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Frost damage and its cascading negative effects on *Aesculus glabra*

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Abstract Frost damage and re-foliation are seldom quantified for forest species, but are of ecological and evolutionary importance. This study of *Aesculus glabra* (Ohio buckeye) in a deciduous forest remnant in Illinois, USA, quantified frost damage to leaves and flowers after sub-freezing temperatures in April 2007. It also documented re-foliation and later growth, reproduction, and survival in 2007–2009 for the 355 study individuals of four life stages growing 0–200 m from the forest edge. Life stages differed in % leaf damage because of differences in phenology during the frost. Large saplings with fully expanded, immature leaves had higher % damage and lower % canopy fullness after re-foliation than smaller saplings with partially or fully mature leaves and canopy trees undergoing shoot expansion with folded leaflets. Percent damage increased for saplings closer to edges. Large saplings with heavier frost damage to leaves had partial re-foliation in deep shade, lower % canopy fullness, earlier senescence, a shorter growing season, and greater death of next year's buds. By 2008, large saplings with greater damage in 2007 had more dead branches and lower % canopy fullness. By 2009, 11% of large saplings had died. In 2007, frost damaged no flowers, but final fruit crop size was negatively related to % leaf damage. Edge trees with total leaf damage aborted all fruits. The frost event differentially affected individuals in their length and time of growing season, energy budget, and, ultimately, reproduction, and survival. The population's local-scale demography and spatial pattern also changed as large saplings died.

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Introduction

A rare event, such as a late spring frost that causes plant damage, may be of particular ecological and evolutionary importance (Inouye 2000; Gutschick and BassiriRad 2003). Counter-intuitively, a plant's risk of frost damage may be increasing with global warming (Gu et al. 2008; Inouye 2008). However, due to frost's rarity and unpredictability, short- and longer-term responses to late spring frost have seldom been quantified for deciduous tree species (Spurr 1957; Tryon and True 1964). Frost immediately affects an individual's organs and modules (Luken 1990), affecting its resource acquisition. It also may act as a selective force, differentially affecting growth (Strain 1966), survival (Mooney 1977), reproduction (Inouye 2008), and the population's demography (Inouye 2000).

Life stages at different phenological phases may differ in frost damage (Kramer and Kozlowski 1979;

Augspurger 2009). In general, developing leaves are more vulnerable than expanding buds and emerging shoots (Sakai 1981; Sakai and Larcher 1987). Additionally, soft, expanding leaves are more vulnerable than fully expanded, tough leaves (Spurr 1957; Sakai 1981; Crawley and Long 1995). Life stages may differ in phenological phase and amounts of frost damage, in part, because of a vertical gradient in temperature affecting time of bud break and rate of leaf development. In deciduous forests, spring temperatures are warmer at lower strata (Spurr 1957; Augspurger 2004) and leaf development progresses from smaller life stages through canopy trees (Augspurger and Bartlett 2003).

On calm, clear nights with temperature inversions, colder near-ground temperatures bring greater radiation frost damage at lower vegetation levels, and in low topographic areas (Clarke 1946; Tryon and True 1964). An advective frost occurs when freezing temperatures combine with wind. Wind both amplifies the effect of cold temperatures and mixes cold air, reducing the vertical temperature gradient. Additionally, wind increases dehydration, especially of expanding and newly mature leaves with thinner cuticles, thereby increasing damage.

Frost damage may be less in a forest interior than in nearby clearcuts (Langvall and Löfvenius 2002) or forest edges. Freezing temperatures are more common on edges than the protected interior (Geiger 1965). Wind mixes cold air from edge areas into the interior, although wind speed decreases from edge into the interior (Geiger 1965). Edges with different orientation to wind direction may have different temperature gradients. Thus, an advective frost may bring great dehydration and frost damage, especially at and near edges facing the wind.

A woody plant's response to leaf frost damage is complex, and negative effects may accumulate past the frost year. The immediate response is to activate dormant buds and re-foliate (Kramer and Kozlowski 1979), but creation of a mature canopy is delayed and shifted to a time of deeper shade. Understorey plants may normally have much carbon gain prior to forest canopy closure (Augspurger et al. 2005). Stress may hasten leaf senescence (Augspurger 2008). Both late foliation and early senescence reduce the growing season. Frost may negatively affect the plant's energy acquisition, storage, growth, reproduction, and next year's buds in the current year, and canopy development, architecture, and even survival in subsequent years.

