Being fast-growing and short-lived relative to conifers, these broadleaved trees play critical roles in meeting wildlife habitat needs and maintaining ecosystem processes and functions, in addition to being used in various forest products.

Spring frosts and insect outbreaks are common in Canadian boreal forests. Among boreal trees, white birch, balsam poplar, and trembling aspen break bud relatively early in spring (Cayford et al. 1959), and these flushing buds and elongating shoots are vulnerable to freezing temperatures (Zalasky 1976; Hiratsuka and Zalasky 1993; Lamontagne et al. 1998; Wolken et al. 2009). Spring is also the time when larvae of forest tent caterpillar (*Malacosoma*

disstria Hbn.), the most serious defoliator of these broadleaves in Canada (Peterson and Peterson 1992), emerge and feed on expanding leaves (Hildahl and Campbell 1975; Fitzgerald 1995). The outbreak of this insect, typically 3–6 years in duration every 6–16 years, can affect large areas (Hildahl and Campbell 1975). At the peak of the most recent outbreak in Ontario, from the early 1990s to early 2000s, nearly 19 million ha of boreal forest were moderately to severely defoliated (Fleming et al. 2000). If repeated severe defoliation occurs over several years, tree growth can be greatly reduced and they may even die (Hildahl and Campbell 1975; Man and Rice 2010). The long-term health of white birch, balsam poplar, and trembling aspen can be at higher risk of defoliation and freezing with the warming climate. Increased temperatures during the winter months help forest tent caterpillar populations to survive and build, prolonging outbreak duration (Daniel and Myers 1995; Roland et al. 1998; Cooke and Roland 2003), and may result in earlier budbreak, making trees more susceptible to damage from late spring frosts (Cannell and Smith 1986; Man et al. 2009).

The effect of spring frost on broadleaved trees depends on temperature. Freezing temperatures above -4°C do not usually result in physical damage to flushing tissues (Perala and Alm 1990; Bigras

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and Hébert 1996), although even mild freezing temperatures may cause physiological shock (Lamontagne et al. 1998; Oksanen et al. 2005). Temperatures between -6 and -10 °C are less common, but can cause leaf necrosis leading to partial or complete foliage loss (Korstian 1921), as well as death of developing shoots or even whole trees (Hiratsuka and Zalasky 1993; Bigras and Hébert 1996). Damaged trees often produce a second leaf flush several weeks later (Cayford et al. 1959; St. Clair et al. 2009). However, it is not clear whether the secondary flush is from buds on the previous year's shoots, those on new elongating shoots, or some combination of both.

Similarly, damage resulting from forest tent caterpillar defoliation is closely associated with the level of foliage loss. Partial defoliation does not usually affect tree growth (Ives and Wong 1988) and one hypothesis for the mechanism is that remaining leaves compensate for foliage loss through increased stomatal conductance and photosynthesis (Hart et al. 2000; Frey et al. 2004). In contrast, more severe defoliation reduces tree growth and vigour (Ghent 1958; Hildahl and Campbell 1975; Peterson and Peterson 1992), suggesting that there is a limit beyond which increased defoliation cannot be offset by compensatory increases in photosynthesis.

The objective of this study was to improve our understanding of the responses of seedlings of three boreal broadleaved tree species, white birch, balsam poplar, and trembling aspen, to varying levels of foliage damage. We experimentally simulated two natural stresses that affect broadleaved species in boreal forests in the spring, freezing and defoliation. Specifically, we assessed the effects of these two stresses on shoot physiology (photosynthesis), morphology (leaf size and dormant bud flushing), and diameter and height growth of the current season.

