Effects of duration of a simulated winter thaw on dieback and xylem conductivity of *Betula papyrifera*

R. M. COX and J. W. MALCOLM

*Canadian Forest Service–Atlantic Forestry Centre, Natural Resources Canada, P.O. Box 4000, Fredericton, N.B. E3B 5P7, Canada*

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**Summary** Stems or roots + stems of potted, 2-year-old paper birch (*Betula papyrifera* L.) were subjected to simulated winter thaws of various durations in climate-controlled chambers. The simulated thaws induced dieback of shoots of the treated plants. Although the stem thaw treatment did not significantly increase dieback, there were significant (*P < 0.05*) correlations between growing degree days above 4 °C and both shoot dieback and percent reduction in conductive xylem. All trees that received > 60 growing degree days (GDD) > 4 °C died back to some extent. Plants in the root + stem thaw treatment that received more than 60 GDD > 4 °C showed a significant (*P < 0.05*) increase in dieback and a significant (*P < 0.05*) loss of conducting xylem after a period of growth and recovery in the greenhouse, especially in the xylem of 1-year-old stems. Furthermore, higher correlations between GDD > 4 °C during a thaw and both the extent of dieback and the loss in conductive xylem were found in trees subjected to the root + stem thaw treatments than in trees exposed only to the stem thaw treatments (*P < 0.05*). The root + stem thaw treatments also resulted in highly significant relationships (*P < 0.05–0.001*) between loss in conductive xylem and dieback. The occurrence of dieback in response to winter thaws, and its close correlation with irreversible losses of xylem conductivity due to embolisms, coupled with an inability to refill the xylem because of root damage, support the view that these processes may be key factors in initiating birch decline.

**Keywords:** bud expansion, embolism, paper birch, root damage.

**Introduction**

Current evidence suggests that mean global surface temperatures have risen during the last century and a half, with a greater increase in winter than in summer (see review by McElroy 1994). It has been predicted that there will be future increases in temperature and that these will be greater in high latitudes (Hansen et al. 1988). In addition, sulfate particulates from industrial sources may cause cooling, offsetting the warming trend at times (Charlson et al. 1987, Wigley 1989). Increased temperature variation could result in longer, more frequent, winter thaws than at present, which could have a greater effect on forest vegetation than slight changes in mean temperature.

The birch decline that occurred during the 1930s in eastern North America resulted in an estimated stem volume loss of 1400 million m$^3$ of yellow and white birch over an area of 490,000 km$^2$ (Pomerleau 1991). Winter thaws have been implicated in this decline (Braathe 1957, Auclair 1987, Braathe 1995), although Millers et al. (1989) have questioned the assumption. Thaws have also been proposed as the cause of the recent dieback in all but a few hardy commercial apple cultivars in New Brunswick, Canada (Coleman 1992).

Pomerleau (1991) reported evidence of a link between birch tree decline and root depth. He also linked winter thaws and deep soil frost with birch decline. A similar relationship between deep soil frost and decline has also been noted in sugar maple by Bertrand et al. (1994).

Sperry et al. (1988a) concluded that one mechanism of freeze–thaw-induced damage in sugar maple was the seasonal occurrence of xylem embolisms, which reached a maximum of 84% in February. They suggested that small bubbles, formed by ice sublimation, grow during a thaw cycle and later expand to block xylem elements. Recovery from cavitation was driven by springtime root pressure. Sperry et al. (1994) observed that when root pressure in birch was artificially suppressed by overlapping cuts across the stem, existing embolisms were not reversed and shoot dieback was extensive.

Extensive xylem cavitation was documented in birches showing crown dieback in New Brunswick (Greenidge 1951); however, at the time, it was not attributed to winter freeze–thaw cycles. Sperry and Sullivan (1992) determined that in the two diffuse-porous species, *Betula occidentalis* Hook. and *Populus tremuloides* Michx., growing in Salt Lake City at an elevation of 1370 m, more than 90% of vessels cavitated by the end of the winter. Auclair (1993) noted that the long time interval between winter cavitation and the development of symptoms has made it difficult to recognize the cause of the injury.