A widespread frost in early April 2007 occurred in the eastern deciduous forest USA. It followed an unusually warm March so that trees were in vulnerable phenological phases at the time of frost. Damage was widespread regionally (Gu et al. 2008), including Illinois, USA (Angel 2007). A comparative study indicated that damage and re-foliation in response to this advective frost differed greatly among 20 species and life stages in a deciduous forest in central Illinois, USA (Augspurger 2009). The variation was explained, in large part, by variation in phenological phase at the time of frost. The most damaged individuals had fully expanded, but soft, immature leaves. *Aesculus glabra* Willd. (Ohio buckeye) saplings had heaviest frost damage because they were the earliest to break bud and had immature leaves, resulting in both high frost damage and low re-foliation.

This study of Ohio buckeye expands on the previous study (Augspurger 2009) by including life stages from small saplings through canopy trees, adding a spatial dimension as the study site is a small forest remnant influenced strongly by edge effects, and detailing the current and two subsequent years' response of individuals heavily damaged by frost.

The objectives of the study were to examine: (1) differences among individuals of different phenological phase (and life stages) in extent of frost damage and re-foliation; (2) relationship of frost damage and re-foliation to proximity to edge of the forest remnant; and (3) effects of damage on subsequent re-foliation, dates of full leaf expansion and senescence, length of growing season, stem growth, bud health, and reproduction in the year of the frost, canopy fullness and basal shoot growth in the following year, and survival in the following 2 years. The study tested three hypotheses: (1) frost damage depends on an individual being at a vulnerable phenological phase at the time of frost, (2) frost damage is related to the extent of an individual's exposure to low temperatures and strong winds, affected by its location relative to the forest edge, and (3) the extent of frost damage determines the extent of developmental and demographic consequences in the current and subsequent years.

Materials and methods

Study site and selection of individuals

The study occurred in Trelease Woods, a mixed mesophytic, upland deciduous, old-growth forest located 5 km northeast of Urbana, Illinois, USA (40°09′N, 88°10′W). Average canopy height is 25 m. The 24-ha flat remnant (400 m E to W and 600 m N to S) has a 1.5 m high fence, then road and crop field to the west, and prairie buffer strips and then crop fields on the other three sides.

All study individuals were in the NW quarter of the remnant. The vegetative structure is similar on N and W edges. The edge is mowed regularly and thus is sharp with a narrow zone of about 1–2 m of dense sub-canopy vegetation, including the invasive *Lonicera japonica* Thunb and saplings of *Aesculus glabra*, before the canopy trunks dominate. At the time of the frost, all woody vegetation in the zone was leafless, except *A. glabra.*

Study individuals of the canopy tree species, *Aesculus glabra* (Ohio buckeye), included both forest (non-N-edge) and N-edge individuals. The forest individuals included four life stages: 15 reproductive canopy trees, 200 large saplings (height = 2–5 m; diameter at 100 cm = 2–7 cm), 40 medium saplings (height = 0.5–1.1 m), and 40 small saplings (<20 cm tall). Canopy trees (crown positioned in top of forest) were >25 m from any edge. Large saplings were selected 2–200 m from the N and/or W edges because prevailing winds were from N-NW during the frost (see below). This sample of 200 saplings was comprised of the first 12–13 saplings encountered while walking S in each of sixteen 50 × 50 m plots. Medium and small saplings co-occurred in an area with 40 of the large saplings and at distances 2–125 m from the N and/or W edges. Finally, the N-edge individuals were 60 large saplings and canopy trees (mean DBH = 10.1 cm; range = 2–37 cm) that grew along the N edge. All individuals ≥2 cm DBH on the N edge were included in this sample that was included to document the amount of frost damage on clearly defined edge individuals. Edge saplings broke bud a week later than interior saplings; this difference in phenology could substantially impact frost damage.

Phenology

Phenological observations of the 15 canopy trees and 10 of the large saplings have been continuous since 1993. These 25 individuals were observed weekly from March 17 to October 20, 2007 for leaf development, senescence, and reproduction. All other saplings were observed casually beginning in early March; they were selected and weekly observations began on April 22–27, 2007, when frost damage was evident, and continued through October 20, 2007.

Reproductive status of the 15 canopy trees was noted weekly as: none, flower buds, flowers, or fruits. Leaf development was documented for the 15 canopy trees and 10 large saplings. The phases were defined as: (1) bud break (bud swollen with scales parted, revealing underlying tissues, (2) shoot expansion (shoot emerging from bud scales and elongating, but leaflets folded and no major leaf expansion initiated), and (3) leaf expansion (leaf undergoing major expansion). Leaf expansion was completed when leaves were full sized, flattened, and in normal orientation. Leaf phases of the additional saplings were observed casually until frost damage was evident; all were at full leaf expansion at the time of the frost.