Methods

Experimental materials

Seeds from single trees provided by the National Tree Seed Centre at Fredericton (New Brunswick) were collected at the Petawawa Research Forest (Ontario) ($46^{\circ}00'N$, $77^{\circ}42'W$) for white birch and trembling aspen and near Kemptville (Ontario) ($45^{\circ}02'N$, $75^{\circ}65'W$) for balsam poplar. Seeds were sown in late June 2010 in 3.8 cm \times 21 cm SC-10 Super Cell tubes filled with 2:1 peat moss/vermiculite (v/v) mixture and grown in a greenhouse at the Ontario Forest Research Institute in Sault Ste. Marie (Ontario). The greenhouse was programmed to provide 26 °C day – 18 °C night and a 16 h photoperiod. Seedlings were watered as required and fertilized weekly with 20–8–20 (N–P–K) (Plant Products Co. Ltd., Brampton, Ontario, Canada) at 100 ppm N. Beginning early September 2010, photoperiod followed ambient conditions and temperatures ranged from 3 to 9 °C day and 1 to 8 °C night. Fertilization was adjusted to 20–20–20 at 50 ppm N. In mid-October, fertilization was discontinued but watering continued as needed.

By the end of November, leaves had abscised from all seedlings. In mid-December seedlings were sealed in plastic bags, boxed, and stored in a freezer at -3 °C. In mid-March, after 3 months in frozen storage, seedlings were moved to refrigerated storage at 2 °C. In early May, seedlings were removed from boxes and returned to the greenhouse and grown at temperatures of 20 °C day – 8 °C night, a 16 h photoperiod at 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux density (PPFD), and 70% humidity. Budbreak occurred after 15–18 days in the greenhouse. Terminal buds of aspen and balsam poplar seedling flushed 1–2 days earlier than lateral buds; both terminals and laterals of white birch flushed at the same time. Among the three species, white birch appeared to have a 1–2-day delay in budbreak.

Treatments

Experimental treatments were applied in early June, 4 weeks after seedlings had been returned to the greenhouse following refrigerated storage and about 2 weeks after budbreak. Mean elongation of current shoot growth at this time was about 1 cm for white birch and balsam poplar and 4 cm for trembling aspen.

The experimental design was a randomized complete block, with four replications and four treatments, as follows: two defoliation levels (partial (50%) and complete (100%) leaf removal), one freezing temperature (-5 °C), and an untreated control. Each of the treatments was applied to 20 seedlings within a replication. For the partial defoliation treatment, every other leaf was clipped at the petiole, and for the complete defoliation treatment all leaves were removed. In the freezing treatment, seedlings were placed inside a programmable freezer (Thermotron[®] SM-32-C, Holland, Michigan, USA), with temperatures first held at 2 °C for 1 h for equilibration and then lowered at a rate of 2 °C $\cdot\text{h}^{-1}$ to the target temperature (actual temperatures reached ranged from -5 °C to -5.5 °C according to two thermocouples placed inside the freezing chamber), held at the target temperature for 2 h, and then gradually increased to 2 °C at a rate of 2 °C $\cdot\text{h}^{-1}$. After freezing, seedlings were held at 2 °C for 4 h.

After treatment, seedlings were returned to the greenhouse to grow for 3 weeks under the conditions they received prior to the treatment. Seedlings were then relocated to an outdoor holding area where they were exposed to natural conditions from late June until mid-October, when the experiment ended.

Data collection and analysis

Photosynthetic responses to freezing and defoliation were assessed immediately (1 day post) and 1 and 3 weeks after treatment, using a gas exchange system (LI-6400 Li-Cor, Lincoln, Nebraska, USA) equipped with the 6400-15 extended reach 1 cm chamber. The light source was a Philips 9 W PAR30 L LED bulb mounted above the leaf chamber providing 1600–1700 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD. Measurements were made on the leaves that initiated prior to treatment at a CO_2 concentration of 400 $\mu\text{mol}\cdot\text{mol}^{-1}$, temperature of 23 °C, air flow of 200 $\mu\text{mol}\cdot\text{s}^{-1}$, and relative humidity of 30%–35%. Six seedlings were repeatedly measured for each treatment by replication combination and stable levels of maximum net photosynthesis were recorded after 4–6 min. Owing to lack of functioning leaves on seedlings in the complete defoliation treatments, only newly developed leaves were measured 3 weeks after defoliation.