We have developed an experimental approach for examining the role of midwinter thaws on birch dieback in controlled-environment chambers. We also measured changes in the amount of conductive xylem in the stems of treated plants, to gain a better understanding of the underlying physiological and biophysical mechanisms leading to dieback.
Materials and methods

Paper birch (*Betula papyrifera* L.) was grown from bulk seed collected at two southern New Brunswick sites. Individual plants were grown in pots for 2 years (1–1.4 m high), then set in the ground (still in pots) at the Hugh John Flemming Forestry Centre, Fredericton, New Brunswick. Before the experiment began on February 4, the potted birch trees had been exposed to air temperature changes from > 0 to < −3 °C (thaw/freeze events) on 19 occasions.

Experimental design

The design consisted of seven plots arranged randomly in each of four blocks. Five plots in each block were assigned thaw treatment periods of 11, 15, 19, 29 or 39 days (chambers), and two plots were left as controls (nonchambered trees). Treatment plots each contained three potted trees, whereas control plots had two potted trees.

On February 3, 1992, one potted tree per plot was removed from the frozen ground with a power chisel. The insulated bases of the chambers were then put in place and sealed around the stems of the two remaining plants. These plants, with their pots remaining frozen in the ground outside the chambers, comprised the stem thaw treatment (ST plants). The trees that were removed from the ground were placed on the insulated base of their respective chambers before erection of the chamber canopies (Figure 1). The plants with pots and stems within the chambers comprised the root + stem thaw treatment (RST plants). The thaw periods began on February 4. Simulated thaw days followed a diurnal temperature curve (Figure 2) throughout the thaw period. Once the RST plants were thawed, they were watered three times a week with 400 ml of water delivered to the pot through a tube connected to a water inlet on top of the chamber (Figure 1).

At the end of each period of a simulated thaw, the trees from one plot per block and one randomly selected control tree per block were removed (with a power chisel if the pot was in frozen ground) and placed in the dark in a freezer at −10 ± 1 °C. After 10 days, the RST plants and one ST plant per plot were placed in a growth cabinet at 4 °C (12-h photoperiod, 70% RH) for 12 days, and then transferred to a greenhouse where they were grown for 7 weeks in a 16-h photoperiod at a day/night temperature of 23/15 °C, 70–80% RH, with automatic watering to maintain the pots at field capacity, and N,P,K fertilization (11,41,8 for 2 weeks then 20,8,20). The remaining ST plants (one per plot) were left in the freezer until examined for percent conductive xylem.

Chamber design and operation

The chambers (Figure 1) consisted of a slightly raised, circular PVC collar with an insulated base through which the stems of the plants protruded. The canopy of the chamber consisted of two concentric polyethylene film sleeves of different diameters tied at the top to a vent. A blower delivered air through a heated PVC tube to the base of the chamber, and the resultant air pressure supported the sleeves. Air passed from the inner sleeve, through the top vent to the outer sleeve and finally to the outside through basal vents.

Temperature transducers inside the chambers were linked to a computer (software developed in collaboration with Interlab Inc., Fredericton, NB, Canada) that controlled the temperature, according to a predetermined profile, by varying power to the delivery-tube heating elements. Figure 2 shows the diurnal

![Figure 1. Diagram of chamber used for simulated winter thaw, showing positions of potted plants and sensors.](image-url)
temperature profile for a representative day. Figure 3 shows the
mean temperatures in the pots within the chambers and in the
pots in the ground below the chambers. Relative humidity in
the chambers ranged between 15 and 90%.

Bud expansion

Three terminal buds per tree were photographed one day be-
fore installing the chambers and again at the end of the thaw
treatment. Photographs were taken from a fixed distance
(about 30 cm), with a reference scale bar displayed in each
frame. Bud lengths and widths were then digitized with a
digitizing tablet (Jandel Scientific software, Numonics Corp.,
Montgomeryville, PA) and calibrated against the scale bars.

