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Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest

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Summary

1. Climate change is predicted to bring earlier bud break and perhaps a greater risk of frost damage to developing leaves and flowers. Given the rarity and unpredictability of major frost events and limited community-level phenological observations, comparisons among deciduous forest species experiencing frost damage and refoliation are rare.

2. This study used phenological observations ongoing at the time of a hard freeze to compare leaf and flower development, frost damage and leaf refoliation of 20 deciduous woody species in Trelease Woods, Champaign Co., IL, USA. Freezing temperatures from 5 to 9 April 2007 followed 22 days after very warm temperatures began in March.

3. Bud break was the earliest in 17 years. Frost caused damage to leaf buds, developing shoots and/or expanding leaves of canopy trees of six species and saplings of two species. Undamaged species were inactive, or in bud break or shoot expansion. Among damaged species, 11–100% of individuals exhibited some frost damage. Mean damage level per individual ranged from 20% to 100% among species.

4. Refoliation from dormant buds led to mean final canopy fullness that ranged from 46% to 99% among damaged species, but time of full leaf expansion was extended by 16–34 days for refoliating species.

5. Frost damaged flowers, but not flower buds or developing fruit, of five of eight species that flowered during the frost period.

6. The extent of frost damage in 2007 was unusual; damage was greater than any of the other 4 years with frost damage from 1993 to 2009 because record-breaking March temperatures in 2007 caused more species to be at later vulnerable stages with the advent of subfreezing temperatures in April.

7. Differences among individuals and species in frost damage and ability to refoliate caused strong selection on individuals and differences in carbon gain that could, in the long-term, affect species' abundances. The frost also reduced fruit/seed abundance for insects and mammals.

Key-words: bud break, climate change, extreme event, intraspecific- and interspecific-variation, leaves and flowers

Introduction

Extreme events affecting an individual's growth, survival and reproduction are rare, unpredictable and seldom documented. One such potentially catastrophic event for temperate deciduous forests is freezing temperatures in spring causing frost damage to developing leaves and flowers. Recent modelling studies have predicted that warmer spring temperatures occurring more frequently in recent decades cause earlier leaf and reproductive phenology, but the studies differ in whether they predict a greater risk of frost damage (Cannell & Smith 1986; Murray, Cannell & Smith 1989; Hänninen 1991; Kramer 1994; Leinonen 1996). Climate predictions include not only an increase in mean temperatures in temperate latitudes but also greater variability in temperatures (Rigby & Porporato 2008). If the temporal scale of this variability includes short-term temperature changes during spring, then warm temperatures followed by sudden freezing temperatures will result in a greater risk of frost damage in the future. The formerly rare event of frost damage may become more common.

A pattern of warmth followed by frost is insufficient to cause damage. The sequence of temperatures in relation to the phenological phase is critical (Fuchigami *et al.* 1982).

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Whether such damage occurs depends on the phenological phase at the time of frost, as well as the sensitivity of particular phases of leaf development and reproduction. Differences among organs, individuals, life stages and species exist in their phenological response to warm spring temperatures, rate of development and sensitivity to frost damage (Tryon & True 1964; Sakai & Larcher 1987; Larcher 1995; Carol K. Augspurger, personal observation).

Plants in temperate deciduous forests experience a trade-off between leafing out early, thereby maximizing resource-acquisition over the entire growing season, and leafing out later, thereby minimizing the risk of frost damage (Lockhart 1983; Saxe *et al*. 2001). Individuals and species with the earliest phenology face the greatest risk because the probability of frost decreases with time, and older tissues become less sensitive to frost (Sakai & Larcher 1987). Frost damage to leaves can be partially compensated for by refoliation, either from activation of dormant buds or development of adventitious buds (Kramer & Kozlowski 1979; Neilson & Wullstein 1983). Refoliation is, however, costly in requiring additional resources and time, thus reducing the length of the growing season.

Differential frost damage and refoliation have consequences at multiple ecological levels from the individual through the ecosystem. Despite its overarching impact, they have seldom been studied, except for economically important plants. Documentation is rare for entire communities of natural vegetation because it requires ongoing phenological observations of multiple species at the time of the frost (for herb studies, see Inouye 2000, 2008). Community-wide phenological observations of trees and frost damage are rare. A few anecdotal studies report widespread frost damage to leaves and flowers in temperate forests (Nixon & McCain 1969) and to roots and shoots in boreal forests (Bourque *et al*. 2005), as well as interspecific variation among tree species in susceptibility to frost damage (Korstian 1921; Tryon & True 1964), but I am not aware of any study that reports the refoliation response of a community after frost damage.