Morphological measurements of all 20 seedlings included leaf dimensions (length and width), bud flush, and growth (height and stem diameter at the base). The dimension of the largest leaf on each seedling was measured prior to and 3 weeks after treatment. Leaves initiated before (old leaves from freezing, control, and 50% defoliation treatments) and after (new leaves from control, 100% defoliation, and 50% defoliation treatments) treatment were measured separately.

The number of flushing buds was counted at 1 and 3 weeks post-treatment. Buds from the previous year's shoots were separated from those from the current year shoots. Seedling height and stem diameter at the beginning (after cold storage) and end (mid-October) of the experiment were measured for all live seedlings.

Analysis of variance (ANOVA) was performed separately for each species following a randomized complete block design with repeated measures for photosynthetic measurements based on plot means (e.g., the mean of six seedlings) using the SAS Proc Mixed Procedure (SAS Institute Inc. 2003). Covariance structure SP(POW) (spatial power law) was used for photosynthetic measurements, which were assessed at unequally spaced time intervals (Littell et al. 1996). Multiple contrasts were conducted for photosynthetic measurements among treatments of the same measurement time with critical p value adjusted using the

Table 1. Summary of *P* values for photosynthesis, leaf dimension, bud flush, and growth of broadleaved seedlings by freezing and defoliation treatments.

Response variables	Factor	White birch	Balsam poplar	Trembling aspen
Maximum net photosynthesis	Time (Tm)	0.001	0.002	<0.001
	Treatment (Tr)	<0.001	<0.001	<0.001
	Tm × Tr	<0.001	<0.001	<0.001
Leaf length	Treatment	<0.001	<0.001	<0.001
Leaf width	Treatment	<0.001	<0.001	<0.001
Previous year bud flush	Treatment	1.000	0.637	0.189
Current year bud flush	Treatment	<0.001	0.436	<0.001
Stem diameter growth	Treatment	<0.001	<0.001	<0.001
Height growth	Treatment	<0.001	<0.001	0.01

Bonferroni method, whereas a multiple comparison of treatment means was performed along with *p* value correction for leaf dimension, bud flush, and growth (Tukey method in SAS 9.2; SAS Institute Inc. 2003) when significant treatment effects or interactions were indicated ($\alpha = 0.05$). In leaf dimension analysis, six treatment types were involved including three old leaf types that initiated prior to treatments (freezing, control, and 50% defoliation) and three new types that initiated after treatments (control, 50% defoliation, and 100% defoliation).

Results

Freezing damage

Freezing at -5°C damaged about 80% of elongating terminal shoots on white birch and trembling aspen and 95% in balsam poplar. Most flushed lateral buds survived freezing. Of 80 seedlings per combination of species and treatments, mortality in the freezing treatment was 5% for trembling aspen and balsam poplar and 10% for white birch, while <3% of the nonfrozen seedlings died.

Photosynthetic response to treatments

In the first week after freezing, photosynthetic rates in seedlings subjected to freezing were substantially lower than those of seedlings in the control and 50% defoliation in all three species (Table 1; Fig. 1). In all instances, mean photosynthetic rate was higher in seedlings after 50% defoliation than in the control at weeks 1 and 3, but the difference was not statistically significant. Three weeks after freezing, the photosynthetic rates had substantially recovered in white birch and trembling aspen seedlings, whereas those of frozen balsam poplar remained significantly lower than those of nonfrozen seedlings (Fig. 1).

