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Effects of winter temperatures on two birch (*Betula*) species

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Summary In Massachusetts, low winter temperatures delay the onset of flowering in black birch (*Betula lenta* L.), but not in gray birch (*B. populifolia* Marsh.). During the winter of 2006, male inflorescences and twigs of black birch had higher water contents than those of gray birch, and the inflorescences of black birch experienced greater frost kill than those of gray birch. Vessels diameters were greater in black than in gray birch, a difference associated with a higher incidence of winter xylem embolism, as indicated by reduced xylem hydraulic conductance. In both species, recovery of hydraulic conductance in twigs that survived the winter coincided with the development of root pressure. Frost kill to male inflorescences or associated damage to plant tissues may account for the difference between species in the effect of winter temperature on the time of first flowering. In a comparison of 24 birch species, sensitivity of the first flowering date to temperature was also correlated with water content in male inflorescences.

Keywords: cavitation, climate change, embolism, flowers, freezing, global warming, inflorescences, Massachusetts, phenology, xylem.

Introduction

The timing of plant phenological events has changed worldwide as a result of recent climate warming (Parmesan and Yohe 2003, Root et al. 2003). In most cases, spring events, such as leaf out and flowering, have occurred earlier. However, not all species have been affected in the same way. For example, in England, some species now flower up to a month earlier than 50 years ago, whereas in other species flowering times remain unchanged (Fitter et al. 1995). Among species in which the timing of phenological events is changing, the pace of change varies dramatically (Miller-Rushing and Primack 2008). Differences in phenological response to changing temperature may have large impacts on the outcome of individual, species and community interactions. Effects of temperature-induced phenological change have been reported on both reproductive biology (Gross and Werner 1983, Kudo et al. 2004) and intertrophic relationships (Both et al. 2006) .

In most temperate plant species, the timing of spring phenological events is dependent on both day-length and temperature cues (Cannell and Smith 1983) in ways that vary among species (Murray et al. 1989) and among ecotypes within species (Myking and Heide 1995). However, the structural or physiological traits that explain differences in phenological responses to temperature, particularly among closely related species, are largely unknown. It has been suggested that freezing-induced cavitation may delay flowering or leaf out by delaying the flow of water to buds in the spring (Wang et al. 1992, Strati et al. 2003). Roots, buds and the signaling compounds that they produce are also critical determinants of flowering phenology (Bernier et al. 1993) and may have a role in mediating effects of climate change.

The question of why the phenologies of closely related species respond differently to climate change is of particular ecological significance. Closely related species co-occur more often than expected by chance (Williams 1947, Webb 2000), and differences in phenology are important in maintaining reproductive isolation and niche differentiation (Hendry and Day 2005). Thus, if flowering times of co-occurring, closely related species respond differently to climate change, the difference between their flowering times will change, affecting the frequency or hybridization and competition for pollinators and other resources (Miller-Rushing et al. 2007). To predict how these ecological relationships will change in response to possible climate warming, it is necessary to understand the mechanisms underlying phenological responses to environmental cues, and in particular, to temperature.

Here we report a study of black (*Betula lenta* L.) and gray (*B. populifolia* Marsh.) birch, closely related species which differ in their responses to winter temperatures. In eastern Massachusetts, black and gray birch often co-occur in mixed stands, where black birch, unlike gray birch, consistently flowers earlier in years with warmer winters than in years with colder winters (Miller-Rushing and Primack 2008). Thus, black birch flowers earlier in response to warm winter temperatures, in contrast with many tree species in which flowering is delayed following a warm winter (Samish 1954, Perry 1971, Cannell and Smith 1983, Murray et al. 1989).

We hypothesize that the time of first flowering in black birch is delayed in cold years because of frost damage to tissues or freezing-induced xylem cavitation resulting in reduced hydraulic conductivity. To test this hypothesis, we observed:

(1) the developmental time course of male inflorescences in relation to freezing damage; (2) overwinter water content of male inflorescences and twigs, as a measure of susceptibility to frost damage; (3) overwinter xylem cavitation in flower-bearing shoots; (4) xylem vessel diameters, as a possible index of susceptibility to frost-induced xylem cavitation; and (5) root pressure immediately before the onset of flowering, as a factor affecting stem hydraulic conductivity.