A rare combination of temperatures occurred in spring 2007 in Trelease Woods in east central Illinois, USA (Angel 2007), as well as much of the eastern deciduous forest in North America (Gu *et al*. 2008). Phenological observations of the woody community in Trelease Woods were ongoing during a very warm March followed by freezing temperatures in early April. Therefore, a rare opportunity arose to compare the effect of this extreme event on this woody community. The objectives for this study were to: (i) compare the frost damage among 20 woody species, between two life stages, among individuals, and among vegetative and reproductive phases; (ii) relate frost damage to daily temperatures and phenological phases; and (iii) document for damaged individuals the timing and extent of leaf and flower recovery via activation of dormant buds.

Although the study's focus was 2007, the frequency and extent of frost damage from 1993 to 2009 also were examined to evaluate the rarity of the frost event in 2007 and to begin to understand the combination of temperature patterns and phenological development necessary to predict frost damage.

Materials and methods

STUDY SITE AND STUDY SPECIES

The study site was Trelease Woods, a 24-ha forest fragment located 5 km northeast of Urbana, Illinois, USA (40°09′N, 88°10′W). The mixed mesophytic upland deciduous forest is an old-growth remnant of 'The Big Grove' (Pelz & Rolfe 1977). Its 20 canopy tree species have an average canopy height of 25 m. The site has no slope. The remnant has a road to the West and prairie buffer strips on the other three sides. The University of Illinois has managed it without human disturbance since 1917.

The 20 study species were 13 species of canopy trees, three species of vines and four species of understorey treelets/shrubs ($<$ 5 m) (see Table 1). In addition, subcanopy, non-reproductive individuals, hereafter saplings ($>$ 2 m to $<$ 5 m), of *Aesculus glabra* and *Acer saccharum* were observed. All species have broad distributions within the eastern deciduous forest; the study site is not near the northern or southern limits of the distribution of any species. Nomenclature follows Mohlenbrock (1986).

Except for saplings, individuals were of mature, reproductive size. Sample size per species averaged 11 individuals (range 2–20). Individuals were located in the interior of the northern half of the forest and at least 50 m from any edge. All species except species of *Vitus* exhibited a flush type of leaf emergence in spring (Kikuzawa 1991). *Vitus* species in this forest have indeterminate growth in summer.

TEMPERATURE DATA

The Illinois State Climatologist Office provided temperature data for 1889–2009 from a weather station that is maintained by the Illinois State Water Survey in Champaign, IL (http://www.sws.uiuc.edu/atmos/statecli/Champ-Urb/CU.htm). This station is ≈8 km SW of the study site. The station and study site are similar in their exposure; both have flat topography and are surrounded by non-forested, open areas. The temperatures at the station more likely reflect temperatures of the open canopy than the closed subcanopy and lower strata. Spring temperatures are typically slightly warmer at low levels than in the canopy in this forest (Augspurger 2004).

PHENOLOGY, FROST DAMAGE AND REFOLIATION

Phenological observations of tagged individuals of the study species have been ongoing from 1993 to 2009 (for methods and summary of data for canopy tree species for 1993–1995, see Augspurger & Bartlett 2003). From February to May 2007, the author made observations with binoculars on a single day at weekly intervals. The observational unit was the entire crown of each individual. Both reproductive and leaf phenology were recorded weekly for each individual. The reproductive status was noted as: none, flower buds, flowers or fruits. The reproductive phase declared represented the majority of an individual's visible reproductive units. For leaves, three stages within each of three phenological phases were defined: (i) bud break (bud swollen with scales parted, revealing underlying tissue (stages 1–3); (ii) shoot expansion (shoot emerging from bud scales and elongating, but no major leaf expansion initiated) (stages 4–6); and (iii) leaf expansion (leaf undergoing major expansion (stages 7–9). The period of leaf

Table 1. Phenological stage at weekly censuses for 20 species (two species with saplings) for 17 March to 2 June 2007 (Julian days 76–153) in Trelease Woods, Champaign Co., IL, USA

