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Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing

Carol K. Augspurger[1]

Department of Plant Biology, University of Illinois, Urbana, Illinois 61801 USA

Abstract. Climate change, with both warmer spring temperatures and greater temperature fluctuations, has altered phenologies, possibly leading to greater risk of spring frost damage to temperate deciduous woody plants. Phenological observations of 20 woody species from 1993 to 2012 in Trelease Woods, Champaign County, Illinois, USA, were used to identify years with frost damage to vegetative and reproductive phases. Local temperature records were used in combination with the phenological observations to determine what combinations of the two were associated with damage. Finally, a long-term temperature record (1889–1992) was evaluated to determine if the frequency of frost damage has risen in recent decades.

Frost $\leq$–1.7°C occurred after bud-break in 14 of the 20 years of observation. Frost damage occurred in five years in the interior and in three additional years at only the forest edge. The degree of damage varied with species, life stage, tissue (vegetative or reproductive), and phenological phase. Common features associated with the occurrence of damage to interior plants were (1) a period of unusual warm temperatures in March, followed by (2) a frost event in April with a minimum temperature $\leq$–6.1°C with (3) a period of 16–33 days between the extremes.

In the long-term record, 10 of 124 years met these conditions, but the yearly probability of frost damage increased significantly, from 0.03 during 1889–1979 to 0.21 during 1980–2012. When the criteria were "softened" to $\leq$–1.7°C in April and an interval of 16–37 days, 31 of 124 years met the conditions, and the yearly damage probability increased significantly to 0.19 for 1889–1979 and 0.42 for 1980–2012.

In this forest, the combination of warming trends and temperature variability (extremes) associated with climate change is having ecologically important effects, making previously rare frost damage events more common.

Key words: climate change; extreme event; flowers; frost damage; global warming; leaves; long-term study; phenology; temperature pattern; trees; warm spring.

Introduction

Rare events may be of disproportionate ecological and evolutionary importance (Inouye 2000, Gutschick and BassiriRad 2003). For example, in temperate deciduous forests, a rare and unpredictable frost can cause damage that affects an individual plant's resource acquisition, thus acting as a selective force through differential growth (Strain 1966), survival (Augspurger 2011), and reproduction (Inouye 2008, Augspurger 2011). At larger scales, frost damage may affect the demography and evolution of populations (Inouye 2000), species abundance and spatial patterns (Korstian 1921, Clarke 1946, Augspurger 2011), and ecosystem-level carbon uptake (Gu 2008, Hufkens et al. 2012).

Vulnerability to frost damage depends in part on phenology (see Plate 1). Species differ in their phenologies overall (Augspurger and Bartlett 2003) and in the extent that their phenologies have advanced in response to earlier, warmer springs (Menzel 2000). Therefore, species differ in their probability of being exposed to a spring frost, and the phenological phase at which it is experienced (Augspurger 2009, Hufkens et al. 2012). Specific phenological phases differ in their frost sensitivity. In general, sensitivity is greater for reproductive than vegetative phases, and for developing leaves than for expanding shoots or opening buds (Sakai and Larcher 1987).

Recent climate change includes earlier, warmer spring temperatures (Trenberth et al. 2007). In response, dates of leaf and reproductive development of woody temperate plants are advancing (Menzel 2000, Schaber and Baldeck 2005), potentially making them more vulnerable if frosts occur late in the spring. In temperate latitudes, climate analyses also indicate greater temperature variability in recent decades (Rigby and Porporato 2008). As changes in frequency of extreme events such as frost depend more on variability than on overall temperature trends (Katz and Brown 1992), the counterintuitive prediction of an increased risk of plant frost damage with climate warming has arisen (Cannell and Smith 1986, Gu 2008, Inouye 2008).

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[1] E-mail: carolaug@illinois.edu

Three approaches have been used to estimate temporal changes in frost risk for temperate trees. The first, using temperature analyses alone, suggests that frost potential is decreasing for any given day (Easterling 2002) and that the latest frost date is earlier (Cooter and LeDuc 1995, Robeson 2002). Worldwide, the annual number of frost days decreased in the second part of the 20th century (Frich et al. 2002) as warmer temperatures occurred earlier (Karl and Easterling 1999) and minimum temperatures increased more than maxima (Scheifinger et al. 2003).

The second approach has been to develop models predicting phenology and frost risk based on plant chilling and thermal time requirements, combining them with scenarios of climatic warming. Studies differ in whether they predict greater or reduced risks of frost damage for a variety of woody species (Cannell and Smith 1986, Leinonen 1996, Bennie et al. 2010).