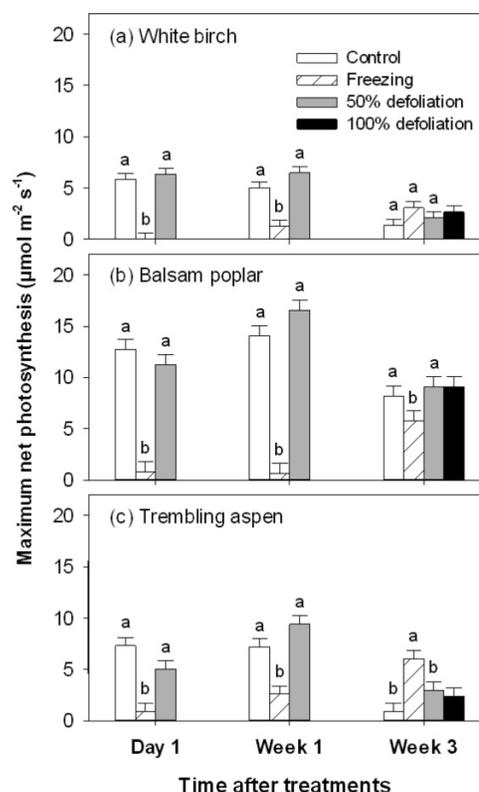
Three weeks after 100% defoliation, the new leaves that were initiated after treatment had photosynthesis rates similar to those of old leaves in seedlings subjected to 50% defoliation (Figs. 1).

Morphological responses

Both balsam poplar and trembling aspen reached nearly maximum leaf size after 4 weeks of growth in the greenhouse, prior to treatments being carried out, whereas white birch leaves in the control and 50% defoliation treatments continued expanding over the 7-week period of observation after cold storage. In all three species, leaf growth stopped after freezing treatment (Table 1; Fig. 2). Interestingly, leaves initiated after defoliation were the same size or larger than the new leaves of control seedlings.

For white birch, all the previous year's buds had flushed prior to treatment and as a result no additional flushing occurred afterwards (Fig. 3a). In comparison, in balsam poplar and trembling

Fig. 1. Maximum net photosynthesis of (a) white birch, (b) balsam poplar, and (c) trembling aspen after freezing or defoliation. Within measurement times, bars with different letters differ significantly. Values for 100% defoliation of post-treatment newly developed leaves are provided for comparison.



aspen some of the buds remained dormant during the 4-week period in the greenhouse prior to treatment, and only a few flushed afterwards (Table 1; Figs. 3b, 3c). The freezing treatment stimulated flushing of axillary buds on the newly elongated (current year) shoots, with a mean of 2.4 new lateral shoots for white birch and 2.6 new lateral shoots for trembling aspen seedlings (Figs. 3a, 3c). Leaves on axillary shoots were notably smaller than those formed on the terminal shoot. Defoliation did not induce new leaf growth from axillary buds on the main stem; instead, all refoliation was from elongation of the undamaged shoot apical meristem, which continued elongating and producing new leaves.

At the end of growing season, 4 months after the treatments, stem diameter and height increments were generally largest for seedlings in the control and lowest for those in the freezing treatment (Fig. 4). Seedlings that survived freezing increased in height from the flush of the previous (balsam poplar) or current (white birch and trembling aspen) year's buds.

Discussion

White birch, balsam poplar, and trembling aspen leaves that survived freezing treatment showed an immediate reduction in photosynthetic rate (Fig. 1). As Dang et al. (1992) reported for black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch), the impaired photosynthetic systems of the three broadleaved trees in the current investigation also had a remarkable recovery. Because of large intervals between remeasurements, we were unable to distinguish the depth of photosynthetic depression and the speed of its recovery, as shown by Dang et al. (1992). However, within 3 weeks, the damaged photosynthetic systems recovered almost fully in seedlings subjected to freezing,

Fig. 2. Dimensions of white birch, balsam poplar, and trembling aspen leaves that initiated prior to (old) and after (new) freezing or defoliation. Measurements were conducted 3 weeks after treatments. Within species, means of bars with different letters differ significantly. Pretreatment leaf dimension values are provided for comparison.