Senescence was quantified for all individuals. Beginning of senescence at the whole-plant level was declared when >1/3 of leaves showed first breakdown of chlorophyll revealing underlying pigments. Beginning of leaf drop occurred when >1/3 of leaves had abscised. Completion of senescence and leaf drop occurred when >5/6 of leaves reached the phase. Growing season was defined as the number of days between completion of leaf expansion and beginning of senescence at the whole-plant level.

Frost damage, re-foliation, shoot growth, survival, and reproduction

Variables measured for each forest (non-N edge) individual were: % damage to leaves (April 7–28), flowers (mid-April), and fruit (June 3); re-foliation (May 5–12); final % canopy fullness (June 3); shoot growth (relative to 2006); and damage to next year's buds (Oct. 6 to Nov. 3). Methods for quantifying damage are detailed in Augspurger (2009). In summary, percentages of shoots/leaves and flower buds/

flowers/fruits damaged by frost were estimated by visual inspection of the individual's crown at each weekly census. Terminal buds on shoots developed during shoot growth of 2007 were described as healthy, shriveled, or missing, and counted. Percent fruit aborted was quantified.

Re-foliation from activation of dormant lateral buds or continued development of damaged units was noted. Four responses (and a mix of the four) were possible: (1) no re-foliation response; original shoot and leaves had 0–5% of units damaged; (2) continued development of leaves on damaged shoot (oldest proximal leaves damaged, brown, and eventually dropped, while younger, more distal leaves expanded, but smaller than usual and partially brown); (3) epicormic and lateral bud activation on thick branches; and (4) up to 15 cm extension of original damaged shoot (from new terminal bud as would occur normally in subsequent year; most terminal buds of new shoot opened with new leaves, but some stayed as buds for next year's growth). After full leaf expansion from original and new buds, a coarse estimate of % "normal" canopy fullness was made, based on long-term observations of general leaf size and proportion of branches with leaf clusters on all size of individuals during non-frost years.

Variables measured for N edge individuals were: % damage to leaves (April 22–27), flowers (mid-April), and fruit (June 3); re-foliation responses (see above); and % canopy fullness (July 8–15). Percentage of leaves from the lateral buds versus new terminal shoots was also estimated.

Two shoot lengths were measured: from the proximal end of the terminal bud to the proximal end of ring scars from 2006's terminal bud (=2007 elongation) and from proximal end of 2006 bud scars to proximal end of 2005 bud scars (=2006 elongation). Elongation was measured on all terminal shoots of each medium sapling and up to 16 terminal shoots on major accessible branches (>1 cm diameter) of each large sapling.

Variables measured for each forest sapling in 2008 were: % canopy fullness, number of major branches dead and alive, number of shoots originating from base of trunk, and survival (June 14–July 5). An individual survived into 2008 if leaves were present on 2007 branches and/or produced new basal sprouts. Survival for all 355 individuals was also quantified in spring 2009.

Results

Phenology in relation to temperatures

Details of temperature patterns in March to April 2007 are in Augspurger (2009). In summary, two warm periods (March 9 to 14 and March 19 to April 3, 2007) with some days of record-breaking warm temperatures (78–80°F (25.6–26.6°C)) resulted in very early leaf bud break for Ohio buckeye. Small and medium saplings began to break bud in the second week of March, large saplings by March 17, and canopy individuals by March 24. N-edge large saplings broke bud about 1 week after large saplings in the forest; canopy individuals were similar at edge and interior.

Minimum daily temperatures were below freezing on 8 days from 4 to 14 April, 2007, including a record-breaking 21°F (−6.1°C) on April 7 (Augspurger 2009). N to NW winds occurred 4–6 April. On April 7, 16–29 km/h W winds brought cold air and mixed air strongly, both horizontally and vertically; it was an advective, not radiation, frost (Angel 2007). Twenty-five days elapsed between first warm temperature and coldest temperature on April 7. Therefore, shoot and leaf expansion was underway or completed prior to April 7.

Damage to leaves was partially apparent on April 7 and totally apparent on April 14. Damaged leaves wilted, eventually became brown/black and brittle, and dropped. Re-foliation began after April 28 and was completed by May 12.