Dieback

Dieback of each tree was measured after 7 weeks of growth in
the greenhouse. The lengths of current-year and 1-year-old
branches and of the 2-year-old main stem were measured. The
presence and the length of dieback on each branch, identified
by discoloration, shrinkage of the bark, or presence of unex-
panded buds, were recorded.

Xylem conductivity

Percentage conductive xylem in 1-year-old branches and 2-
year-old main stems was measured by the dye perfusion
method described by Sperry et al. (1988b). Branch segments
at least 25 cm long were cut and immediately submerged in tap
water. While keeping the segment immersed, sharp secateurs
were used to cut several small pieces from each end to a final
length of 15 cm. After shaving each end with a razor blade,
gaskets and short water-filled lengths of Tygon tubing were
fitted to the apical ends, to provide both watertight seals and a
reservoir above the apical end of the segment to prevent intro-
duction of air to the stem. Stem segments were then quickly
attached to the perfusion apparatus.

Each perfusion apparatus consisted of a horizontal manifold
with five vertical ports and an exit line providing a vertical
drop of 100 cm (static head of −9.8 kPa). Stem segments were
attached parallel to the vertical ports of the manifold, with their
basal ends suspended in beakers of dye solution (0.1% safranin
in 0.5% formalin, filtered at 0.22 μm). The static head in the
liquid-filled apparatus was applied for 45 min to draw the stain
up through the segments. The staining solution was then re-
placed with a rinse solution (0.5% formalin) and after a further
45 min of perfusion the segments were removed and allowed
to air-dry.

Small (0.5 cm) sections were removed at 5.0 and 10.0 cm
from the base of the segments, and the bark carefully removed.
Total cross-sectional area and unstained area were measured
for each section with an image-digitizing area meter (Delta-T
Devices, Cambridge, U.K.). Stained areas were assumed to be
conducting xylem (Sperry et al. 1988b).

Statistical analysis and data transformation

All percent values were arcsin transformed to normalize the
data distribution. Mean values ± 1 SE were calculated for each
combination of treatments. Statistical analysis was carried out
with the SAS software package (SAS Institute, Cary, NC,
1989). Percent change in bud length and width were calculated
as: Percent change = ((Value after a thaw – Value before a
thaw)/Value before a thaw)100.

Results

Dieback

There was wide variation in individual plant response to the
stem thaw treatments (ST plants), and variation was greater
among treated trees than among untreated controls (Figure 4a).
The root + stem thaw treatments (RST plants) produced
more damaging effects than the stem thaw treatments (Fig-
ure 4b). There was a threshold between 55.5 and 87.1 accumu-
lated growing degree days (GDD) > 4 °C of thaw, above which
complete dieback of previous-year growth occurred on all
individuals tested. Dieback also occurred on untreated individuals (up to 40% of their branches in some individuals).

**Bud expansion**

Dieback occurred without any indication of bud swelling or growth during the treatments. Many buds tended to shrink with increasing duration of the thaw treatment. In the ST plants, percent changes (arcsin) in bud length, including negative values (shrinkage), were strongly negatively correlated with GDD > 4 °C ($r = -0.477$, $P = 0.0002$, $n = 56$). A weaker but significant correlation for this relationship was observed in RST plants ($r = -0.451$, $P = 0.046$, $n = 20$). Because there was no indication of bud expansion or growth during the experiment, we concluded that bud expansion was not a reliable indicator of physiological susceptibility to dieback.

**Xylem conductivity**

In ST plants, the percentage of cross-sectional area made up of nonconducting xylem exhibited much variation with duration of the thaw treatment (Figures 5a and 5b). This variation was evident both directly after refreezing ST plants (Figure 5a) and 7 weeks after ST plants had been transferred to the greenhouse (Figure 5b) and may reflect phenotypic variation among the plants in vulnerability to winter cavitation.