Species	76	83	90	97	104	111	118	125	132	139	146	153
Fraxinus americana White Ash						*1·0*	4·1	7·3	*9·0*			
Toxicodendron radicans Poison Ivy						1·0	4·2	8·0	8·7	*9·0*		
Ulmus rubra Slippery Elm					*1·0*	1·5	3·7	7·0	8·9	*9·0*		
Gymnocladus dioicus Ken. Coffee Tree					*1·0*	*1·0*	2·5	5·9	8·0	9·0		
Carya cordiformis Bitternut Hickory				*1·0*	*1·7*	2·2	4·5	7·0	8·5	*9·0*		
Acer saccharum Sugar Maple			*1·0*	*1·5*	*1·8*	*2·4*	5·3	8·7	*9·0*			
Carya ovata Shagbark Hickory			*1·0*	*1·5*	*2·0*	2·8	5·3	8·1	*8·7*	*9·0*		
Tilia americana Basswood			*1·0*	*1·7*	*1·8*	2·7	5·1	8·2	*9·0*			
Parthenocissus quinquefolia Virginia Creeper			*1·5*	*1·6*	2·1	4·3	7·7	9·0				
Acer saccharum S. Maple sapling *			*1·8*	3·3	3·9	5·7	7·9	*9·0*				
Vitus spp. Grape			*2·0*	*4·0*	*5·0*	2·7	4·3	8·0	8·0	8·0	8·0	8·0
Ulmus americana American Elm *			*3·0*	*4·0*	*4·0*	3·5	5·0	8·0	*9·0*			
Juglans nigra Black Walnut *			*2·1*	3·0	3·1	3·6	5·2	7·4	8·1	*8·9*	*9·0*	
Lindera benzoin Spicebush			*2·7*	3·6	3·9	5·4	7·1	8·9	9·0			
Quercus rubra Red Oak *			*1·2*	2·0	2·1	2·9	3·9	7·5	8·9	*9·0*		
Quercus macrocarpa Bur Oak *			1·6	2·8	2·9	1·1	1·6	5·9	7·9	8·8	*9·0*	
Celtis occidentalis Hackberry *			1·8	5·8	0·0	0·2	1·0	8·0	9·0			
Asimina triloba Pawpaw		*1·0*	1·9	2·6	2·8	3·5	4·8	6·4	7·9	8·2	*9·0*	
Xanthoxylum americanum Prickly Ash		*1·0*	1·9	4·1	4·1	5·4	7·1	8·0	8·0	8·4	*8·8*	*9·0*
Carpinus caroliniana Blue Beech		*1·0*	2·8	4·2	4·5	5·8	7·3	8·8	*9·0*			
Aesculus glabra Ohio Buckeye *		*1·5*	5·9	7·6	7·6	8·2	8·9	*8·0*	*9·0*			
Aesculus glabra O. Buckeye sapling *	1·0	4·2	8·2	9·0	0·0	0·0	0·0	8·0	9·0			
Community	*1·0*	*2·2*	*2·7*	*3·8*	*3·3*	*3·6*	*5·3*	*7·7*	*8·5*	*8·6*	*8·8*	*9·0*

See Table 2 for sample sizes. Values represent mean phenological stage: [0 = no activity, 1–3 = bud break (light grey), 4–6 = shoot expansion (medium grey), 7–9 = leaf expansion (dark grey)] at each census date. Italicized values indicate asynchronous intraspecific phenology, i.e. < 100% of individuals had any active phenological development during the previous week; early values indicate that some individuals had not begun bud break, while late values indicate that some individuals had completed leaf expansion by the previous census date(s). The bottom row has the mean phenological stage of all individuals in the community in the census.
*Species with frost damage. Freezing temperatures occurred on days 94–100 and 103, as indicated by thick black borders around subsequent census days.

development was determined as the number of days between the onset of stages 1 and 9. The three stages represent the vegetative unit's (bud, shoot or leaf) completion of one-third, two-thirds or all of a given phenological phase. For example, a bud at stage 2 would be *c.* 2/3 swollen to the full size it reaches prior to shoot emergence, a leaf at stage 7 would have expanded to *c.* 1/3 of its final size, whereas at stage 9, the leaf would be fully expanded, flattened and in its normal orientation. Completion of a phase, e.g. fully swollen or fully expanded, was based on many prior years of observation of the size of units. Phenological stages were sometimes not synchronous over an individual's entire crown. In addition, entire crowns of canopy trees were not always visible. Therefore, the one stage declared for each individual on a given observation day represented the majority of the visible vegetative units.

The percentages of buds/shoots/leaves and flower buds/flowers/fruits per individual damaged by frost were estimated by visual inspection of the crown at each weekly census. For each species, the earliest stage with frost damage and the most developed stage with no damage were identified, and related to daily maximum and minimum temperatures to which they were exposed.

Refoliation from activation of dormant buds on damaged individuals was noted if present at each weekly census. Using observations during refoliation and after completion of all leaf expansion, an estimate of the percentage of the 'normal' canopy fullness based on non-frost years was made for each damaged individual. Additionally, the portion of this percentage comprised of leaves from the first cohort of buds (undamaged) vs. the second cohort that arose after frost damage was estimated.

Results

PHENOLOGY IN RELATION TO TEMPERATURES

The second warm period in March and the cold period in April 2007 (Fig. 1) were the second warmest and second coldest periods in those months in the past 121 years. Daily maximum temperatures were consistently warmer than average in March 2007, including several record-breaking temperatures (Fig. 1). They were well above the 121-year March average of 9·4 °C (49°F) from 9 to 14 March (Julian days 68–73), including a new daily record of 25·6 °C (78°F) on March 13 (72). A second prolonged period of very high temperatures, including two new daily records of 26·7 °C (80°F), occurred from 19 March to 3 April (78–92). Ten days in March had temperatures ≥23·9 °C (75°F); this period was 9·2 °C (16·6°F) above the long-term average. First bud break for *A. glabra* saplings began on 17 March (76) (Table 1). Plant development then proceeded at a rapid rate and continued through censuses of 24 March (83) and 31 March (90) (Table 1).