Hypothesis 1: Damage depends on phenology (and life stage)

Phenology progressed from small saplings through canopy trees. Leaves differed in size and maturity. Small saplings had earliest bud break and their leaves were full-sized, fully mature at frost; medium saplings leaves were full-sized, semi-mature; large sapling leaves were full-sized, immature; and canopy tree leaflets were folded and protected in the expanding shoot, and/or were beginning to expand and were immature.

Life stages (and phenological phases) differed significantly in mean % leaves damaged by frost (1-way ANOVA $df = 3, 131$, $F = 94.859$, $P < 0.0001$). The % damage increased from small to medium to large saplings, while canopy trees had intermediate damage similar to medium saplings (Fig. 1a).

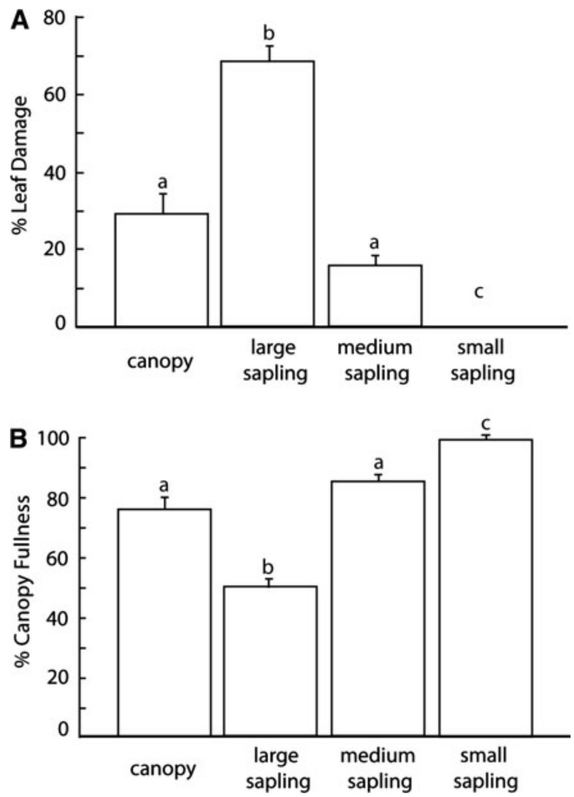

Fig. 1 Comparison among life stages of **a** % leaves damaged by frost/individual and **b** % final canopy fullness/individual on May 9, 2007. Values = means ± 1 SE. Data were analyzed with 1-way ANOVA, followed by Scheffé's *F*-test for post-hoc comparisons

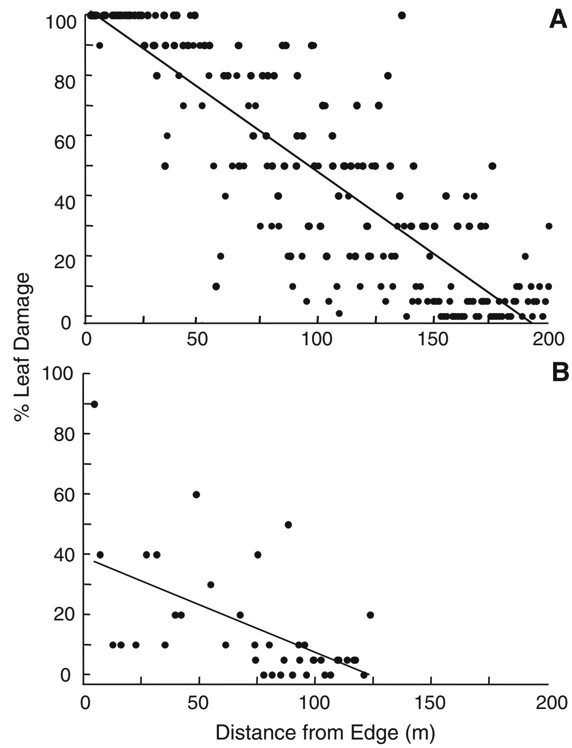

Fig. 2 **a** For large saplings, % leaves damaged by frost/individual as a function of distance from forest edge (line = $y = 102.308 - 0.545x$); **b** Same for medium-sized saplings (line = $y = 38.944 - 0.317x$)

Frost damage to reproduction

All canopy trees (forest and N edge) had flower buds or flowers at frost. None showed any frost damage to flowers. For forest canopy trees, 11 of 15 trees had many mature seeds; they had an average of 26% leaves damaged and 81% canopy fullness. In contrast, four individuals with rare or no seeds had greater damage (42.5%) and lower canopy fullness (57.5%). Of 14 N edge trees with flowers, all surrounded by damaged shoots/leaves, eight trees began to produce fruit, but none developed mature seeds.