Values of percent nonconducting xylem determined for plants allowed to recover in the greenhouse were lower than for plants measured directly after refreezing, by about 20 and 4% in 1- and 2-year-old segments, respectively (Figures 5a and 5b, Table 1). This decrease includes the contribution of the new conducting xylem produced during growth in the greenhouse. The same comparisons for untreated (control) trees indicated a similar extent of xylem recovery for 1- and 2-year-old segments. We observed a significant increase in percent nonconducting xylem of RST plants over ST plants after thaws of 89.7 GDD > 4 °C ($P = 0.011$, $F = 13.33$ MS = 4563, DF = 1) (Figures 5b and 6).

The relationship between percent nonconducting xylem (arcsin) and two measures of dieback from the same plants were examined (Table 2). These correlations were significant ($P > 0.05$) for the two branch ages and both measures of dieback in the combined data set, and for the data subset from RST plants. The subset from ST plants did not exhibit any significant correlations at $P = 0.05$.

Correlations between GDD > 4 °C of winter thaw and percent nonconductive xylem (arcsin) of sections of 1- and 2-year-old branches from ST and RST plants after a 7-week
Table 1. Effect of thaw treatments of differing duration on mean percent unstained area (arcsin) of stem cross sections sampled from the top and base of 15-cm stem segments after dye perfusion. Values are means of up to four replicates ± 1 SE. Abbreviations: ST = stem thaw treatment, RST = root + stem thaw treatment, and GDD = growing degree days.