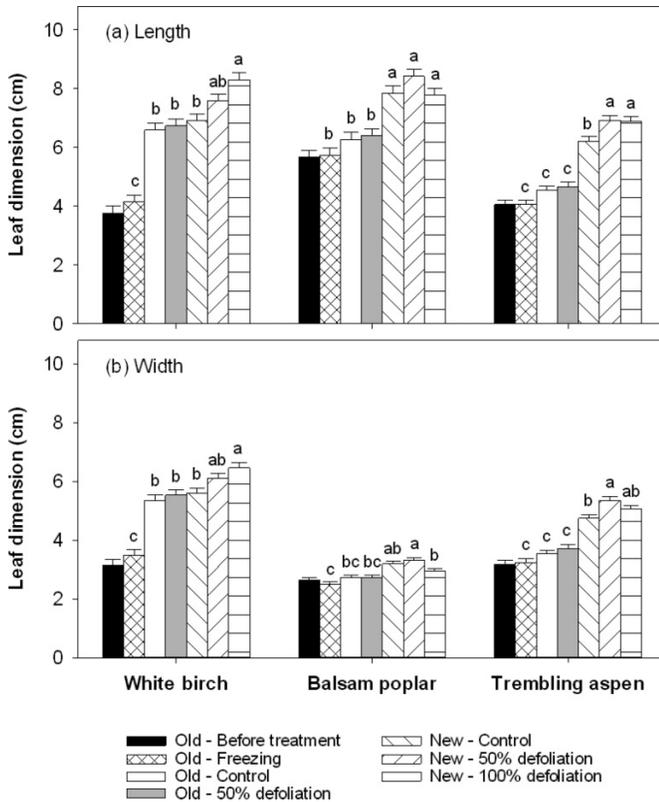
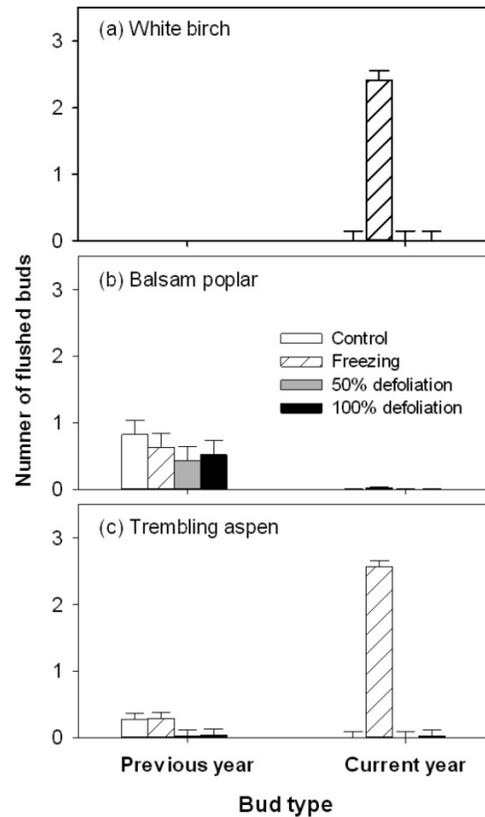


Fig. 3. Flush of previous and current year buds of (a) white birch, (b) balsam poplar, and (c) trembling aspen after freezing or defoliation.

