Variation in responsiveness of woody plant leaf out phenology to anomalous spring onset

ROBERT T. FAHEY†,[1]

Department of Research, The Morton Arboretum, 4100 Illinois Route 53, Lisle, IL 60532 USA

Abstract. Timing of leaf out in woody plants is being affected by global climate change, with cascading effects on associated organisms and ecosystem processes. However, the timing and responsiveness of this important phenological event are not well understood, especially in relation to the geographic origin of species and populations. This study assessed the effect of anomalous spring warming on leaf out timing for woody plant species and individuals from a range of taxa and geographic origins. Timing of leaf out was assessed across 4 years (2011–2014) for 478 plants, representing 96 species and 21 genera, planted together in a common environment at The Morton Arboretum, Lisle, Illinois, USA. An anomalously warm spring in 2012 strongly affected leaf out timing, advancing mean leaf out date for every species by an average of 31 days across all individuals. Responsiveness was related to species traits, as species classified as early-successional, with diffuse-porous wood anatomy, or with a weak chilling requirement were much more responsive. There was strong variation among individuals within a species in leaf out timing and responsiveness. These patterns were somewhat related to geographical origin of the individual, but were not consistent among species or genera. High responsiveness of leaf out to anomalous spring warming, which is forecasted to be more common with global climate change, could have important implications for climate change adaptation, assisted migration, and ecological interactions. Chilling requirements may have limited responsiveness for some species, which could affect competitive dynamics within plant communities. Through such interactions and direct effects on woody plant species, variation in spring leaf out phenology will likely affect biodiversity and functioning in many ecosystems.

[1] Present address: Department of Natural Resources and the Environment and Center for Environmental Science and Engineering, University of Connecticut, Storrs, CT 06279 USA.

†E-mail: rfahey@mortonarb.org

INTRODUCTION

Global climate change is predicted to have significant impacts on the timing of plant phenological events, including leaf development (Cleland et al. 2007, Körner and Basler 2010, Polgar and Primack 2011). These shifts will strongly affect the plants themselves as well as competitive dynamics among species (Wolkovich and Cleland 2010). For example, alteration of leaf out timing in trees could result in damage to leaves (through freezing) or branches (through snow or ice loading) leading to reductions in productivity in the short term (Augspurger 2013). However, growing season extension could increase productivity for many species and would likely alter competitive relationships in the longer term (Cleland et al. 2012). Changes in the timing of leaf out could also have cascading effects on ecosystems and landscapes (Walther et al. 2002, Polgar and Primack 2011). For example, mismatches of leaf unfolding and maturation with timing of insect

herbivore emergence could lead to reduced populations or changes to emergence patterns, both of which could affect this key food source used by migratory birds (van Asch and Visser 2007).

Although the effects of plant phenological response to climate change are likely to be significant, much is still unknown about how species and populations are likely to respond (Körner and Basler 2010). One specific change in climate that will likely have an especially strong effect on phenology is alteration of the timing and pattern of spring warming (Polgar and Primack 2011). This change will likely take the form of earlier spring warming and greater variation among years in timing of spring warming (Schwartz et al. 2006). For example, in eastern North America the spring of 2012 was especially early and warm relative to historical patterns (Ellwood et al. 2013). Such early spring warming followed by a return to cold temperatures could cause widespread damage to vegetation (Augspurger 2013). The frequency of such anomalous events is predicted to increase in the future (Schwartz et al. 2006) and the responsiveness of leaf out in plants to such events is likely to be an important part of their overall response to climate change.

The timing of leaf out in woody plants is highly variable among taxa (Panchen et al. 2014) and also appears to vary among populations within species based on the climatic associations of the populations (Vitasse et al. 2009a). Leaf out timing can also vary greatly from year to year and has been shown to have changed greatly as a result of changes in local climate (Polgar et al. 2014). Leaf out in plants is driven by a combination of chilling requirement to break dormancy, heat accumulation in spring (forcing), and photoperiod (day length relative to night). Recent work has indicated that species vary greatly in the way in which these factors combine to prompt the onset of leaf out (Laube et al. 2014, Polgar et al. 2014, Zohner and Renner 2014). Some species require very long chilling periods or specific photoperiod conditions to be met before they can be forced into leaf out by warm temperatures. Both requirements are likely adaptations to limit the potential for damage during anomalous spring warming. Differences among species in the importance of these cues are not likely to be straightforward, but there is some evidence that

long-lived, late-successional species often have higher chilling requirements than pioneer species (Caffarra and Donnelly 2011) and that species with diffuse-porous wood anatomy leaf out earlier than ring-porous species (Panchen et al. 2014). Leaf out date has also been shown to vary among individuals from different climates when planted in a common garden, suggesting a variable role for these cues among populations (Vitasse et al. 2009b).