<table>
<thead>
<tr>
<th></th>
<th>Period 1</th>
<th>Period 2</th>
<th>Period 3</th>
<th>Period 4</th>
<th>Period 5</th>
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<tbody>
<tr>
<td><strong>Measurements made directly after refreezing</strong></td>
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<tr>
<td>One-year-old segments of control plants</td>
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<td></td>
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</tr>
<tr>
<td>Top</td>
<td>48.24 ± 1.91</td>
<td>90.00 (^3)</td>
<td>54.74</td>
<td>21.88 ± 4.86</td>
<td>66.10</td>
</tr>
<tr>
<td>Base</td>
<td>2.26 ± 0.91</td>
<td>90.00</td>
<td>54.74</td>
<td>24.32 ± 1.85</td>
<td>63.90</td>
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<td>Two-year-old segments of control plants</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Top</td>
<td>52.59 ± 1.79</td>
<td>90.00</td>
<td>30.88</td>
<td>47.85 ± 5.81</td>
<td>53.45 ± 26.11</td>
</tr>
<tr>
<td>Base</td>
<td>57.92 ± 10.61</td>
<td>61.46</td>
<td>30.96</td>
<td>39.00 ± 4.92</td>
<td>54.19 ± 21.69</td>
</tr>
<tr>
<td>One-year-old segments of ST plants</td>
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<tr>
<td>Top</td>
<td>51.20 ± 15.10</td>
<td>64.47 ± 15.58</td>
<td>60.62 ± 26.12</td>
<td>73.87 ± 17.13</td>
<td>58.42 ± 6.87</td>
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<tr>
<td>Base</td>
<td>35.45 ± 9.84</td>
<td>60.96 ± 17.09</td>
<td>67.50 ± 22.50</td>
<td>69.02 ± 20.98</td>
<td>53.99 ± 4.54</td>
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<td>Two-year-old segments of ST plants</td>
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</tr>
<tr>
<td>Top</td>
<td>65.48 ± 10.13</td>
<td>51.79 ± 14.45</td>
<td>37.40 ± 9.70</td>
<td>48.45 ± 5.36</td>
<td>61.58 ± 10.00</td>
</tr>
<tr>
<td>Base</td>
<td>60.19 ± 7.65</td>
<td>51.17 ± 7.12</td>
<td>36.50 ± 10.53</td>
<td>38.24 ± 6.69</td>
<td>54.49 ± 10.61</td>
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<tr>
<td><strong>Measurements made after a 7-week period of growth in the greenhouse</strong></td>
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<tr>
<td>One-year-old segments of control plants</td>
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</tr>
<tr>
<td>Top</td>
<td>17.06 ± 2.70</td>
<td>37.01 ± 12.54</td>
<td>34.06</td>
<td>28.83</td>
<td>46.09 ± 11.22</td>
</tr>
<tr>
<td>Base</td>
<td>24.70 ± 0.96</td>
<td>36.87 ± 9.82</td>
<td>44.23</td>
<td>32.84</td>
<td>45.92 ± 6.06</td>
</tr>
<tr>
<td>Two-year-old segments of control plants</td>
<td></td>
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<tr>
<td>Top</td>
<td>36.23 ± 2.50</td>
<td>33.67</td>
<td>23.63</td>
<td>29.47 ± 3.84</td>
<td>33.88 ± 2.52</td>
</tr>
<tr>
<td>Base</td>
<td>39.24 ± 0.90</td>
<td>32.46</td>
<td>33.53</td>
<td>30.39 ± 2.18</td>
<td>52.37 ± 5.33</td>
</tr>
<tr>
<td>One-year-old segments of ST plants</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Top</td>
<td>32.21 ± 4.20</td>
<td>34.38 ± 7.33</td>
<td>45.51 ± 22.35</td>
<td>28.33 ± 5.84</td>
<td>61.08 ± 10.81</td>
</tr>
<tr>
<td>Base</td>
<td>38.45 ± 3.90</td>
<td>33.20 ± 7.97</td>
<td>40.50 ± 9.96</td>
<td>28.26 ± 6.52</td>
<td>55.65 ± 10.25</td>
</tr>
<tr>
<td>Two-year-old segments of ST plants</td>
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</tr>
<tr>
<td>Top</td>
<td>42.15 ± 4.07</td>
<td>43.15 ± 3.67</td>
<td>25.99 ± 3.13 (^2)</td>
<td>36.68</td>
<td>51.40 ± 13.50</td>
</tr>
<tr>
<td>Base</td>
<td>45.57 ± 4.36</td>
<td>43.94 ± 2.81</td>
<td>26.79 ± 3.80 (^2)</td>
<td>33.81</td>
<td>49.57 ± 13.10</td>
</tr>
<tr>
<td>One-year-old segments of RST plants</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Top</td>
<td>43.63 ± 5.52</td>
<td>37.14 ± 6.91</td>
<td>30.56 ± 3.90</td>
<td>28.88 ± 9.53 (^1)</td>
<td>59.78 ± 10.40</td>
</tr>
<tr>
<td>Base</td>
<td>39.01 ± 6.10</td>
<td>41.83 ± 10.90</td>
<td>18.76 ± 4.96</td>
<td>64.40 ± 19.70</td>
<td>56.95 ± 12.04</td>
</tr>
<tr>
<td>Two-year-old segments of RST plants</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Top</td>
<td>36.88 ± 3.27</td>
<td>45.45 ± 5.78</td>
<td>27.37 ± 2.73</td>
<td>68.50 ± 21.50</td>
<td>51.38 ± 14.38</td>
</tr>
<tr>
<td>Base</td>
<td>43.12 ± 4.39</td>
<td>39.56 ± 7.85</td>
<td>23.73 ± 2.65</td>
<td>63.84 ± 15.89 (^1)</td>
<td>53.20 ± 13.36</td>
</tr>
<tr>
<td>GDD &gt; 4 °C</td>
<td>22.00 ± 3.59</td>
<td>43.80 ± 0.96</td>
<td>51.50 ± 2.33</td>
<td>89.70 ± 2.38</td>
<td>118.70 ± 8.59</td>
</tr>
</tbody>
</table>

\(^1\) Significantly different from treatment period 1 (protected Duncan’s multiple range test, alpha = 0.05).
\(^2\) Significantly different from treatment period 1 (P < 0.05) (Student’s t-test).
\(^3\) SE not calculated because n < 2.

recovery period in the greenhouse were higher for branch sections from RST plants than from ST plants (Table 3). Three out of the four data subsets of RST plants showed a significant (P < 0.05) relationship, whereas the relationship in ST plants was only significant (P < 0.05) for the base sections of 2-year-old branches. When plants were examined directly after refreezing, only very low coefficients were found, none of which demonstrated a significant relationship between the two variables.