The third approach combines temperature records and direct phenological observations. For example, in central Europe, Scheifinger et al. (2003) found that last-frost temperatures have been moving earlier and at a slightly faster rate than most plant phenologies, suggesting a declining probability of frost damage. Schwartz et al. (2006) concluded that dates of last freezes and rates of change in phenology differed between Northern Europe and East Asia, and showed complex geographic relationships in North America. In the southeastern United States, the historical change in the relationship between early phenological development and last frost date varied with location (Marino et al. 2011).

None of these approaches appraised directly whether climate change has resulted in an increase in frost damage (but see Cannell and Smith [1984] for conifers, Inouye [2008] for herbs). In order to address that, in the springs of 1993–2012, I made weekly phenological observations of vegetative and reproductive development on 20 woody species in a temperate deciduous forest, recording the extent of frost damage with respect to phenological phase. Here, I analyze this long-term data set to address three questions: (1) Which phenological phases and species experience damage and with what frequency? (2) Which combinations of temperature conditions and phenology cause damage? (3) Has the frequency of such combinations, and thus the occurrence of frost damage, increased over a 124-year period (1889–2012)?

Methods

Study site and observation protocols

The study site was the north half of Trelease Woods, a 24-ha old-growth forest remnant 3 km northeast of Urbana, Illinois, USA (40°9′ N, 88°10′ W). The site is level and the mixed mesophytic upland deciduous forest has an average canopy height of 25 m. The study included 13 species of canopy trees, three woody vines, four understory treelets/shrubs, all of reproductive size (Appendix A), and saplings (nonreproductive individuals 2–5 m tall) of *Aesculus glabra* and *Acer saccharum*. An average of 11 individuals per species (range 2–20) were tagged and monitored in the forest interior, at least 50 m from any edge. Additional, non-tagged individuals were monitored 0–5 m in from the edge.

Weekly observations were conducted between 15 February and 31 May, from 1993 to 2012 (see Augspurger [2009] for detailed methods). Data recorded included leaf development (scored as bud break, shoot expansion, or leaf expansion), reproductive status (scored as none, flower buds, flowers, or fruits), and crown frost damage (scored as damage or no damage). Frost damage to leaves was manifested as initial wilting and subsequent turning brown/black and brittle. Damaged flower buds and petals also turned brown/black. Damage was counted at the species level when at least one individual had some damage. Extent of an individual's damage and percentage of individuals of a species damaged varied (see Augspurger [2009] for details).

For each species, the number of years of exposure to frost, the phenological phase(s) experiencing frost damage, and the number of years with such damage were tabulated. The highest minimum temperature causing damage and the lowest temperature causing no damage were also determined for each species and phenological phase.

Temperature combinations causing frost damage: 1993–2012

Field observations showed unusual warmth in March promoted early bud break. Typically, if frost occurred shortly thereafter, no visible damage resulted. However, if the subsequent development interval were long enough, a frost in April would damage leaves and/or flowers.

To determine the frequency with which specific temperature combinations caused phenological phases and species to experience frost damage, a model was developed based on the weekly observations and coincident temperature data. Temperature data for 1889–2012 were downloaded from the Illinois State Water Survey in Champaign, Illinois for a station ~8 km from the study site (data *available online*).[2] As the weather station and study site had similar exposure to open areas, those data likely reflect temperatures of the canopy or forest edges; the closed subcanopy and lower strata were typically slightly warmer. Based on the field observations, for this study, "frost" conditions are equated with a minimum temperature of −1.7°C or lower.

Early-season warm temperatures were characterized first, by summing growing-degree days (GDD) using a 10°C basal temperature, starting at the January date

[2] http://www.isws.illinois.edu/atmos/statecli/cuweather

TABLE 1. Annual pattern of spring temperatures for 1993–2012.

Year	GDD	No. days	First date	Maximum March temperature (°C)	Interval	Minimum April temperature (°C)
1993	10	1 + 0	30	23.3	4	−4.4
1994 I	13	1 + 1	22	25.0	16	−8.9
1995 I	64	4 + 2	13	24.4	21	−6.7
1996	19	1 + 0	14	21.1	26	−4.4
1997 I	44	1 + 1	21	25.6	19	−7.2
1998	77	1 + 3	26	25.6	9	0.6
1999	67	2 + 0	17	21.7	30	1.1
2000 I	100	3 + 2	7	26.1	33	−6.1
2001	140	0 + 0		16.7	17	−1.7
2002	10	0 + 0		20.6	28	−4.4
2003 E	108	4 + 1	16	23.9	21	−1.7
2004	53	1 + 1	18	23.9	21	−1.1
2005	179	1 + 1	29	23.9	26	0.6
2006	46	1 + 1	30	23.9	10	−2.2
2007 I	181	4 + 6	13	26.7	25	−6.1
2008	8	0 + 0		19.4	31	−2.2
2009 E	61	2 + 1	6	23.9	32	−1.7
2010	104	1 + 1	10	25.0	30	−0.6
2011	37	4 + 0	17	22.8	16	0
2012 E	325	4 + 12	12	28.3	30	−1.7