Materials and methods

Species and sites

Two co-occurring populations of black birch and gray birch in eastern Massachusetts were studied. We monitored at least 10 adult wild individuals of each species at Hammond Woods in Newton, MA (42°20′13″ N, 071°12′33″ W, 30 m a.s.l.) and at the Arnold Arboretum of Harvard University in Jamaica Plain, MA (42°18′35″ N, 071°07′13″ W, 52 m a.s.l.). We made weekly observations from January through April 2006.

Black and gray birch are both native to eastern Massachusetts, and both are wind pollinated and deciduous. Black birch is found in both wet and dry habitats, whereas gray birch is found primarily in dry habitats. To our knowledge, the specific flowering requirements of black and gray birch have not been described. Analyses of historical flowering times indicate that the first flowering times of black birch are significantly correlated with January temperatures ($r = -0.590$, $P = 0.016$), whereas those of gray birch are not ($r = -0.141$, $P = 0.602$) (Miller-Rushing and Primack 2008). January was usually the coldest month in the years for which we have flowering observations. In neither species were first flowering times significantly correlated with February, March or April temperatures, or with precipitation in the months January–April. Historical records likely describe only the flowering of male inflorescences, not female inflorescences. Therefore, we monitored only male inflorescences.

Male inflorescence mortality and growth

For 10 trees of each species per site, we recorded the percent of male inflorescences that exhibited freezing-induced mortality each week from January 21 through April 6. Freezing-induced mortality was indicated by desiccation of the inflorescence (i.e., bruising, wilting or cracking). Some dead inflorescences were shed, so the percent of desiccated inflorescences was less than the total inflorescences that had died since the beginning of the winter.

Each week, we estimated volume growth (Perry 1971) of 45 marked male inflorescences of each species at each site (three inflorescences per branch × three branches per tree × five trees per site). We estimated the volume of each inflorescence as a cylinder from its length and its mean diameter at one- and two-thirds of its length. Measurements were continued until an inflorescence either died (usually by freezing-induced mortality) or began to shed pollen.

Xylem conductance

To estimate the incidence of xylem cavitation, we measured percent loss of hydraulic conductivity in one twig from each of five trees of each species each week from March 16 through April 13. We used twigs with a diameter of about 0.5 cm without signs of desiccation. We stored freshly cut twigs at 4 °C in double-bagged Ziploc bags with wet paper towels until hydraulic conductivity was measured (within 24 h of harvest). Hydraulic conductivity was measured by attaching each twig to tubing and allowing gravity-forced (15.6 kPa) filtered, distilled, degassed, deionized water to flow through each twig (e.g., Atkinson et al. 2003, Cobb et al. 2007). We measured the volume of water from each twig per unit time. We then placed the measured twigs into a bucket of filtered, distilled, degassed, deionized water under a vacuum overnight, to remove embolisms. The next day we remeasured the hydraulic conductivity to obtain an estimate of maximum potential hydraulic conductivity. Finally, we calculated the percent loss of hydraulic conductivity of each twig (Sperry et al. 1988). Absolute hydraulic conductivity might have been higher had we perfused twigs with an ionic solution instead of distilled water (Zwieniecki et al. 2001). However, we assume that, being relative values, our measurements of percent loss of hydraulic conductivity were similar to values that would have been obtained had we used an ionic perfusion solution.

Root pressure, water content and vessel diameter

We observed root pressure by making a hole with a needle in the main stem or a large branch of each tree and observing if a bubble formed at the opening or if sap flowed from the hole, in which case root pressure was assumed to be positive. Measurements were made within 2 h of sunrise.

We measured water content of inflorescences and twigs of each tree by weighing them immediately after removal from the tree and after oven drying to constant mass.