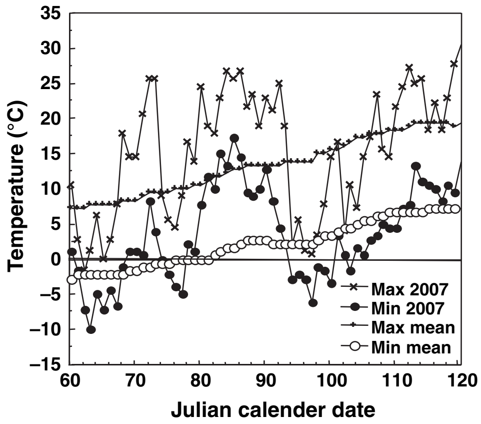

Fig. 1. Daily maximum and minimum temperatures (°C) for March to April 2007 at Champaign, IL, USA. Note one early warm period during the second week of March (days 68–73) and one prolonged warm period in late March to early April (days 78–93), followed by 8 days of subfreezing temperatures in April, including the record-breaking −6·1 °C (21°F) on 7 April, day 97. Also shown are the mean values for 1889–2009.

Minimum daily temperatures were below the freezing point on 8 days in early April, four of which occurred between censuses on 31 March (90) and 7 April (97), including a record-breaking daily minimum temperature of −6·1 °C (21°F) on 7 April (97) (Fig. 1). The other four days were between censuses on 7 April (97) and 14 April (104). 7 April also had winds ranging from 16 to 29 km h^{-1} that strongly mixed air both horizontally and vertically (Angel 2007). The interval between the start of warm temperatures on 13 March (72) and the first subfreezing temperature on 4 April (94) was 22 days, or 25 days based on the coldest temperature of −6·1 °C (Fig. 1). This interval was sufficient for all but four of the 20 species to have begun leaf development prior to the extreme cold of 7 April (Table 1). All but two species had undergone leaf bud break prior to the last frost day. Mean values for *Vitus* spp. in Table 1 decrease after the frosts; this decline was not because of frost damage to the lone individual active during frost, but rather because the majority of individuals had late bud break.

VARIABILITY IN FROST DAMAGE AND RECOVERY

Some species had already reached a phase vulnerable to frost when frost damage to vegetative structures began to be apparent on 7 April (97). Leaves were wilted and eventually became brown/black and brittle. By 14 April (104), frost damage was totally apparent, except for *Quercus rubra*, which did not exhibit frost damage to leaves or shoots until 28 April (118).

Species and individuals differed in whether they had vegetative damage and in their amount of damage. Canopy trees of six of thirteen species and saplings of both species experienced some damage (total = 7 species), but no species of vine or understorey treelets/shrubs was damaged, even though some species were in the middle of shoot expansion (Table 1). Per cent individuals damaged per species ranged from 11% to 100% (Fig. 2). Per cent vegetative units damaged per individual ranged among species from 20% to 100% (Fig. 2). *Quercus macrocarpa*, *Celtis occidentalis* and *A. glabra* had both a high per cent of individuals damaged and a high per cent of damage per individual. Saplings of *A. saccharum* and *A. glabra* suffered more than canopy trees, both in per cent individuals damaged and per cent damage per individual (Fig. 2).

Species (and individual) differences in vegetative damage depended, in part, on their stage at the onset of freezing temperatures. For example, saplings had earlier bud break than conspecific canopy trees, were at more advanced stages when the freezing temperatures occurred and incurred more damage (Table 1). Damage was certain during leaf elongation (two of two species had damage) and was unlikely in bud break (five of seven species had no damage); it was highly unpredictable for species in shoot elongation (Fig. 3). To add complexity, *Juglans nigra* and *Q. rubra* had rare individuals in later stages not damaged, while earlier stages were damaged. The earliest damaged stage was in bud break (stages 2–3) for the two *Quercus* species; the latest stage was full leaf expansion (stage 9) for saplings of *A. glabra* (Fig. 3). Among damaged species, all non-damaged individuals were in bud