In order to study variation in leaf out timing and responsiveness among species and populations individual plants must be subjected to a common environment. Experimental research can be used to create specific environmental conditions, but is very difficult to conduct with mature woody plants. Therefore, most studies focus on young plants (e.g., Vitasse et al. 2013) or cuttings from mature trees (e.g., Caffarra and Donnelly 2011, Polgar et al. 2014), which may be more representative of mature trees than seedlings (Vitasse and Basler 2014). Provenance trials have been used to assess within-species variation in phenology (Chmura and Rozkowski 2002), but are difficult to conduct with more than a few target species. Common garden studies are another useful avenue (Alberto et al. 2011), but take a long time to establish for tree species, although some studies have focused on seedlings (Vitasse et al. 2013). Arboretum collections offer a chance to study tree phenology on a wide variety of species in a mature common garden structure (Primack and Miller-Rushing 2009, Panchen et al. 2014, Zohner and Renner 2014). In addition, some collections often have detailed accession and provenance information for individuals that can be used to study within-species variation in phenology (Primack and Miller-Rushing 2009).

In this study, the extensive collections of The Morton Arboretum were used as a common garden to study the phenology of a broad range of woody plant species, both natives to eastern North America and nonnative species from Asia and Europe, planted together in a common environment. The data set included multiple individuals across a large number of species, and many individuals had information on the geographic location of their collection from wild populations. This information allowed for the study of variation in leaf out among individuals within a species in relation to source population location

and climate (Van Dijk et al. 1997, Olsson and Ågren 2002). The phenological data set included the highly anomalous 2012 spring (Ellwood et al. 2013), which allowed testing of phenological responsiveness outside of a manipulative experiment.

The primary objective of this study was to assess how woody plant leaf out timing and responsiveness to variation in the pattern of spring warming vary with latitudinal and climatic origins of species and individuals. I hypothesized that species with more southern native ranges would not only have later leaf out dates due to greater heat-sums required for stimulation of leaf out (Zohner and Renner 2014) but also be more responsive to early onset of spring warming. Similarly, within species I expected that individuals accessioned from more southern areas within a species' range would leaf out later, but be more responsive to early onset of spring conditions (Clark et al. 2014). Support for these expectations could either indicate a greater effect of chilling requirements on leaf out timing in northern species and individuals, or the greater impact of forcing relative to photoperiod as a driver of leaf out timing (Laube et al. 2014). I also hypothesized that species categorized as late-successional, ring-porous, and having strong chilling requirements would be less responsive to early spring onset (Caffarra and Donnelly 2011, Polgar et al. 2014).

Materials and Methods

Study location and data sets

The study was conducted on the grounds of The Morton Arboretum, in Lisle, IL, in the western part of the Chicago metropolitan region (41.8127°, −88.0727°). Mean temperatures in the area range between −5.3°C in January and 22.3°C in July (Angel 2011). Meteorological records are collected on-site for the NOAA National Climatic Data Center Global Historical Climatology Network (http://www.ncdc.noaa.gov/). To evaluate variation in heat accumulation among years, daily temperature data collected at this station were used to calculate Growing Degree Accumulation Base 30 (hereafter "GDD")—the cumulative number of degrees above 30°F (−1°C) for average daily temperature—for each date from 2005 to 2014 (Fig. 1a). In addition, to assess variation in

chilling among years the total number of days with average temperature below 41°F (5°C) was recorded for the period November 1 to April 30 for the winters of 2010–2011 through 2013–2014 (Fig. 1b).

This study focused on the Morton collections, which house over 222,000 live accessioned plants. Leaf out status was recorded weekly by research assistants in the Morton Arboretum Forest Ecology Lab from mid-March until leaf out was complete. The full data set included 479 individuals across 96 species and 21 genera (see Appendix A for full list). For leaf out data collection, field assistants randomly selected three branches on each plant and recorded percentage leaf out (defined as having young leaves unfolding or expanding with their final shape at least partially visible; Panchen et al. 2014).