Hypothesis 2: Damage depends on exposure to temperature/wind

Percent damage decreased significantly with increasing distance from edge for large saplings ($R^2 = 0.723$, $P < 0.0001$) (Fig. 2a), and, to a lesser extent, for medium sapling ($R^2 = 0.318$, $P < 0.0001$) (Fig. 2b). Damage was unrelated to plant size of tall or medium saplings (data not shown). Damage to canopy trees was unrelated to distance from edge. Small saplings had no damage regardless of location in the forest.

Among N edge individuals of all sizes, 87% had all leaves damaged; subsequently all leaves were dropped. The other individuals retained 10–30% of original leaves; they were expanding shoots or had immature leaves at frost.

Hypothesis 3: Developmental and demographic consequences

Life stages of forest individuals differed in the extent of re-foliation, leading to significant differences in mean % canopy fullness (1-way ANOVA df = 3,131, $F = 75.054$, $P < 0.0001$). Fullness was inversely related to damage (Fig. 1a, b). Large saplings had least fullness, while small saplings had complete fullness; medium saplings and canopy trees had similar intermediate fullness.

Other responses described below focused on large forest saplings, the life stage with heaviest damage. Large saplings displayed many modes of re-foliation, even within an individual, by May 7, 2007 (Table 1). In general, individuals with the highest damage close to the edge showed the greatest extent of lateral bud and terminal shoot activation (Table 2). Nevertheless, when re-foliation was completed, % canopy fullness was negatively related to % damage (Table 3). Two cohorts of leaves were apparent then, those from original terminal buds and new buds. Leaf size varied greatly among leaves originating from both types of buds, even on the same individual (Table 4). In general, larger leaves came from original terminal buds than lateral buds. Individuals with the heaviest damage, and those with most leaves from lateral buds, had the smallest leaves (data not shown).

Stem elongation in 2007 and % damage of large saplings in 2007 were negatively correlated, but with only marginal significance (Table 3). The mean ratio of growth 2007/2006 was 0.83, but the ratio was unrelated to % damage.

Mean dates of beginning and completion of whole-plant senescence were July 10 and August 1, respectively. Date of beginning of senescence and % damage were negatively correlated (Table 3). All other senescence and leaf drop variables were highly

Table 1 Summary for May 9, 2007 of % of large and medium saplings displaying different modes of foliation from original buds and re-foliation from new buds after frost damage in April, 2007

Large saplings		Medium saplings	
Mode	%	Mode	%
1	12.0	1	37.5
2	41.0	2	20.0
2, 3	24.5	2, 3	15.0
2, 3, 4	11.5	2, 3, 4	5.0
3	8.0	3	12.5
3, 4	2.0	3, 4	7.5
4	1.0	4	2.5

1 = no new buds activated; 2 = expansion of non-damaged leaves from original shoot; 3 = new leaves expanding from lateral buds; 4 = new leaves on extension of old terminal shoot (See "Materials and methods" for more details). Many individuals showed multiple modes

Table 2 Extent of re-foliation response for large saplings with different levels of frost damage

% damage	*N*	Much	Moderate	Rare	None
0–10	63	0/0	0/0	1/0	62/63
20–40	40	0/0	0/0	10/3	30/37
50–70	36	1/0	5/0	17/6	13/30
80–100	61	28/6	16/3	13/11	4/41

Number of individuals with re-foliation via lateral buds (response 3 in Table 1) is to the left of the slash above and number of individuals with re-foliation via terminal shoot (response 4 in Table 1) is to the right of the slash above

correlated with beginning of senescence (data not shown). Length of growing season averaged 59 days, all in deep shade of the full forest canopy.

Some terminal buds on major branches (>1 cm diameter) were missing or damaged on 41% of large saplings. A mean of 43% of buds were damaged or missing per individual with damage; five saplings had no healthy buds. Percent buds healthy and % damage were negatively correlated (Table 3).

Effects of frost damage of large saplings in 2007 were still evident in 2008 and 2009. Branches with shriveled terminal buds or no buds in 2007 were dead by spring 2008. Number of dead branches in 2008 and % leaf damage in 2007 were positively correlated, while % canopy fullness in 2008 and % leaf damage in 2007 were negatively correlated (Table 3). While 59% of large saplings had full canopies in 2008 and 17% had 80–99% full canopy, 13% did not produce any leaves in 2008 from old branches of 2007. By 2009, 9% of living individuals had % canopy fullness lower in 2009 than 2008.