Notes: Growing-degree days ("GDD") are until first cold temperature in April. "No. days" are number of days in March with temperature ≥21.1°C + number of days ≥23.9°C. "Interval" is the number of days from the first day ≥21.1°C (or warmest day if <21.1°C) in March to the coldest temperature in April. Also shown are the first date in March with a warm temperature, maximum March temperature, and minimum April temperature. In the first column, "I" shows temperature with damage to forest interior study individuals; "E" shows temperature with damage to edge individuals only.

with the coldest average temperature and ending at the April date with the coldest minimum temperature, and second, by identifying days in March with maximal temperatures reaching ≥18.3°, 21.1°, 23.9°, and 26.7°C. Note that no species responded visibly to earlier warm periods, presumably because their chilling requirements were unmet. The number of days from the first warm March date to the April frost (≤−1.7°C) was also recorded. If damage occurred following more than one day with frost, the lowest temperature was taken as that causing damage.

The complete weather data set thus contained GDD, the number of warm days in March, the April frost date and minimum temperature, and the interval between the March warm and April frost events. To determine the combination of factors that predicted best frost damage in at least one species, these parameters were considered both singly and in combination. Error matrices (Story and Congalton 1986) assessed the accuracy of the model by summarizing, for each set of parameters, the number of damage years predicted correctly and the number of non-damage years incorrectly included. The best overall model was chosen as that which made no error, i.e., the parameter(s) predicted all frost damage years without including any non-damage years in the 1993–2012 data set. Additional analyses were used to explore the variability among life forms and species and their fit to the overall model. To prevent bias driven by one extreme year, a jackknife procedure (resampling without replacement) was completed on the chosen model (Dixon 1993).

Changes in frost risk: 1889–2012

To determine whether the risk of frost damage has increased over the last century, the best overall model for 1993–2012 was used to predict retroactively those years with probable frost damage between 1889 and 1992. Frost damage frequencies were compared for two intervals (1889–1979 and 1980–2012) using a chi-square test. This "change point" is the time at which global land temperatures moved consistently above the 1961–1990 long-term average, and has been used by the Intergovernmental Panel on Climate Change in evaluating temporal patterns of many climate variables (Trenberth et al. 2007). As an alternative method to address this question, the fraction of years with predicted frost damage in a running 31-year window from 1889 to 2012 was also analyzed.

RESULTS

Phenology, frost exposure, and frost damage: 1993–2012

Twenty years of field observations involving 20 species were combined to address the questions: Which phenological phases and species are exposed to frost, experience damage, and with what frequency? The years differed substantially in their temperature patterns (Table 1). Six years had no frost temperatures in April or May and no frost damage (Table 1). Five years had no warm days in March and no frost damage. In three

TABLE 2. Number of species in three vegetative and three reproductive phenological phases exposed to temperatures ≤ -1.7°C each year during 1993–2012.

Year	Date	BB	SE	LE	FB	FL	FR
1993	89	3			1		
1994	81	1					
1994	88	5	1				
1994	95	7	2(1)	1(1)		1	
1995	93	8	3(1)	1(1)	5	3(1)	1
1996	95	4	1		2	1	
1997	77	1	1				
1997	84	1	1				
1997	91	4	1		4	1	1
1997	98	13	2	1(1)	9	5	1
1998	none						
1999	none						
2000	70	5	1				
2000	77	5	1		6	3	
2000	83	5	1		6	3	
2000	91	8	2	1	7	3	2
2000	98	16	6(3)	1(1)	7	7(2)	2
2001	84	1			2		
2001	93	4	1		4	1	
2001	105	14	19	5	7	9	2
2002	76	2	1				
2002	83	2	1		5	1	
2002	88	4	1		3	2	
2002	93	5	1		3	2	
2003	84	5	1		5	2	
2003	91	8	2	1(1E)	3	3	
2004	none						
2005	none						
2006	77	3			5	1	
2006	84	3			5	1	
2006	98	7	3	1	5	4	
2007	76	1	1				
2007	90	15	2	1(1)	9	4	2
2007	97	2(2)	11(4)	2(2)	8(2)	7(4)	2
2008	95	1			5	1	
2008	102	5	1		9	3	
2009	97	6	1	1(1E)	3	3	1
2010	none						
2011	none						
2012	96	8	14(3E)	18(10E)	3	4	8