Vessel diameters were measured in two hand-cut transverse stem sections, which were stained with safranin. The diameters of twelve randomly selected vessels from each slice were measured from digital images taken with the aid of a microscope.

Temperature-response experiment

To test whether water content or male inflorescence size affected the relationship between first flowering date and spring temperature, we monitored flowering date in excised shoots with male flowers from 24 birch species incubated in controlled environment chambers (Table 1). Samples were collected on March 8, 2006 from 29 trees of 22 species growing at the Arnold Arboretum. On March 11, 2006, we collected twigs with male inflorescences from 10 wild individuals of black and gray birch, half from the Arnold Arboretum and half from Hammond Woods. Immediately after collection, two twigs from each tree were placed with their cut end in water in a controlled environment chamber at 21, 19, 11 or 6 °C with a 14.5-h photoperiod, typical of May in Massachusetts. The date of first flowering (pollen shedding) of each twig was recorded.

Volume and water content of inflorescences from each tree were measured.

Analysis

Characteristics of black and gray birch were compared with *t*-tests. Relationships between water content or inflorescence size and time to flowering in the temperature-response experiment were investigated by regression analysis.

Results

Male inflorescence growth and mortality

Field monitoring, beginning in January, showed no change in male inflorescence size in either black or gray birch until just before pollen shedding. At both sites, male inflorescence mortality was significantly greater in black birch than in gray birch. At Hammond Woods, an average of 26 ± 3% of black birch male inflorescences were frost killed compared with 0.9 ± 0.4% of gray birch (paired $t = 6.86$, two-tailed $P = 0.001$; $n = 6$). Of the 11 black birch trees monitored at Hammond Woods, two suffered 100% male inflorescence mortality, whereas in the most severely damaged gray birch tree, mortality was only 33%. At the Arnold Arboretum, the difference between species in male flower mortality was less: 5 ± 0.8% mortality in black birch and 2 ± 0.9% in gray birch (paired $t = 3.14$, two-tailed $P = 0.026$; $n = 6$). The heaviest mortality in black birch at the Arnold Arboretum was 40% compared with 22% for gray birch. Many inflorescences were shed following frost kill without being recorded. Thus, our estimates of mortality are conservative, particularly in the case of black birch, which suffered the heaviest mortality.

Table 1. Mean water content (WC) and mean dimensions of male inflorescences of 24 birch (*Betula*) species. Individuals were cultured at the Arnold Arboretum unless otherwise noted: AA indicates a wild population at Arnold Arboretum; and HW indicates a wild population at Hammond Woods.

Species	WC (%)	Male influorescence	
		Length (mm)	Diameter (mm)
B. alleghaniensis	56	27.5	4.0
B. alnoides	21	26.9	3.6
B. chinensis	11	19.4	3.1
B. costata	50	22.1	3.8
B. davurica	11	29.9	3.8
B. ermanii	31	28.2	3.9
B. globispica	10	23.2	4.0
B. grossa	49	32.9	3.7
B. lenta AA	53	25.0	3.9
B. lenta HW	44	20.7	3.5
B. litwinowii	51	25.8	3.3
B. mandshurica	52	20.4	3.3
B. maximowicziana	33	51.2	4.6
B. nigra	45	29.5	3.3
B. obscura	47	31.5	3.1
B. papyrifera	44	36.8	4.2
B. pendula	46	30.4	3.4
B. platyphylla	50	31.1	3.2
B. populifolia AA	48	29.1	3.1
B. populifolia HW	38	26.0	2.4
B. pubescens	37	23.4	3.3
B. schmidtii	30	23.7	3.1
B. schugnanica	32	29.6	3.0
B. turkestanica	26	24.4	3.5
B. uber	49	13.3	3.6
B. verracosa	38	21.1	3.3

Xylem conductance

During the first 2 weeks (mid to late March), loss of hydraulic conductivity was greater in twigs of black birch than of gray birch (March 16, $t = 2.65$, $P = 0.038$; March 23, $t = 2.84$, $P = 0.047$; Figure 1). Mid-March was the last winter period with temperatures well below freezing (Figure 2). Percent loss of hydraulic conductivity decreased in both species in late March, and the difference between the species disappeared (March 30, $t = -0.28$, $P = 0.785$; April 6, $t = -0.75$, $P = 0.484$). By April 13, full hydraulic conductivity had been restored in all individuals of both species (Figure 2).