There was a highly significant (P < 0.001) relationship between the extent of thaw (GDD > 4 °C) and dieback in the RST plants (Table 4). Although the ST plants demonstrated lower coefficients for this relationship, they were significant (P < 0.05) for percent branches with dieback.

**Discussion**

Most stands of white-barked birches in the Maritimes region show some dieback symptoms (Auclair 1987, Magasi et al. 1994). Our finding of some dieback in untreated control trees may indicate that many birch trees are under stress.

Exposure of roots and shoots to thaws (RST plants) exceeding 51.5 GDD > 4 °C caused dieback on all branches and reductions in conductive stem xylem of about 20–30%. This
damage to the water transport system, if permanent, may be responsible for the dehydration and dieback observed. Sperry et al. (1994) have shown that artificially suppressing root pressure development in birch with cavitated xylem causes dieback. We postulate that failure to refill embolisms in these plants is due to root damage incurred while the roots refreeze after a thaw in excess of the 51.5 GDD > 4 °C.

Recent investigations (Sperry and Sullivan 1992, Sperry 1993, Sperry et al. 1994) have shown extensive xylem embolisms (cavitation) in hardwood species resulting from accumulated injury throughout the winter. Variation in the responses of our treated plants may be associated with variation in vulnerability to xylem cavitation in response to freeze-thaw cycles as was demonstrated in *Betula papyrifera* and *B. occidentalis* (Sperry et al. 1994). Evidence suggests that the process of embolism formation occurs more readily in large diameter vessels than in small diameter vessels (Ewers 1985, Cochard and Tyree 1990, Sperry et al. 1994). Thus, in our study, the higher initial degree of cavitation in the older stem than in the younger stem may relate to vessel volume distributions.

Evidence for stem pressure development has been noted in sugar maple (Tyree and Sperry 1989). The contrasting responses in percent conductive xylem of 2-year-old and 1-year-old segments between treatment periods of 22 and 51.5 GDD > 4 °C may be attributable to stem pressure development that displaces the embolisms toward the extremities; alternatively, compared with the younger stem, higher pressures may develop in the older stem that are more effective at dissolving the embolisms.

We found that duration of stem thaw was directly related to incremental damage to xylem conductivity and dieback (Tables 3 and 4). However, the contribution of a single stem

Table 3. Values of $r$ determined for the relationship between GDD > 4 °C accumulated during the stem thaw and root + stem thaw treatments and percent of nonconducting xylem, as indicated by percent of stem cross section not stained (arcsin) in sections sampled 5 cm from the top and base of the 1- and 2-year-old segments. Values in parentheses indicate sample number; $^* = P < 0.05$, $** = P < 0.01$, and $*** = P < 0.001$.

<table>
<thead>
<tr>
<th>Stem section</th>
<th>Freezer plants</th>
<th>Stem-thawed greenhouse plants</th>
<th>Root + stem-thawed greenhouse plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>One-year-old</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Top</td>
<td>0.217 (25)</td>
<td>0.260 (28)</td>
<td>0.467** (18)</td>
</tr>
<tr>
<td>Base</td>
<td>0.221 (25)</td>
<td>0.368* (27)</td>
<td>0.559** (19)</td>
</tr>
<tr>
<td>Two-year-old</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Top</td>
<td>0.003 (25)</td>
<td>0.287 (24)</td>
<td>0.490** (18)</td>
</tr>
<tr>
<td>Base</td>
<td>0.067 (25)</td>
<td>0.431** (24)</td>
<td>0.486 (17)</td>
</tr>
</tbody>
</table>

1 Greenhouse plants includes control plants.

Table 4. Values of $r$ for the relationship between GDD > 4 °C accumulated during the stem thaw and root + stem thaw treatments and two measures of dieback. Values in parentheses indicate sample number; $^* = P < 0.05$ and $** = P < 0.001$.