In 2008, basal sprouts developed on 10 large saplings, including nine of 10 with 0% canopy fullness in 2008; by 2009, only seven of nine had living basal sprouts. For large saplings, 16 of 200 in 2008 and 22 of 200 in 2009 had no basal sprouts or leaves on old branches; thus, by 2009, 11% of large saplings died in response to the frost of 2007. Mortality was concentrated in large saplings in the far NW corner, nearest edges with the most direct wind during frost. All individuals in other life stages survived into 2009.

All responses to frost damage of large saplings were correlated. The strongest negative responses to % frost damage were % canopy fullness in 2007 and 2008, date of senescence, and % buds healthy

Table 3 For large and medium saplings, Pearson correlations (r) and partial correlations between % damage to vegetative units by frost in 2007 and subsequent response variables in 2007 and 2008

Sapling size	Response variable	Correlation	P value	Partial correlation
Large	% Canopy full 2007	−0.773	<0.0001	−0.633
	Mean branch elongation 2007	−0.182	<0.0138	0.056
	% Buds healthy 2007	−0.631	<0.0001	−0.540
	Date senescence begins 2007	−0.470	<0.0001	−0.012
	% Canopy full 2008	−0.436	<0.0001	−0.013
	Number dead branches 2008	0.325	<0.0001	−0.067
Medium	% Canopy full 2007	−0.463	<0.0023	−0.468
	% Canopy full 2008	−0.366	<0.0197	−0.142
	Number dead branches	−0.357	<0.0232	−0.062

$N = 183$ (large) and 40 (medium) saplings. Higher order Pearson partial correlations were calculated to determine the correlation between % damage and each specific response after the linear effect of the other responses was removed. The partial correlations were calculated as $PC_{ij} = -IC_{ij}$/square root of $IC_{ii} * IC_{jj}$, where PC = partial correlation matrix and IC is inverse of correlation matrix

Table 4 Percentage of large saplings with different size and condition of the majority of mature leaves on June 3, 2007

Dominant origin	Small	Medium	Large	Damaged
Lateral buds	56	19	25	0
Terminal buds	19	29	37	15

Each estimate was based on a subjective appraisal by the author of the sapling's predominant leaf size/condition; variation existed among an individual's leaves. $N = 190$ as 10 individuals had no or almost no leaves. Estimates were made for individuals whose predominant origin of leaves was either lateral buds (36) or original terminal buds ($n = 154$)

(Table 3). Partial correlation analyses revealed that the most important negative relationships were between % damage in 2007 and % canopy fullness in 2007 and % buds healthy, both direct outcomes of frost damage (Table 3).

Medium saplings showed less damage and weaker subsequent re-foliation responses than large saplings. Only 42.5% of individuals had any re-foliation responses, largely from lateral buds (Table 1). Greater damage was negatively related to % canopy fullness in 2007 and 2008, particularly 2007 (Table 3).

Consequences of damage for edge individuals

All N edge individuals had strong re-foliation responses by May 3, 2007; 6.7% re-foliated from only lateral buds (response 3), 31.7% from only newly extended terminal shoots (response 4), and 61.7% from both sources. By July 8, 2007, leaves that arose from lateral buds were dark green, but 29% of leaves from new terminal shoots per individual showed chlorosis at leaf edges.

By 2008, N edge individuals showed few negative effects of frost damage in 2007. Mean % canopy fullness in 2008 was 98.7%. Dead branches occurred in 2008 on 18.3% of individuals that reduced their canopy fullness to 80–95%; all individuals with dead branches were large saplings (2–10 cm DBH). No edge individuals died in 2008 or 2009 and none showed any basal sprouts.

Discussion

Hypothesis 1: Damage depends on phenology (and life stage)

The results support the hypothesis that frost damage of *Aesculus glabra* depends on leaves being at a vulnerable phenological phase. Damage depended on extent of development to a full-sized leaf and to maturation of the full-sized leaf. Damage increased from small to medium to large saplings, and was intermediate for canopy trees. Large and small saplings had extremes in maturation of full-sized leaves, while medium saplings had intermediate maturation of full-sized leaves. Full-sized, but immature leaves (thin, soft, flexible, little cuticle) of large saplings were most vulnerable, while full-sized, mature leaves (thick, touch, stiff, heavy cuticle) of small saplings were invulnerable. In contrast, canopy trees did not have fully expanded leaves. Their expanding shoots with small or unfolded leaflets were intermediate in vulnerability. Likewise, at the community level during April 2007, differences among species in frost damage depended on phenological phase (Augspurger 2009).