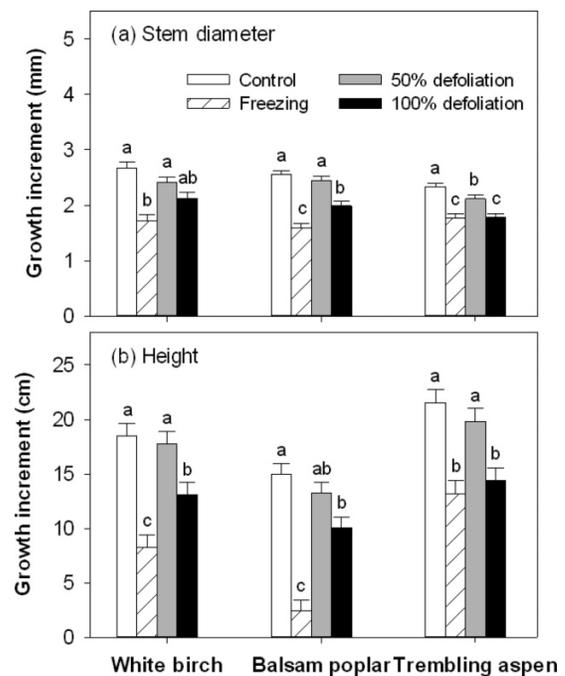


which was not the case for seedlings in the control or 50% defoliation treatments. The causes for considerable reduction of photosynthesis in the control and 50% defoliation treatments 3 weeks post-treatment were not clear. We speculate that with the rapid increase in seedling and foliage size, water and nutrients could have become limiting, despite the regular watering and fertilization schedules applied in this study. It is also possible that foliage in the control and 50% defoliation treatments were physiologically older and had lower photosynthetic capacity (Kitajima et al. 2002) as we noticed that foliage of seedlings that survived freezing and 100% defoliation treatments remained green longer into the fall.

Defoliation has been found to increase photosynthesis in species such as *Eucalyptus globulus* Labill. (Turnbull et al. 2007), red pine (*Pinus resinosa* Ait.) (Reich et al. 1993), and red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.) (Heichel and Turner 1983). This has been attributed to increased specific activity of Rubisco (Turnbull et al. 2007) and improved water relations (Hart et al. 2000; Frey et al. 2004), both of which increase photosynthetic rate in the remaining leaves and any new leaves initiated after defoliation. In the present study, however, the observed increase in photosynthesis in defoliated seedlings was not consistent or large enough to be declared significant.

Boreal broadleaved tree seedlings showed different responses to compensate for foliage loss via freezing and defoliation (Figs. 3 and 4). Freezing killed terminal shoots and released current year buds from apical dominance, while defoliation resulted in larger leaves being produced from the continuous growth of terminal shoots. Contrary to the common belief that refoliation occurs after 75%–100% defoliation (Wargo 1978), complete defoliation did

Fig. 4. Growth of white birch, balsam poplar, and trembling aspen after freezing or defoliation. Within species, means of bars with different letters differ significantly at 0.05.



not stimulate the flush of axillary buds on current year shoots in any of the species in this study. We believe the absence of axillary bud flush was due to correlative inhibition (paradormancy) exerted by the shoot apex (Cline and Deppong 1999), because axillary buds have been noted to flush if terminal shoots are damaged by insects (Peterson and Peterson 1992; Chao et al. 2007) and after manual removal of shoot apices in these species in an unpublished experiment by one of the authors (R. Man, unpublished). Freezing did not result in the flush of current buds in balsam poplar as all current buds were killed, suggesting that growing balsam poplar shoots are slower than those of trembling aspen and white birch to gain cold hardiness.

Compensatory leaf growth and slightly increased rates of photosynthesis may explain why 50% defoliation did not significantly reduce seedling diameter and height growth. This is consistent with the general belief that light defoliation has little effect on tree growth (Ives and Wong 1988; Peterson and Peterson 1992, Frey et al. 2004). Comparatively, freezing treatment at -5°C reduced seedling growth as much or more than 100% defoliation (Fig. 4). In addition to reduced growth, freezing damage to shoot apical meristems encouraged the development of multiple leaders, which, if they persist, will reduce merchantable stem quality (Hiratsuka and Zalasky 1993).

Freezing temperatures and insect defoliation are common stressors of trees in Canadian boreal forests. The results of this study suggest that broadleaved trees have some capacity to compensate for foliage loss through enhanced photosynthesis and larger leaf size. When terminal shoots are damaged, foliage from flushing of axillary buds later in the growing season can contribute to replacing lost foliage. These physiological and morphological responses could allow broadleaved trees to maintain growth in a future that may include increasing climatic extremes, and more frequent risk of spring frost damage (Cannell and Smith 1986; Colombo 1998; Man et al. 2009) and insect defoliation (Soja et al. 2007). However, caution is required when applying the findings of this study to natural forests because of differences in stress tolerance levels between trees and seedlings, differences between the effects of natural and simulated stresses on trees (Chen et al. 2002), and possible repetition of stresses in nature relative to a single instance in this study (Hildahl and Campbell 1975; Hiratsuka and Zalasky 1993; Man and Rice 2010).

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