Root pressure, water content and vessel diameter

Both species showed root pressure in the spring, starting slightly earlier in black birch than in gray birch. The first tree to develop root pressure was a black birch at the Arnold Arboretum on March 30. The following week, root pressure was evident in all black birch trees and 54% of the gray birch. In the week of April 13, all trees of both species showed root pressure.

Inflorescences and twigs had higher percent water contents in black birch than in gray birch at both study sites. At the Arnold Arboretum, the water contents of black birch inflorescences and twigs were 52.6 ± 0.4% and 46.7 ± 0.4% by mass, respectively, compared with 48.0 ± 0.5% and 42.3 ± 0.3% for gray birch (inflorescences, $t = 7.01$, $P < 0.001$; twigs, $t = 8.29$, two-tailed $P < 0.001$). At Hammond Woods, black birch inflorescences and twigs contained 44.0 ± 2.2% and 42.2 ± 0.9% water by mass, respectively, compared with 38.3 ± 1.9% and 36.5 ± 0.9% in gray birch (inflorescences, $t = 1.97$, $P = 0.064$;

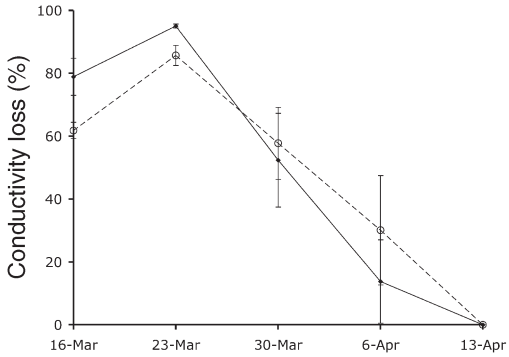

Figure 1. Percent loss of conductance in black birch (*Betula lenta*; ◆, solid line) and gray birch (*B. populifolia*; ○, dashed line) during March and April 2006. Error bars show standard errors.

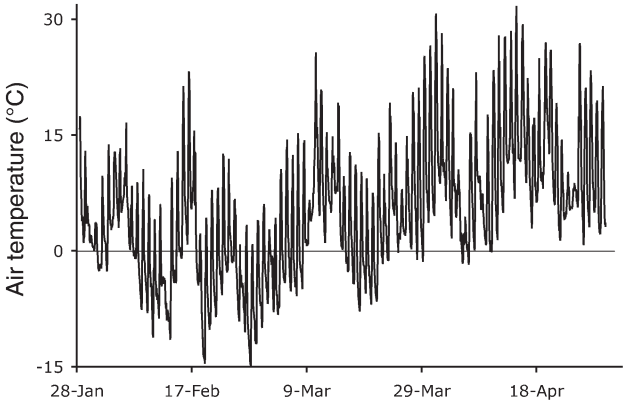

Figure 2. Air temperature during the study measured at 30-min intervals in 2006.

twigs, $t = 4.34$, two-tailed $P < 0.001$).

At both study sites, xylem vessel diameters were significantly greater in twigs of black birch than of gray birch. At the Arnold Arboretum, xylem vessels of black and gray birch had mean diameters of 33.1 ± 0.7 and 28.1 ± 0.5 μm, respectively ($t = 5.48$, two-tailed $P < 0.001$; $n = 120$ for each species). At Hammond Woods, mean diameters for black and gray birch were 30.6 ± 0.6 and 27.5 ± 0.5 μm, respectively ($t = 3.88$, two-tailed $P < 0.001$; $n = 120$ for each species). The distribution of xylem vessel diameters is shown in Figure 3. Because hydraulic conductivity of a vessel is proportional to its diameter to the fourth power (Hagen-Poiseuille relationship), mean hydraulic conductivity of gray birch vessels (27.8 ± 0.4 μm) was thus 59% that of black birch vessels (31.8 ± 0.5 μm).