Notes: The number of species with frost damage is in parentheses; "E" refers to damage to forest edge individuals only. "Date" refers to the day of the year of the census preceding the frost that occurred between that date and the next weekly census. Phenological phases are: BB, bud break; SE, shoot expansion; LE, leaf expansion; FB, flower bud; FL, flower; FR, fruit.

years, the interval between March warmth and April frost was short and there was no frost damage.

Frost exposure.—Phenological phases and species differed in their frost exposure. Opening buds, expanding shoots, and expanding leaves of interior plants were exposed in 14, 13, and 10 years, respectively, and to multiple frosts in some years (Table 2). Eighteen species were exposed at all phases, but in highly variable numbers of years (Appendix A). Most species were exposed during leaf expansion only in 2012 (Table 2), although leaves of *Aesculus glabra* saplings had exposure in nine years (Appendix A). Flower buds, flowers, and developing fruits experienced frost in 13, 13, and 7 years, respectively (Table 2); 16, 15, and 8 species were exposed at flower bud, flower, and fruit phases, respectively, but in highly variable numbers of years (Appendix A).

Frost damage.—Damage occurred to opening buds, expanding shoots, and expanding leaves of interior plants in 1, 4, and 5 years, respectively (Table 2). Expanding shoots and leaves of edge plants had damage in 1 and 3 additional years, respectively. During the 20 years, seven species had no frost damage. Damage to interior plants occurred for eight species at vegetative phases, although in variable numbers of years (Appendix A). An additional five species had damage to leaves of only edge plants. Expanding leaves of *A. glabra* saplings were prominent in having damage in five years to both interior and edge plants and in three additional years to only edge plants. Six species experienced frost damage to reproductive tissues. Damage to flower buds and flowers occurred in 1 and 3 years, respectively (Table 2). Two and four species had damage to flower buds and flowers, respectively, but no fruits experienced damage (Appendix A).

Interior vs. edge effects.—Overall, frost damage occurred to vegetative structures of both interior and edge plants in at least one species in five of 20 years (1994, 1995, 1997, 2000, and 2007) and to only edge plants in three additional years (2003, 2009, 2012; Table 2). Species differed in whether they were damaged only in the interior ($n = 3$ species), only at the edge ($n = 5$ species), or both ($n = 5$ species) (Appendix B). Frost damaged the most species in the interior in 2007, and at the edge in 2012. Reproductive structures of interior plants were damaged in 1995, 2000, and 2007 (Table 2).

Temperature patterns associated with frost damage: 1993–2012

The overall goal here was to develop a community-level model that would predict all years in which frost damage occurred to at least one species. Secondary goals were to identify temperature patterns that distinguished damage at forest edge only and damage also in forest interior, damage to understory individuals only and damage also to canopy individuals, and the responses of specific species and life stages.

Weather summary.—The mean last frost date (minimum temperature ≤ -1.7°C) was 5 April (range, 22 March–1 May). In the 14 years with April frosts, the number of growing-degree days (GDD) prior to frost ranged from 8 to 325 (Table 1). In five years, March was cold, with 0 or 1 day above 21.1°C. In two years, March was extremely warm: in 2007, 10 days were above 21.1°C (maximum 26.7°C) and in 2012, 16 days (maximum 28.3°C). The interval ranged from 4 to 33 days between March warmth and April frost.

Frost temperatures ranged from −1.7 to −8.9°C (Table 1). The highest minimum temperature preceding damage to interior plants was −6.1°C, although −8.9°C caused no damage in some cases (Appendix A). Edge plants experienced damage when minimum temperatures fell to −1.7°C (Table 1).

Table 3. Error matrix for parameter(s) used to predict number of years between 1993 and 2012 with frost damage or no damage.