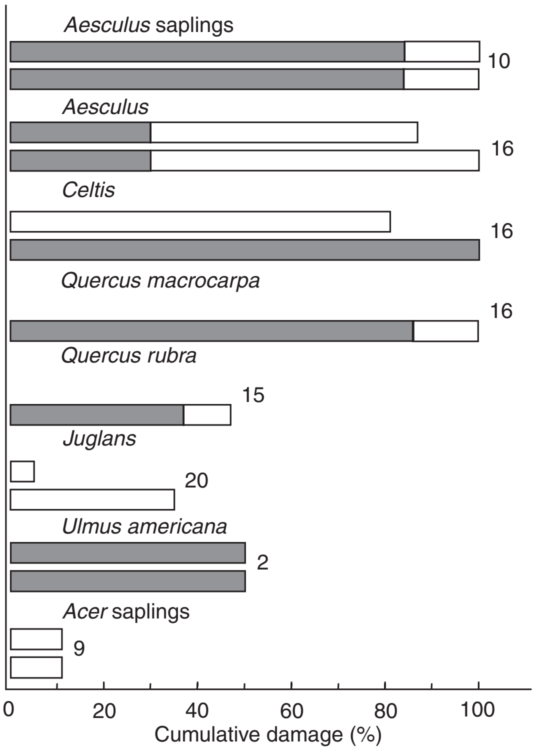

Fig. 2. For those species with frost damage in spring 2007, cumulative vegetative damage observed after subfreezing temperatures on or before day 97 (top bar) and day 104 (bottom bar). Open bars indicate per cent individuals damaged. Grey bars indicate mean per cent damage per individual; the latter value was 20% for *Acer saccharum* saplings, 50% for *Juglans nigra* and 100% for *Celtis occidentalis*. Sample size of number of individuals observed is next to each bar; see Fig. 4 for number of individuals with damage.

break or shoot expansion. Similarly, the 12 species with at least some active individuals during freezing temperatures but with no frost damage for any individual, were in the stages of bud break (five species) or shoot expansion (seven species) (Fig. 3).

Damage was not dependent solely on date of bud break. *Aesculus glabra* was the earliest to break bud, had rapid leaf development and had the greatest proportion of individuals

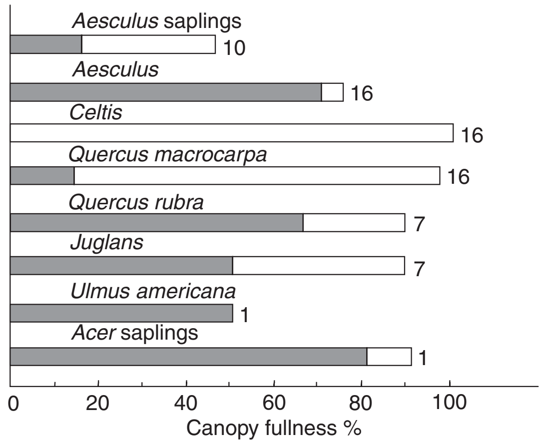

Fig. 4. For those species with frost damage in spring 2007, mean per cent of canopy filled with leaves after leaf expansion was completed (open bars), and mean per cent of canopy fullness arising from non-damaged leaves from bud cohort 1 (grey bars). The difference between the two values represents the mean per cent of canopy arising from new leaves developed from adventitious buds after frost damage (cohort 2). Sample size of damaged individuals is next to each bar.

damaged (Table 1; Fig. 2). In contrast, although *Asimina triloba*, *Xanthoxylum americanum* and *Carpinus caroliniana* also had early bud break, they escaped damage because their rate of development was slower and their phase exposed to frost was not vulnerable. *Celtis occidentalis* was later in breaking bud, but had very rapid leaf development and suffered damage as severe as *A. glabra*.

For damaged individuals, no further development of shoots or leaves occurred by 21 April (111) (Table 1). On these damaged individuals, leaf refoliation began by 28 April (118), when lateral buds and some adventitious buds began to open and new shoots appeared, often simultaneously with further development of older shoots and leaves non-damaged by frost. By 5 May (125), any addition of new shoots/leaves was evident, although some of the new cohort of leaves did not reach full expansion until 26 May (146) (Table 1).

The amount and rate of refoliation differed among species. Mean final per cent canopy fullness per species ranged from 46% to 99% (Fig. 4). The final canopies of damaged

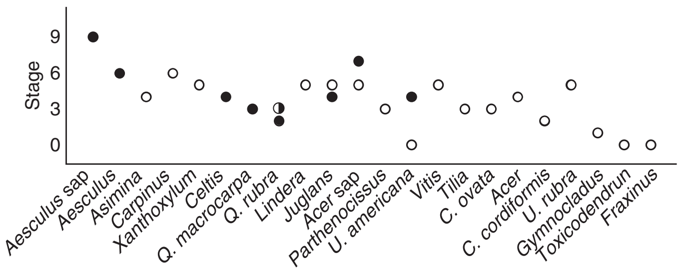

Fig. 3. For each species in spring 2007, the vulnerability of vegetative stages to frost damage on census days 97 or 104. Stages 0 = no activity; 1–3 = bud opening; 4–6 = shoot expansion; 7–9 = leaf expansion. Filled circles: least developed stage on any individual with damage; open circles: most developed stage on any individual with no damage; half-filled circle: some individuals damaged; others not damaged. Damage was evident by day 97 for all seven species except the two *Quercus* species; additional damage occurred on day 104 to all species except *Ulmus americana* and saplings of *Aesculus glabra* and *Acer saccharum*.