Temperature-response experiment

In all species, the date of pollen shedding was advanced with increase in temperature (Figure 4). Black and gray birch were among the last birch species to reach anthesis, gray birch flowering earlier than black birch at every temperature. Male inflorescence size had no effect on flowering date at any temperature ($P > 0.12$ for individual regressions within each treatment, and $P = 0.112$ with all treatments considered together). Percent water content of male inflorescences was positively correlated with date of anthesis at all temperatures, but the effect was significant only at 19 °C (as determined by linear regression: 19 °C, $P = 0.032$, $n = 25$; 21 °C, $P = 0.15$, $n = 26$; 11 °C, $P = 0.12$, $n = 24$; 6 °C, $P = 0.48$, $n = 10$; Figure 5). Considering all temperatures in a single regression, with water content and treatments as independent variables, water content had a significant effect on days to flowering ($r^2 = 0.64$, $P = 0.004$). There was no statistically significant effect of temperature on the relationship between water content and days to flowering ($P > 0.48$ for each interaction term).

Discussion

We identified differences in the behavior of black birch and gray birch during the winter that are likely related to the response of flowering date to climate. Frost kill of male inflorescences was greater in black birch than in gray birch. Frost kill reduces the number of male inflorescences during particularly cold winters, which may explain the delay in date of first flowering in black birch, simply because a reduction in the number of inflorescences narrows the range of flowering times. Such an effect of population size has been observed in a study of flowering times in other plant species (Miller-Rushing and Primack, unpublished data), and in studies of bird migration dates (Sparks et al. 2001, Tryjanowski and Sparks 2001). Freezing damage to inflorescences may be correlated with damage to twigs or other tree tissues that may delay flowering by, for example, limiting water movement.

The freezing-induced mortality we observed may have been caused by ice formation in flower tissues or by xylem embolisms, resulting in desiccation. Water contents of male inflo-

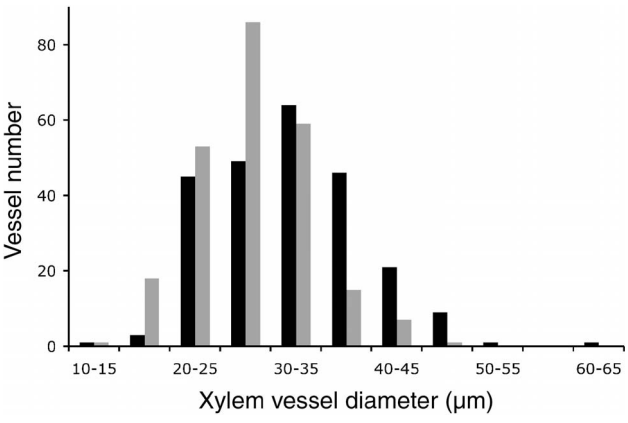

Figure 3. Distribution of xylem vessel diameters in black birch (*Betula lenta*; black bars) and gray birch (*B. populifolia*; gray bars) populations at the Arnold Arboretum and Hammond Woods. We measured 12 vessels × 2 twigs × 5 trees × 2 sites, for a total of 240 vessels per species.