Parameter	Damage years correctly predicted	Non-damage years incorrectly included
One parameter		
GDD		
≥8	8	12
≥13	8	9
≥20	7	8
≥40	7	7
≥60	6	5
≥80	4	3
≥100	4	3
≥150	2	1
≥200	1	0
≥300	1	0
≥400	0	0
March temperatures		
2 d ≥15.6°C (60°F)	8	12
2 d ≥17.3°C (65°F)	8	9
2 d ≥21.1°C (70°F)	8	7
2 d ≥23.9°C (75°F)	3	1
2 d ≥26.7°C (80°F)	2	0
1 d ≥21.1°C + 1 d ≥23.9°C	8	5
April temperature		
≤1.1°C (34°F)	8	12
≤0°C (32°F)	8	9
≤−1.7°C (29°F) (edge only)	8	6
≤−2.2°C (28°F)	5	6
≤−4.4°C (24°F)	5	3
≤−6.1°C (21°F) (interior)	5	0
Interval March–April		
≥4 d	8	12
≥16 d (understory)	8	9
≥21 d	6	7
≥25 d (canopy)	4	6
Two parameters		
1 d ≥21.1°C + 1 d ≥23.9°C		
+ ≤−1.7°C (edge)	8	1
+ ≤−2.2°C	5	1
+ ≤−4.4°C or ≤−6.1°C (interior)	5	0
1 d ≥21.1°C + 1 d ≥23.9°C		
+ 16–24 d (understory)	8	3
+ ≥25 d (canopy)	4	2
≤−1.7°C + 16–24 da	8	4
≤−1.7°C + ≥25 da	8	3
≤−6.1°C + ≥25 da	5	3
Three parameters		
1 d ≥21.1°C + 1 d ≥23.9°C + ≤−6.1°C + 16–24 d (understory)	5 (+3)†	0
1 d ≥21.1°C + 1 d ≥23.9°C + ≤−6.1°C + ≥25 d (canopy)	2 (+1)†	0
1 d ≥21.1°C + 1 d ≥23.9°C + ≤−1.7°C + 16–24 d (understory)	8‡	0
1 d ≥21.1°C + 1 d ≥23.9°C + ≤−1.7°C + ≥25 d (canopy)	3‡	0

Notes: Single and combinations of parameters tested were: growing-degree days (GDD) (from day in January with lowest mean temperature to day in April with lowest minimum temperature; reported as number of days), temperature patterns in March and April (reported as °C), and the interval between March warmth and April cold (reported as a range of days). The number of years correctly predicted by the parameter(s) is in the column damage years; the number of non-damage years incorrectly predicted as having damage (errors) is in the non-damage years column. A perfect parameter(s) accurately predicted all years that had damage and included none that did not have damage (i.e., made no errors).

† Interior (+ edge).

‡ Edge.

Model evaluations.—Error matrices incorporating temperature parameters were used to determine the best model that correctly predicted all damage years for at least one species, but no non-damage years in 1993–2012 (Table 3).

Models using GDD prior to April frost alone or in combination with April temperature did not accurately predict the occurrence of frost damage, requiring extreme values to eliminate all non-damage years, while concurrently reducing the number of damage years retained (Table 3). Using only GDD accumulated after 1 March (to eliminate phenologically unimportant accumulations in January and February) did not improve its predictive value (data not shown). GDD models also failed to account for the interval between warmth and cold, which observations showed was required to have structures at a vulnerable stage when the frost occurred.

Single-parameter models using March temperatures only, April temperature only, or the interval between them had similar deficiencies (Table 3). The most effective, yet still imperfect, two-parameter model used a combination of March and April temperatures. When an April low of $\leq$–1.7°C was used to predict damage, all eight damage years were included, but one non-damage year was not excluded. Alternately, requiring an April temperature of $\leq$–6.1°C eliminated the single non-damage year, but excluded three years with damage at the forest edge.

The best model for the five damage years for interior plants included all three temperature parameters with these values: (1) in March, $\geq$1 day $\geq$21.2°C and $\geq$1 day $\geq$23.9°C; (2) in April, $\geq$1 day of $\leq$–6.1°C; and (3) $\geq$16 days between the extreme temperatures for understory individuals and $\geq$25 days for canopy individuals (Table 3). Hereafter, that model is referred to as the "strict" model. It selected all five damage years and no non-damage years. The best model for edge plants was similar, but with an April cold threshold of $\leq$–1.7°C (Table 3). The jackknife procedure showed that these results were not unduly influenced by any one year. Deleting any one year from the dataset, the same criteria for March and April temperatures applied. The minimum interval for understory damage increased from 16 to 19 days.