individuals were composed of leaves from both initial buds (Cohort 1) and refoliation buds (Cohort 2). Species differed in mean per cent of their final canopies that were comprised of Cohort 1 leaves (0–80%) vs. Cohort 2 leaves (0–99%). Only *Ulmus americana* showed no refoliation. *Celtis occidentalis* and *Q. macrocarpa* were notable in the extent to which they recovered (99% and 96% respectively), given their total or nearly total loss of the first cohort of leaves to frost. *Aesculus glabra* saplings had the greatest consequence of frost because they had high frost damage combined with low refoliation. The refoliation period was very short for *C. occidentalis*, but more prolonged for the two *Quercus* species and *J. nigra*, whereas *A. glabra* was intermediate (Table 1).

The period of leaf expansion (bud break through full leaf expansion) was lengthened greatly for all species with frost damage, relative to years without frost, except for *A. glabra* canopy trees (Table 1). It was an average of 16, 17, 25 and 34 days longer for *Q. rubra*, *Q. macrocarpa*, *C. occidentalis* and *A. glabra* saplings in 2007 than in 1993–1995 (Augspurger & Bartlett 2003). However, senescence was 2–3 weeks later for *Celtis* and the *Quercus* species in 2007 than in 1993–1995 (Carol K. Augspurger, unpublished data), such that the growing season was actually 2–4 weeks longer for these species in 2007 than in 1993–1995. In contrast, senescence was 3 weeks earlier for *A. glabra* saplings in 2007 than in 1993–95 (Carol K. Augspurger, unpublished data), so that their growing season was 5 weeks shorter than their normally very short season (Augspurger & Bartlett 2003).

Damage to reproductive structures differed among species and depended on their phase, relative to the frost dates (Table 2); some species had already past and some had not yet reached vulnerable phases at the time of frosts. Damage was restricted to flowers whose petals became brown/black. The nine species with flower buds during frosts had no damage. Five of eight species with flowers during frosts incurred flower damage on at least some individuals (Table 2). Damaged individuals formed no new flowers and produced no fruits. *Ulmus americana* and *U. rubra* were developing fruits during frosts; their fruits incurred no visible damage.

Comparison to other years

All 20 study species experienced temperatures ≤0 °C at bud break or later phenological phases in at least 1 of 17 years of observation (1993–2009). *Aesculus glabra* saplings, the earliest to break bud in each year, were exposed in the most years (15 of 17). However, frost damage to buds, shoots or leaves was uncommon, both in number of years (5 of 17) and number of species (9 of 20 in at least 1 year). *Aesculus glabra* saplings had greatest frost damage, based on number of years (all 5 years), per cent of individuals and per cent of units damaged per individual. Three species, *A. glabra*, *C. occidentalis* and *Q. macrocarpa,* had damage in years in addition to 2007; *Lindera benzoin* and *C. caroliniana* had damage only in years other than 2007. Four new species, *A. saccharum saplings*, *U. americana*, *J. nigra* and *Q. rubra*, had frost damage only in 2007.

Although flowers of 12 of 20 study species were exposed to freezing temperatures in at least 1 of 17 years, only six species

Table 2. For each species in spring 2007, sample size, number flowering, flower damage and timing relative to time of frost

Species	N	Number with flowers	Per cent individuals with flower damage	Time of flowering relative to frost
Acer saccharum	14	0	–	–
Vitus spp.	5	0	–	–
Parthenocissus quinquefolia	7	0	–	–
Ulmus americana	2	2	0	Before
Ulmus rubra	10	9	0	Before
Xanthoxylum americanum	13	2	0	During
Lindera benzoin	7	7	29	During
Quercus rubra	15	4	75	During
*Quercus macrocarpa**	14	2	100	During
Celtis occidentalis	16	15	100	During
Carpinus caroliniana	12	2	0	During/After
Fraxinus americana	12	6	0	During/After
Juglans nigra†	20	20	5	During/After
*Asimina triloba**	11	8	13	During/After
Gymnocladus dioicus	12	9	0	After
Toxicodendron radicans	5	1	0	After
Carya cordiformis	4	2	0	After
Carya ovata	15	11	0	After
Tilia americana	16	16	0	After
Aesculus glabra	16	14	0	After

*Both had flower buds, not flowers, destroyed by frost.
†Only one individual had flowers during frost and they were damaged.

had damage to flower buds or flowers. Exposed developing fruits of the two *Ulmus* species never showed damage.