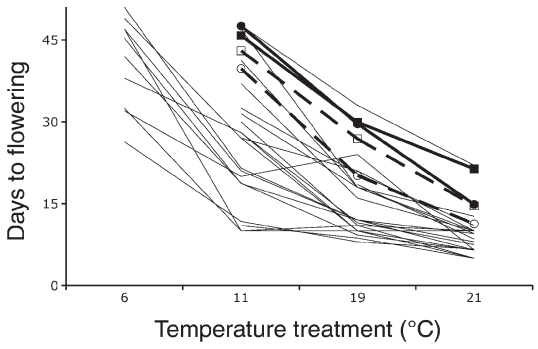

Figure 4. Effect of temperature treatment on number of days to flowering for male inflorescences of 24 species of birch (*Betula*). Results for black birch (*B. lenta*; ●, ■, solid lines) and gray birch (*B. populifolia*; ○, □, dashed lines) are highlighted. Circles and squares denote populations growing at Arnold Arboretum and at Hammond Woods, respectively. Other birch species are shown as thin solid lines. Several species did not flower in the 6 °C treatment.

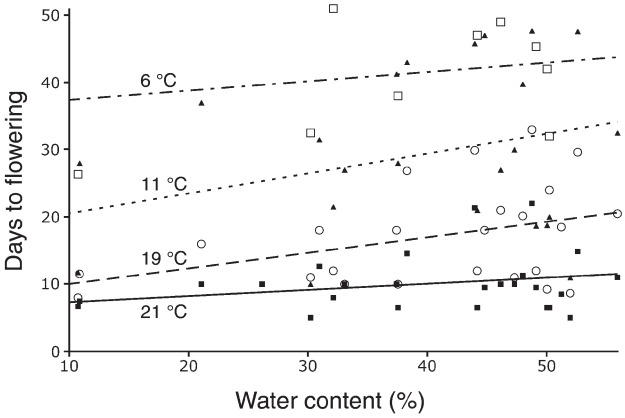

Figure 5. Effect of temperature treatment on the relationship between percent water content of male inflorescences and days to flowering in 24 species of birch (*Betula*). The relationship was significant only in the 19 °C treatment ($r^2 = 0.19$, $P = 0.032$; ○, dashed line). Other treatments: 21 °C = ■, solid line; 11 °C = ▲, dotted line; and 6 °C = □, dot-dashed line.

rescences were higher in black birch than in gray birch, which might have increased their susceptibility to ice formation. Low bud water content has been shown to protect against freezing damage in various species (Weiser 1970), including birches (Rinne et al. 1994, Welling et al. 1997). Comparisons among species show that those with low bud water contents tend to have the greatest cold hardiness (Kadir and Proebsting 1994). Black birch had a higher incidence of twig xylem cavitation than gray birch, likely reflecting greater xylem vessel diameter in black birch than in gray birch (Figure 3). Vessel diameter is related to freeze–thaw cavitation during the winter (Davis et al. 1999). Davis et al. (1999) found that quite small differences in vessel diameter (5–45 μm) lead to large differences in susceptibility to freeze–thaw cavitation. Complete loss of conductivity during the winter might have caused the observed inflorescence and twig mortality through tissue desiccation.

Additional mechanisms that could underlie the observed effect of winter temperatures on flowering time in black birch trees may involve cavitation, root or phloem damage or the production or translocation of signaling compounds. Xylem cavitation may impede water transport sufficiently to affect flowering time. However, root pressure apparently restored xylem conductivity in both species before the onset of flowering. Strati et al. (2003) also observed that birches growing in Scotland restore xylem conductivity after overwinter cavitation through the development of root pressure.

Root damage may be responsible, at least in part, for effects of winter temperatures on flowering times. Many birch species have shallow root systems, which are thus affected by soil freezing when there is no snow pack (Cox and Zhu 2003). The soil depth was shallow at both study sites, and there was no snow pack for most days during the winter. In yellow birch (*Betula alleghaniensis* Britt.), root damage is indicated by reduced root pressure and a lack of full recovery from embolism (Zhu et al. 2000, Cox and Zhu 2003). However, in our study, both black and gray birches developed root pressure and achieved full recovery from xylem embolism before the onset of flowering, indicating that root damage was unlikely to have affected flowering times in either species.