While the overall model used minimum parameter values required to predict damage to at least one species, modification of these values, i.e., adding more March warm days and/or increasing the interval between warm and cold days, resulted in correctly predicting more species and life forms with observed vegetative and reproductive damage (Appendix B). The minimum model with two warm days and an interval of 16 days correctly predicted vegetative damage to only *A. glabra* saplings and *Lindera benzoin*, both in the understory. Modifying the model number of March warm days to 16 days and the interval to 30 days correctly predicted vegetative damage to all 13 species. For damage to reproductive tissues, the minimum model of five warm days correctly predicted only *Asimina triloba*, while an interval of 21 days predicted only *L. benzoin* (Appendix B). Modifying the model number of March warm days to 10 days and the interval to 25 days correctly predicted all six species with reproductive damage.

Changes in frost risk: 1889–2012

Over the 124-yr record, the percentage of years with a given March day having a temperature $\geq$21.1°C ranged from one to 15, increasing through the month (Appendix C), while the percent of years with a given April day having a temperature $\leq$–1.7°C ranged from zero to 22, decreasing with time (Appendix C). Forty-six years had two or more warm days in March, and 37 of the 46 years also had April frosts (minima $\leq$–1.7°C) (Appendix D). When the interval between warmth and cold was applied additionally, 28 years satisfied all three criteria. Three years with frost temperatures unique to May were not included in the analyses below because leaves likely had matured to be non-vulnerable prior to frost (see Augspurger 2011). No frost damage was observed at a temperature of −3.3°C on 1 May 2005.

Using temperatures over 30-year intervals since 1891, days in March that met the warm-temperature criterion increased through the last 120 years, although 1951–1980 marked a cooler period (Appendix E). Warm days in March occurred in 24 years (27%) between 1891–1980, but in 21 years (70%) between 1981–2010. In contrast, cold Aprils changed less through the past 120 years; the April cold criterion was met in 73 years (81%) between 1891–1980 and in 22 years (73%) between 1981–2010 (Appendix E). Fourteen years (16%) between 1891–1980 and 8 years (27%) between 1981–2010 met the strict criterion of $\leq$–6.1°C needed for interior damage. The mean first warm March day advanced by two days, and the first cold April day was later by one day over the 120 years (Appendix E). The interval between the first warm March day and first cold April day increased from 19 to 23 days.

Overall, 10 of 124 years (8%) met the strict criteria for predicting a high probability of frost damage to understory species such as *A. glabra* and *L. benzoin* (Table 4, Appendix D). In only five of 124 years (4%) was the interval long enough ($\geq$25 days) for the slower developing leaves of canopy trees to be at a vulnerable phase for damage.

When the criteria were "softened" to include (1) a warm March (as above), (2) $\leq$–1.7°C in April, and (3) an interval of 16–37 days, 31 of 124 years (25%) had at least some probability of frost damage (Table 4, Appendix D). This softening brought inclusion of edge plants with frost damage at $\leq$–1.7°C, and three non-observation years that slightly exceeded the strict 33 day observed interval, but otherwise met the strict warm and cold criteria, and likely had frost damage (Table 4). The year 1983, with a 47-day interval, likely had no frost damage because leaves would have "hardened" and not have been vulnerable.

TABLE 4. Years with observed and probable frost damage during 1889–2012.

	Damage when early phenology			Damage when later phenology		
Low temp. April	Year	No. March days $\geq$21.1 + 23.9°C	Interval (days)	Year	No. March days $\geq$21.1 + 23.9°C	Interval (days)
$\leq$−6.1°C	1903	0 + 3	18	1972	1 + 1	28
	1939	0 + 3	20	1987	2 + 2	27
	1994 I	1 + 1	16	1990	1 + 3	28
	1995 I	4 + 2	21	2000 I	3 + 2	33
	1997 I	1 + 1	19	2007 I	4 + 6	25
−5.6 to −3.9°C	1894	2 + 2	16	1907	1 + 7	26
	1919	3 + 7†	20	1910	3 + 8‡	35§
	1928	2 + 1	18	1918	6 + 3	36§
				1925	2 + 1	29
				1986	0 + 5	29
				1989	3 + 1	23
−3.3 to −1.7°C	1905	4 + 1	20	1916	2 + 1	31
	1943	0 + 2	16	1921	3 + 3	27
	1946	2 + 2	17	1974	3 + 3	37§
	1963	2 + 1	17	1992	3 + 2	31
	1988	3 + 1	18	2009 E	2 + 1	32
	2003 E	4 + 1	21	2012 E	4 + 12	30

Notes: Observed damage was to interior (I) or edge only (E) plants. April frost temperatures had high ($\leq$−6.1°C), intermediate (−5.6 to −3.9°C), and low (−3.3 to −1.7°C) probability of producing damage. Also shown are number of days in March with temperatures $\geq$21.1° and $\geq$23.9°C and interval (number of days) between first day in March $\geq$21.1°C and first day in April with indicated frost temperature. With an interval of 16–21 days, species with early phenology (understory *Aesculus glabra* saplings and *Lindera benzoin*) were most likely to have had frost damage; if $\geq$25 days, later canopy individuals also became vulnerable to damage.