Among the 5 years with frost damage (1994, 1995, 1997, 2000 and 2007), 2007 was extreme in the extent of damage, based on number of species, per cent of individuals and per cent of vegetative units damaged per individual. It also was the earliest year of bud break for many species after its 10 days of very warm, sometimes record-breaking temperatures in March. The five frost years from 1993 to 2009 had in common multiple days in March with temperatures ≥21·1 °C (70°F), but 2007 was unique in having such a prolonged period of warmth in March. As in 2007, the other years with damage also had a temperature in early April of ≤−6·1 °C (21·1°F), but it occurred as early as 2·5 weeks after the March warmth, while it occurred after 25 days in 2007. Years with a warm March but temperatures −1·7 to 0 °C (29–32°F) in early April had no damage. No year with a warm March had temperatures in the intermediate range between −1·7 and −6·1 °C.

Discussion

PHENOLOGY AND FROST DAMAGE IN RELATION TO TEMPERATURES

The extreme event in spring 2007 resulted from a convergence of multiple conditions: an unusually prolonged warmth in March with multiple record-breaking temperatures bringing early and rapid phenological development, a period of unusually cold temperatures in April and wind convection on the coldest day (Angel 2007). The −6·1 °C (21°F) temperature of April 7 was a record low temperature, but not unusual in its timing; spring freezes are common in the first 2 weeks of April at the study site. The extremely cold temperatures in April alone would not normally result in damage. In 2007, they did so because the frost was preceded by a sufficiently long interval after the March warm temperatures, which caused the vegetation to be in phenological phases vulnerable to frost. Indeed, bud break was the earliest in 17 years of observation at the site.

A single weather system can bring freezing temperatures over a large geographical area. Damage can be widespread, especially at latitudes with most species at a vulnerable stage(s). Spring warming occurs sooner at southern latitudes, and thus a single weather system should produce most damage there. Indeed, in 2007, less frost damage occurred north of the study site, but considerably more occurred in southern Illinois (Angel 2007) and in deciduous forests in the southeastern USA (Gu *et al.* 2008). Forests in the most southern area of this biome were not damaged (Gu *et al.* 2008).

The degree of frost damage in 2007 was unusual. In other years, species had no or less serious damage because those years had no or fewer and less warm March days, temperatures insufficiently below freezing in April, and/or a shorter interval between a warm March and a frost in April. Phenological development had not started or had not reached vulnerable stages in most years with freezing temperatures. The combination of conditions sufficient to cause serious frost damage has occurred once in the last 17 years.

Despite the ability to make some generalizations about conditions required to produce frost damage, such predictions are still limited. How early in March such warm temperatures promote early bud break is unclear. Control of growth in response to warm temperatures and its relation to the state of dormancy remains poorly understood (Saxe *et al.* 2001). How late in April a frost causes damage is not known as all years with damage had frost in early April. Likewise, it is not clear whether the one extremely low temperature on 7 April 2007, the freezing temperatures on seven consecutive days or the combination was primarily responsible for the damage. Also, the temperature below which frost damage is certain cannot be discerned because the full range of temperatures did not occur in the 17 years and the temperatures during spring 2007 ranged from −1 to −6 °C. Sakai & Larcher (1987) reported that leaves of deciduous woody plants have frost damage after air temperatures of −3 °C (26·6°F) to −5 °C (23°F), while flowers are damaged by −1 °C (30·2°F) to −3 °C. Finally, the interval between warm and cold temperatures necessary to produce damage is poorly defined. Too short an interval results in insufficient development to have organs in a vulnerable state, although an extremely long interval may result in the vegetation developing to a mature and non-vulnerable stage (Sakai & Larcher 1987; Crawley & Long 1995). Overall, more concurrent and long-term observations of phenology, temperature patterns and frost damage are needed to further refine our understanding of requisite conditions that predict when frost damage will occur.

VARIABILITY IN FROST DAMAGE AND REFOLIATION

Damage due to the spring weather in 2007 varied for different phenological phases, organs, individuals, life stages and species. This variation arose from a combination of level-specific responses to warming, rate of development and resistance to freezing temperatures. The vegetative phenological phases damaged by frost ranged from late bud break through full leaf expansion. In general, more damage arose for later than earlier phases. Likewise, Strain (1966) found that frost caused damage to leaves but not to buds of *Populus tremuloides*. In general, rapidly differentiating and actively growing organs, e.g. expanding shoots, leaves and flowers, are most susceptible to frost (Sakai & Larcher 1987; Crawley & Long 1995). In this study, flowers were the only reproductive organ with damage. All species with damage to flowers also had damage to vegetative units.