Ultimately, these patterns of frost damage among life stages occurred because of differences in timing of bud break, perhaps due, in part, to differences in the rate of thermal accumulation (degree days) required to initiate bud break. Spring temperatures in this forest are warmer at sapling than canopy levels (Augspurger 2004), so thermal accumulation is faster and bud break sooner for small saplings near the ground than in the exposed canopy trees (Augspurger and Bartlett 2003). Additional factors leading to the vertical gradient in bud break may include the extent and speed of spring repair of cavitated xylem vessels and buildup of root water pressure to move water to expand buds (Hacke and Sauter 1996).

Hypothesis 2: Damage depends on exposure to temperature/wind

As hypothesized, greater damage corresponded with greater exposure to lower temperatures and stronger winds as damage increased with proximity to the exposed edge. Korstian (1921) and Neilson and Wullstein (1983) interpreted a similar pattern to be due to more advanced phenology at edges, not to weather differences. However, phenological phase of large non-edge saplings was generally the same across the 200 m gradient at the time of frost. Therefore, the gradient of damage was likely due to the weather gradient. In contrast, North edge saplings were at earlier phases, yet nearly all suffered 100% damage. Perhaps the more severe weather at the edge made earlier stages more vulnerable.

Hypothesis 3: Developmental and demographic consequences

Frost damage to current foliage and next year's buds was followed by a cascade of negative effects on an individual's canopy fullness, leaf size, length of growing season, growth, reproduction, and, ultimately, survival. Re-foliation occurred on the most heavily damaged individuals. Similarly, Rose (1958) noted that re-foliation of aspen trees occurred only if completely defoliated from frost. Re-foliation was insufficient for complete recover; saplings had both fewer leaves and smaller leaves from lateral buds.

In the higher light of the N edge, individuals of all sizes and extent of damage showed much more extensive re-foliation than forest individuals. They had more shoot extension via a new terminal bud, although, as Strain (1966) observed for aspen leaves, this second cohort of leaves suffered from chlorosis. Edge individuals also had a fuller canopy in both years, later senescence than interior individuals, resulting in a longer growing season, and no mortality.

Damage affected stem elongation in the frost year to a minor extent, probably because it was largely complete prior to frost. In contrast, Strain (1966) found a reduction in radial growth of frost-damaged aspen trees in the year of defoliation. Radial growth of Ohio buckeye may have been affected because its saplings shaded experimentally during the early spring had reduced radial growth (Augspurger 2008).

Fruit production in 2007 was apparently lowered or, for some trees, eliminated by frost damage, especially on edge trees. Similar observations of lower or no fruit production in frost years lowered the food supply for mammals (Nixon and McCain 1969). The lowered reproduction of Ohio buckeye by frost affected its recruitment and demography, but not the mammal community because they do not eat its toxic seeds (C. Augspurger pers. observation).

Frost damage negatively affected the acquisition of energy for maintenance during the current year and energy storage for the subsequent year. First, the delay in re-foliation caused the period of leaf expansion for large saplings to be an average of 34 days longer in 2007 than in 1993–1995, years without late frost (Augspurger and Bartlett 2003). Consequently, achievement of full canopy occurred later in deep shade after canopy closure in the forest. In contrast, in non-frost years, these saplings receive 98% of their light during the high light period prior to canopy closure (Augspurger et al. 2005). Second, their smaller canopy acquired less light due to fewer and smaller leaves. Third, senescence was 3 weeks earlier for saplings in 2007 than in 1993–1995 (Augspurger and Bartlett 2003). Similarly, Ohio buckeye saplings artificially shaded to eliminate their early high light environment had premature senescence (Augspurger 2008). Overall, damaged saplings had a greatly reduced growing season of only 59 days, due to both late leaf development and early leaf senescence. In non-frost years, it is 5 weeks longer (Augspurger and Bartlett 2003).

Consequences of frost damage in 2007 were still evident in 2008. Terminal bud damage led to no growth extension from those branches in 2008. In addition, branches partially died from the tip back or died entirely by 2008, as has been observed for shrubs with frost damage (Luken 1990). Both the lack of new growth and death of existing branches affected tree architecture, leading to a less full canopy to intercept light in 2008.