† The year 1919 had no day $\geq$21.1°C in March; a cold temperature in April occurred 20 days after 10 days of temperatures $\geq$21.1°C in April.

‡ The year 1910 had one warm day on 5 March; a second extended warm period began 19 March. The interval to the coldest April temperature uses the second warm day in March 1910.

§ Interval is greater than the maximum observed interval with frost damage (33 days).

Widespread and heavy damage from frost, as occurred in 2007 to interior plants and 2012 to edge plants, probably occurred rarely in the last 124 years (Table 4, Appendix D). However, based on the strict criteria, the probability of frost damage in April of a given year became significantly greater at the study site from 1889–1979 (0.033) to 1980–2012 (0.212) (χ^2 = 10.484, df = 1, $P < 0.0012$). The increased risk of frost damage over time is also confirmed in the running 31-year window analysis, as the percentage of years with damage increased greatly after 1970 (Fig. 1). Based on the "softened" criteria outlined above, the probability of edge frost damage also became significantly greater from 1889–1979 (0.187) to 1980–2012 (0.424) (χ^2 = 7.281, df = 1, $P < 0.007$). This change in risk was nonlinear, as predicted edge frost damage was more common early and late in the 124 years than in the cool period from 1951 to 1980 (Fig. 1).

DISCUSSION

Plants face an evolutionary tradeoff between developing early to enhance carbon gain and delaying development to avoid frost damage. This study indicates high variability among species and life stages in their phenology and therefore in how often frost served as a potential selective force for traits to avoid frost exposure and/or to resist or tolerate damage.

The risk of frost damage in a given year is low and unpredictable because three conditions must converge: (1) abnormally warm temperatures in early spring must initiate early leaf and flower development, (2) a sufficient number of subsequent above-freezing days must bring development to a vulnerable phase, and (3) a subsequent frost must occur. Evaluating the frequency with which these criteria are met is key to assessing frost damage risk.

Phases and species vulnerable to frost: 1993–2012

The phenological stage at the time of frost affected the extent of frost damage, as was observed by Kreyling et

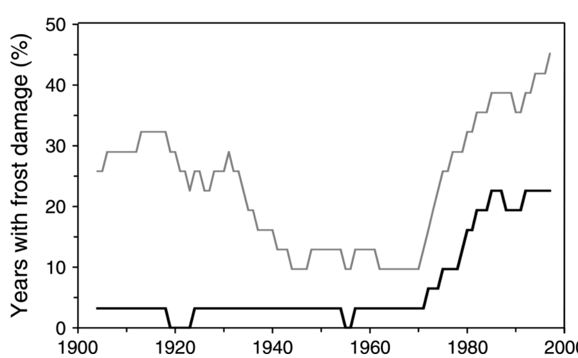

FIG. 1. Running window of the percentage of years with frost damage during 1889–2012. Year on x-axis is the central year of the 31-yr window. The black line is based on "strict" criteria (see *Results: Model evaluations*), and the gray line on "soft" criteria (see *Results: Changes in frost risk 1889–2012*).

PLATE 1. In early spring, in a temperate deciduous forest, species with early leaf phenology (e.g., this *Aesculus glabra* sapling) are particularly vulnerable to frost damage. Photo credit: Steven Buck.

al. (2011). While all species were exposed to frost during bud break, fewer were exposed at shoot expansion, and still fewer during leaf expansion. Conversely, damage was greater at later phases (see also Sakai and Larcher 1987). Although Sakai and Larcher (1987) reported that reproductive structures are more vulnerable, in this study they were less often exposed to frost. No obvious pattern related to life history, time of bud break, or life form emerged in this study to explain differences in damage among exposed species.

Frost damage has negative consequences at the individual (Augspurger 2011), population (Augspurger 2011), and ecosystem levels (Gu 2008, Hufkens et al. 2012). Frost damage can undoubtedly occur to mature, long-lived trees multiple times with no threat to survival, but can cause mortality at earlier life stages. The most vulnerable species in the current study was that which began development earliest in the spring, *A. glabra*, and especially its saplings (Augspurger 2009). In 2007, *A. glabra* saplings with heavy leaf frost damage showed only partial refoliation, low canopy fullness, early senescence, a shortened growing season, and high mortality of next year's buds; by 2009, 11% had died (Augspurger 2011).