In some species, individuals of the same life stage (sapling or canopy tree) showed substantial variation in phenology, thus affecting their relative frost damage. Additionally, individuals may have had different levels of resistance. Strain (1966) found frost damage to leaves to be greater for early- than late-leafing biotypes of *P. tremuloides*.

The sapling life stage had greater damage than the canopy trees of *A. glabra*. This difference may have arisen because of the earlier phenology of saplings, resulting in vegetative units being in a phase more vulnerable to frost, and/or greater resistance developed by canopy trees in response to frost. Sakai & Larcher (1987) found lower resistance in juvenile than adult individuals of *Quercus ilex*. In the current study, it was not possible to compare resistance at the same phenological phase because leaves of saplings and canopy trees of *A. glabra* were at different expansion phases at the time of frost.

Finally, species differed in their phenological response to the March warm period and hence in their relative risk of frost damage. Species in later phenological phases showed more damage than those in bud break or early shoot expansion. Even species in the same phase, e.g. shoot expansion, during the April cold differed in damage. Large differences in damage occur among tree species exposed to a range of midwinter freezing temperatures (Sakai & Weiser 1973; Sakai, Paton & Wardle 1981). As in the current study, the same interspecific variation has been observed for spring freezing temperatures (Tryon & True 1964).

Some species did not respond to the March warmth with bud break and rapid development. These species may use a photoperiod cue and thermal accumulation to initiate bud break. Alternatively, they may have a greater chilling requirement for breaking bud dormancy; if that requirement was not met when the warmth occurred, they would not respond or be vulnerable to frost (Cannell & Smith 1986).

Lechowicz (1984) noted that ring-porous (and semi-ring porous) species tend to have later leaf out than diffuse-porous species. Earlier leafing out species would be more subject to frost damage. In the current study, all canopy tree species are ring-porous or semi-ring porous, except *A. saccharum*, *Tilia americana*, *A. glabra* and *C. caroliniana* (a treelet). The former species leafed out, on average, only about 1 week later than the later group. Furthermore, frost damage occurred in five of ten ring-porous/semi-ring-porous species and two of three diffuse-porous species. Therefore, in this study, no relationship between wood anatomy and leaf frost damage was evident.

Refoliation after damage varied for different life stages, individuals and species. Refoliation is possible because buds, especially adventitious buds, are more frost resistant than leaves in woody plants (Sakai & Larcher 1987). Sipe & Bazzaz (2001) noted differences in recovery among *Acer* species following stem and bud damage of unknown origin. Phillips (1907 in Korstian 1921) reported incomplete refoliation in some tree species following frost damage. Refoliation of frozen oak seedlings was observed to be high in closed, but not open, habitats (Neilson & Wullstein 1983). Rose (1958) observed that refoliation of *P. tremuloides* was complete only following complete defoliation; partial defoliation led to no refoliation.

The late refoliation changed the photosynthetic period of the damaged species and thereby likely reduced their carbon gain. The light available for *A. glabra* saplings that refoliated was lower than normal because the canopy proceeded to close while the saplings refoliated 5 weeks later than normal. These saplings normally complete a substantial part of their photosynthesis in the pre-canopy closure period (Augspurger, Cheeseman & Salk 2005).

IMPLICATIONS

The observed variation in frost damage and refoliation has evolutionary and ecological consequences. First, from an evolutionary perspective, this extreme frost event in 2007 must have resulted in strong directional selection on an individual's phenological cue for bud break, as well as frost resistance and/or tolerance of its developing tissues and organs. Long-term net directional selection on most traits is very small, except for a small subset of traits selected by extreme events (Gutschick & BassiriRad 2003). For example, Agrawal, Conner & Stinchcombe (2004) documented strong selection favouring resistance in an herb species after a late spring frost.

Second, at an ecological level, population demography, forest regeneration and relative species abundance were affected by the frost in Trelease Woods, because many saplings of *A. glabra* with heavy damage and weak refoliation in 2007 were dead by spring 2008 (Carol K. Augspurger, unpublished data). Similar mortality from frost resulted in different species composition in frost pockets in deciduous forest in Pennsylvania (Clarke 1946). Damage to reproductive structures in Trelease Woods in 2007 may have affected trophic interactions. The freeze of spring 1966 in deciduous forests of south-eastern Ohio resulted in no fruit production by *Quercus* and *Fagus* trees, key food items for squirrels; subsequently, their population declined sharply due to a cessation of breeding, and greater emigration and/or mortality (Nixon & McCain 1969). Freeze damage to leaves and flowers reduced acorn yields of *Quercus* trees in both the same and the following year (Goodrum, Veid & Boyd 1971). Given the impact of any extreme event of frost on many ecological levels in the forest, it is important that more focus be given to the frequency, magnitude and timing of both warming and freezing temperatures, phenological responses and damage and refoliation of the forest community, especially in the light of the predicted increase in temperature variability with climate change.

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