Interspecific differences in flowering-related hormones, enzymatic activities or other signaling compounds may contribute to the difference between black and gray birch in flowering responses to winter temperature. The role of biochemical signals in sensing winter temperatures and determining flowering time is increasingly well documented in herbaceous plants such as *Arabidopsis* (Bernier et al. 1993, Henderson and Dean 2004, Kim et al. 2004, Sung and Amasino 2004); however, it is less well understood in woody plants (Arora et al. 2003). Freezing damage to the phloem may influence flowering times, because several signaling compounds and carbohydrates required for flowering are transported by the phloem (Corbesier and Coupland 2006).

One implication of our results is that more black birch inflorescences will survive the winter if winter temperatures continue to warm, leading to an increased duration of flowering. As a result, the overlap in the flowering times of black birch and gray birch may increase, even if the mean dates of flowering do not change.

The high incidence of frost kill of flowers and branches may limit the northern range of black birch, as it does for many other species (Prentice et al. 1992). If winters warm in the Northern Hemisphere, the ranges of these species may expand northward. Individuals at the northern edge of the range may reproduce more prolifically in years following warm winters; although, warmer winters could lead to increased mortality in some northern species by increasing freezing damage and the number of freeze–thaw cycles that cause cavitation (Zhu et al. 2000, Cox and Zhu 2003). The migration of tree populations will also depend on seed germination and seedling survival, which are highly temperature-dependent.

In conclusion, our results suggest that in cold years, mortality of male inflorescences delays first flowering in black birch. Other mechanisms, such as freezing effects on the supply of signaling compounds or phloem function, may also contribute to effects of winter temperatures on flowering dates. In contrast, gray birch experiences little male flower mortality and shows no dependence of first flowering date on winter temperature. We have identified freezing-induced cavitation as a possible mechanism for freezing mortality in black birch male inflorescences, although ice formation in flower buds or other mechanisms may also have caused, or contributed to, the observed mortality.

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References

Arora, R., L.J. Rowland and K. Tanino. 2003. Induction and release of bud dormancy in woody perennials: a science comes of age. HortScience 38:911–921.

Atkinson, C.J., M.A. Else, L. Taylor and C.J. Dover. 2003. Root and stem hydraulic conductivity as determinants of growth and potential in grafted trees of apple (*Malus pumila* Mill.). J. Exp. Biol. 54:1221–1229.

Bernier, G., A. Havelange, C. Houssa, A. Petitjean and P. Lejeune. 1993. Physiological signals that induce flowering. Plant Cell 5: 1147–1155.

Both, C., S. Bouwhuis, C.M. Lessells and M.E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81–83.

Cannell, M.G.R. and R.I. Smith. 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. J. Appl. Ecol. 20: 951–963.

Cobb, A.R., B. Choat and N.M. Holbrook. 2007. Dynamics of freeze–thaw embolism in *Smilax rotundifolia*. Am. J. Bot. 94: 640–649.

Corbesier, L. and G. Coupland. 2006. The quest for florigen: a review of recent progress. J. Exp. Biol. 57:3395–3403.

Cox, R.M. and X.B. Zhu. 2003. Effects of simulated thaw on xylem cavitation, residual embolism, spring dieback and shoot growth in yellow birch. Tree Physiol. 23:615–624.

Davis, S.D., J.S. Sperry and U.G. Hacke. 1999. The relationship between xylem conduit diameter and cavitation caused by freezing. Am. J. Bot. 86:1367–1372.

Fitter, A.H., R.S.R. Fitter, I.T.B. Harris and M.H. Williamson. 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. Funct. Ecol. 9:55–60.

Gross, R.S. and P.A. Werner. 1983. Relationships among flowering phenology, insect visitors and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). Ecol. Monogr. 53:95–117.

Henderson, I.R. and C. Dean. 2004. Control of *Arabidopsis* flowering: the chill before the bloom. Development 131:3829–3838.

Hendry, A.P. and T. Day. 2005. Population structure attributable to reproductive time: isolation by time and adaptation by time. Mol. Ecol. 14:901–916.