Temperature combinations producing frost damage: 1993–2012

Springtime frost temperatures were common, occurring in 14 of 20 years of observation, sometimes with multiple episodes per year, but frost damage of interior plants occurred in only five years; three additional years brought damage to edge plants. This rate is similar to that reported by Inouye (2000) for herbs in a montane habitat. Although this study was restricted to one local site, such damage in forests is not unique (e.g., Korstian 1921, Mock et al. 2007). Major frost events often extend regionally, sometimes to large geographic areas, as in the 2007 regional freeze in the southeastern United States (Gu 2008) and in 2010 in the northeastern United States (Hufken et al. 2012). Minor damage years are probably more local events, and are seldom documented.

The severity of frost damage clearly differs among years. The years 2007 and 2012 were exceptional as long warm periods in March put more species at risk in April. In 2007, the damage was most extreme and affected the most species both in this forest (Augspurger 2009) and regionally (Gu 2008). The warmest year, 2012, had the most species at vulnerable stages; however, the higher April minimum temperature (−1.7°C) restricted damage to the forest edge. Serious damage requires −3°C (Sakai and Larcher 1987).

It is, however, impossible to define the conditions for frost damage unequivocally as the actual conditions experienced in 20 years were a small subset of all possibilities. Particularly lacking were April temperatures between −6.1°C and −1.7°C during shoot and leaf expansion. Similarly, the range of values for the warm-to-cold interval was too limited to accurately define the phenological point at which resistant to frost damage develops.

Increased frost risk in recent decades

Whether using the strict or soft frost criteria, the probability of frost damage in a given year for these woody species appears to have increased in recent decades. Similarly, Inouye (2008) reports increased frost damage to flower buds of montane herbaceous species in recent years; he attributes that increase to an earlier date of spring snowmelt that advances flower development but puts them at risk for frost. Both studies support the prediction of increased frost damage despite overall climatic warming. Based on analysis of the long-term patterns, temperature changes in March but not April were responsible for the increased probability of frost in recent decades at the study site. More of those years had warm March days combined with little or a slight increase in number of years with cold April days. The pattern of extreme cold events is continuing into the 21st century and is not following the upward mean temperature trend, at least in some regions (Walsh et al. 2001, Kunkel et al. 2004).

This study illustrates the importance of simultaneously gathering field observations of temperature, phenology, and frost damage over long-term periods. Studies rarely combine all three components. No other long-term study including field observations of frost damage for most woody species in a temperate deciduous forest is available (but see Gu et al. [2008] for 2007 frost, Hufkens et al. [2012] for 2010 frost). Overall, little is known about the historical temporal and spatial change in spring frost damage (but see Marino et al. 2011). Prospective analyses of future spring frost risk are more common (Leinonen 1996, Bennie et al. 2010).

The retrospective nature of the predictions in this study precludes any direct appraisal of the future likelihood of frost damage. Recent models using only temperature data provide some evidence that increased temperature variability might lead to continuing frost risk in the future in some regions (Vavrus et al. 2006, Kodra et al. 2011). An added complexity for predicting future frost risk is that interacting climatic drivers are likely to determine plant responses (Kreyling et al. 2011). Growth under elevated [CO_2] can lower freeze tolerance, increasing plant vulnerability at warmer freezing temperatures (Barker et al. 2005). Long-term, continuous observations of temperature and phenology that encapsulate these rare and unpredictable events of frost damage are needed to evaluate the uncertainties of CO_2-effects, precipitation, and global warming.

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Supplemental Material

Appendix A

Table presenting, for each study species, number of years from 1993 to 2012 with exposure to frost temperatures and with frost damage to leaf and reproductive phenological phases (*Ecological Archives* E094-006-A1).

Appendix B

Table presenting, for each study species, temperature combinations during 1993–2012 that resulted in frost damage to vegetative and reproductive structures (*Ecological Archives* E094-006-A2).

Appendix C

Figure presenting percentage of years from 1889–2012 with daily temperatures in March $\geq$21.1°C and temperatures in April and May $\leq$0°C (*Ecological Archives* E094-006-A3).

Appendix D

Table presenting yearly pattern from 1889–2012 of warm temperatures in March and cold temperatures in April, and the interval (days) between warmth and cold (*Ecological Archives* E094-006-A4).

Appendix E

Table presenting pattern of temperatures in March, April, and May for 30-yr intervals from 1890–2010 (*Ecological Archives* E094-006-A5).