<table>
<thead>
<tr>
<th>Stem thaw Root + stem thaw</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage of branches with dieback (arcsin)</td>
</tr>
<tr>
<td>Percentage of total length died back (arcsin)</td>
</tr>
</tbody>
</table>

Greenhouse plants includes control plants.
thaw to dieback would depend on the initial xylem conductivity (cavitation) before the particular thaw. The high percent loss in conductive xylem (cavitation) in the untreated control plants, presumably caused by the 19 natural freeze–thaw events before the experiment, may explain the lack of significant correlation between loss of conductive xylem and dieback in these plants. The RST plants showed the highest correlation coefficients for all of the relationships examined (Tables 2, 3, and 4), indicating that the period of thaw of both roots and stems is an important cause of dieback in paper birch. The need for spring refilling of winter embolisms in the xylem of diffuse porous species requires that healthy roots be present in early spring to provide the necessary root pressure. The importance of root health was noted by Pomerleau (1991), who reported that shallow-rooted birch and those that suffered deep root freezing were most affected by dieback (cf. Spalding and MacAlony 1931, Hall 1933). It has been observed that, in winters of reduced snow cover (< 10 cm), soil temperatures at a depth of 2.5 cm can drop 10 °C below the 16-year norm of −2 °C at Fredericton, NB, Canada (Salonius et al. 1977).

Braathe (1995) induced dieback in yellow birch with a simulated early spring thaw followed by refreezing. His observations led him to conclude that frost (−5 °C) damaged the developing buds and twigs, causing the dieback. In contrast, we found that dieback was induced in the absence of bud break. Furthermore, during a 7-week period of recovery in a greenhouse under favorable growing conditions, thaw-treated plants occasionally produced short shoots that dried up, indicating that water was not being transported from the soil to the growing shoots, a phenomenon that was also described by Braathe (1995).

We propose that the onset of birch dieback is triggered by a combination of, first, xylem cavitation brought about by low winter temperatures and freeze–thaw cycles in the stem, causing extensive loss of xylem conductivity; and second, root damage from refreezing after roots had become metabolically active during a thaw and were unable to reharden, thus reducing the ability of the roots to provide sufficient root pressure to drive the refilling of the xylem with sap in the spring.

The relative importance of winter xylem cavitation and spring root activity responses to winter thaws may vary with species or phenotype (Sperry et al. 1994). Amounts of xylem cavitation may also vary with the diameter and volume distribution of the xylem vessels (Sperry et al. 1994). Speed of dehardening in response to root thaw, and hardening in response to refreezing, will also affect the relative impact of these two processes.

We have demonstrated the efficacy of an experimental approach to the study of birch dieback and generated a testable hypothesis of birch dieback. The implication of our hypothesis is that dieback in paper birch will be greatest in winters having large numbers of freeze–thaw events, which will maximize development of xylem embolisms, followed by a prolonged thaw, which will maximize damage to the roots and thus prevent refilling of the cavitated xylem. Prolonged thaws before a −5 °C frost and their distribution have been described for 1936, 1944, 1945 and 1954 and linked to birch dieback (Braathe 1995). These decadal events may become more frequent and occur over wider areas with climate warming, implying increased risk of winter injury to northern-adapted hardwoods in eastern Canada.

We note that dieback is not equivalent to decline; however, it is an important contributing factor. Although the amount of accumulated thaw-induced dieback that triggers irreversible decline has not been quantified and may depend on secondary pathogenic infections, we postulate that it is less than that required for complete death of the previous season’s growth.

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