Kadir, S.A. and E.L. Proebsting. 1994. Various freezing strategies of flower-bud hardiness in *Prunus*. J. Am. Soc. Hortic. Sci. 119: 584–588.

Kim, H.-J., Y. Hyun, J.-Y. Park et al. 2004. A genetic link between cold responses and flowering time through *FVE* in *Arabidopsis thaliana*. Nature Genet. 36:167–171.

Kudo, G., Y. Nishikawa, T. Kasagi and S. Kosuge. 2004. Does seed production of spring ephemerals decrease when spring comes early? Ecol. Res. 19:255–259.

Miller-Rushing, A.J. and R.B. Primack. 2008. Global warming and flowering times in Thoreau's Concord: a community perspective. Ecology. In press.

Miller-Rushing, A.J., T. Katsuki, R.B. Primack, Y. Ishii, S.D. Lee, and H. Higuchi. 2007. Impact of global warming on a group of related species and their hybrids: cherry tree (Rosaceae) flowering at Mt. Takao, Japan. Am. J. Bot. 94:1470–1478.

Murray, M.B., M.G.R. Cannell and R.I. Smith. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. J. Appl. Ecol. 26:693–700.

Myking, T. and O.M. Heide. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. Tree Physiol. 15:697–704.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Perry, T.O. 1971. Dormancy of trees in winter. Science 171:29–36.

Prentice, I.C., W. Cramer, S.P. Harrison, R. Leemans, R.A. Monserud and A.M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. J. Biogeogr. 19:117–134.

Rinne, P., H. Tuominen and O. Junttila. 1994. Seasonal changes in bud dormancy in relation to bud morphology, water and starch content, and abscisic acid concentration in adult trees of *Betula pubescens*. Tree Physiol. 14:549–561.

Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Samish, R.M. 1954. Dormancy in woody plants. Ann. Rev. Plant Physiol. 5:183–204.

Smallwood, M. and D.J. Bowles. 2002. Plants in a cold climate. Phil. Trans. R. Soc. B 357:831–847.

Sparks, T.H., D.R. Roberts and H.Q.P. Crick. 2001. What is the value of first arrival dates of spring migrants in phenology? Avian Ecol. Behav. 7:75–85.

Sperry, J.S., J.R. Donnelly and M.T. Tyree. 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ. 11:35–40.

Strati, S., S. Patiño, C. Slidders, E.P. Cundall and M. Mencuccini. 2003. Development and recovery from winter embolism in silver birch: seasonal patterns and relationships with the phenological cycle in oceanic Scotland. Tree Physiol. 23:663–673.

Sung, S. and R.M. Amasino. 2004. Vernalization and epigenetics: how plants remember winter. Curr. Opin. Plant Biol. 7:4–10.

Tryjanowski, P. and T.H. Sparks. 2001. Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*. Int. J. Biometeorol. 45:217–219.

Wang, J., N.E. Ives and M.J. Lechowicz. 1992. The relation of foliar phenology to xylem embolism in trees. Funct. Ecol. 6:469–475.

Webb, C.O. 2000. Exploring the phylogenetic structure of ecological communities: an example from rain forest trees. Am. Nat. 156: 145–155.

Weiser, C.J. 1970. Cold resistance and injury in woody plants. Science 169:1269–1278.

Welling, A., P. Kaikuranta and P. Rinne. 1997. Photoperiodic induction of dormancy and freezing tolerance in *Betula pubescens*. Involvement of ABA and dehydrins. Physiol. Plant. 100:119–125.

Williams, C.B. 1947. The generic relations of species in small ecological communities. J. Anim. Ecol. 16:11–18.

Zhu, X.B., R.M. Cox and P.A. Arp. 2000. Effects of xylem cavitation and freezing injury on dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw. Tree Physiol. 20: 541–547.

Zwieniecki, M.A., P.J. Melcher and N.M. Holbrook. 2001. Hydrogel control of xylem hydraulic resistance in plants. Science 291: 1059–1062.