Basal sprouting occurred in 2008, especially on saplings with no leaves. It is a common response to frost of some species (Neilson and Wullstein 1983, Luken 1990). Those individuals survived through 2008, but they were greatly reduced in size, had a major change in architecture, and not all survived to 2009. Ohio buckeye saplings experimentally shaded during early spring for 3 years had some basal sprouting, but none survived after 3 years (Augspurger 2008).

Ultimately, frost damage in 2007 led to mortality in 2009 of large saplings with the most extreme damage. Similarly, survival was diminished by repeated frost damage of shrubs (Mooney 1977) and small trees (Clarke 1946). Overall, mortality was probably affected by low nutrient and carbon reserves, and was induced by multiple negative responses related to the initial frost damage: a smaller canopy made up of fewer and smaller leaves in 2007, a shorter and darker period of light acquisition in 2007, and no nutrient uptake from dead leaves. Additionally, reduction in fine root production due to declining photosynthate production may have contributed to mortality.

Comparisons to other species and other years

Among 20 woody species observed at the study site from 1993 to 2009, Ohio buckeye was the most vulnerable to frost damage based on number of years, % of individuals damaged, and % of units damaged per individual (Augspurger 2009). They are likely most vulnerable, in part, because they are earliest to break bud. Additionally, their rapid leaf expansion, similar to other species of *Aesculus* (Lopez et al. 2008), causes leaves to reach a vulnerable phase at a time with greater probability of freezing temperatures than species with later bud break and/or slower leaf expansion.

From 1993 to 2009, Ohio buckeye saplings were the earliest to break bud in each year and were exposed most often to sub-freezing temperatures. Forest saplings were exposed to freezing temperatures during all development phases: bud break (15 of 17 years), shoot expansion (10 years), and leaf expansion (7 years). They had damage in only 5 years (1994, 1995, 1997, 2000, 2007), and only during leaf expansion, despite quite low temperatures during bud break and shoot expansion. Saplings on the W edge had frost damage more frequently than forest saplings. For 11 years of observations in common (1999–2009), edge saplings had damage to expanding leaves in 5 years (1999, 2000, 2001, 2007, 2009), while forest saplings had damage in only 2000 and 2007.

Implications

The 2007 frost had ecological consequences for Ohio buckeye. The death of saplings, particularly near the edge, changed the species' demography, age structure, and spatial pattern, at least within the NW corner. The long-term effects of this frost damage on species' abundance are unclear. It is unknown what percentage of the total population in the forest remnant died and whether future reproduction and recruitment could rebuild the population to levels that existed before the 2007 frost.

The results raise the question why Ohio buckeye persists to flush early if frost damage is fairly common. A biogeographical explanation may be that, over most of its range, it does not experience such frost because this largely southern species is at its NW limit in central Illinois. A physiological explanation may be that it must depend heavily on the higher light and major carbohydrate production during early spring (Augspurger et al. 2005) and could not survive in the community if it were to develop leaves later when most species do. Thus, it risks potential frost to realize the early season carbon gain. Damage by most frosts is light enough to allow it to persist. Even a mortality level of 11%, as in 2007, may be insufficient to "tip the balance". The population would be greatly affected only if it happened several times over several decades.

The study also raises the possibility that frost damage acted as a selective force on this population. It was a source of differential reproduction and survival, although the genetic variation for the various traits affecting frost damage in this species is unknown. To evaluate the evolutionary significance of rare frost events for this species also requires knowing the frequency of such mortality. The frost of 2007 was unusual in the context of the short lifetime of the current saplings, but its frequency is unknown over the centuries of an individual's lifetime or the millennia of this Ohio buckeye population.

To evaluate the frequency of frost damage using meterological data requires quantifying the frequency of unusually early spring warmth, coupled with subsequent freezing temperatures at an interval sufficient for leaf development to have reached a vulnerable phase. Preliminary analysis indicates that the combination of temperatures, as occurred in years with frost damage to Ohio buckeye forest saplings, has occurred in 10 of the last 121 years (Augspurger, unpublished data). This analysis did not incorporate whether the frost was radiative or advective, due to lack of wind data in many years. Radiation frosts have been more common than advective frosts in Illinois (Joos 1960), but the relative consequence for Ohio buckeye of these two types of frosts is unknown. The last spring freezing temperature in Illinois has moved 9.8 days earlier over the last century (Robeson 2002), but the movement of phenological phases over the same period is not known.

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