For each eastern North American species in the data set, the latitude of the species' current range center, northern limit, and southern limit were estimated using data from the Climate Change Tree Atlas (USFS 2014). I determined whether each plant was wild collected based on information recorded in the Morton Arboretum Plants Database (http://quercus.mortonarb.org/). Accession location was recorded for plants that were wild collected and had a specific collection location noted (at least county of origin). Accession location latitude was then used to calculate the latitudinal difference between the accession location and the species range center (hereafter "latitude difference"). In addition, for each accession location I calculated mean temperature (annual, 5 months: January–May, 3 months: March–May) using PRISM gridded climate data (4-km resolution; http://www.prism.oregonstate.edu/). Species range and accession information is included in Appendix B.

Species with existing information on leaf out requirements were classified into chilling requirement groups (mild, moderate, strong) based on data from experimental manipulations in the literature (Basler and Körner 2012, Laube et al. 2014, Polgar et al. 2014, Zohner and Renner 2014). Also, species were classified into successional strategy groups (early, mid, late) and wood anatomy groups (ring, semiring, and diffuse porous; Panchen et al. 2014) based on information from general sources (Walters and
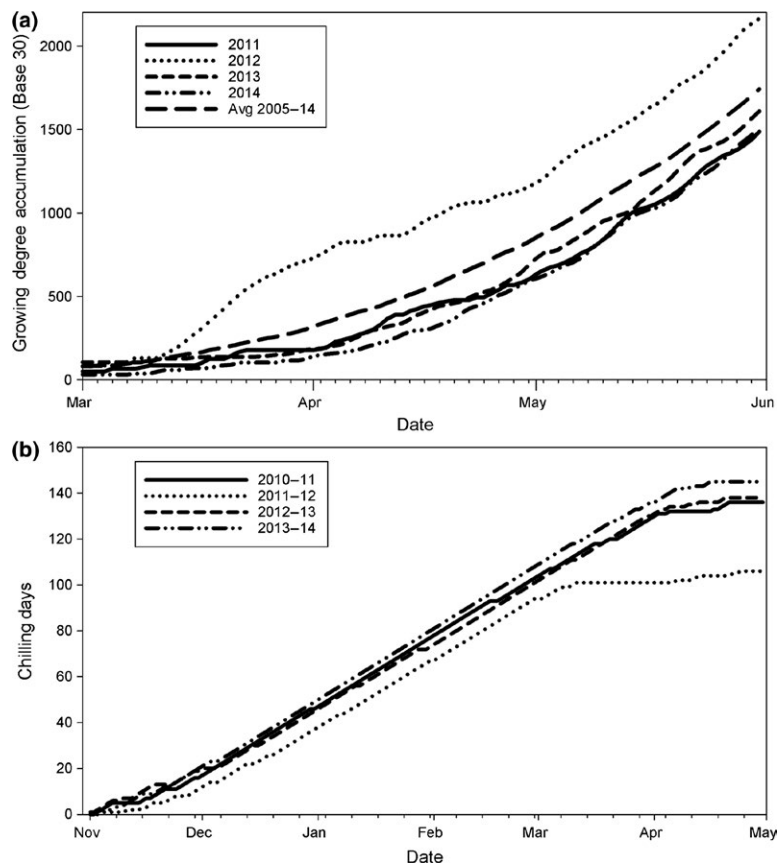
Fig. 1. Pattern of (a) growing degree accumulation (the cumulative number of degrees above 30°F (−1°C) for average daily temperature) over the period from March 1 to June 1 for 2005–2014 and (b) chilling days (cumulative number of days with average temperature <41°F, 5°C) from November 1 to April 30 for 2010 through 2014 at The Morton Arboretum from on-site climatological data.

Yawney 2004). Chilling requirement, succession-al, and wood anatomy group membership for all species are included in Appendix C.

Data analysis

Leaf out date for each individual in each year was defined as the date at which ≥50% of leaves were recorded as having begun to unfold (O'Keefe 2000). Dates were converted to ordinal scale and the mean leaf out date was calculated for each species and genus for each year and for all years combined (Table 1). There was a very large difference in warming pattern in 2012 relative to 2011, 2013, and 2014 (which were near average for the previous decade; Fig. 1). Therefore, leaf out responsiveness to temperature differences was evaluated as the difference between 2012 leaf out date and the mean date for 2011/2013/2014 (hereafter "2012 leaf out response") and also difference in GDD accumulation on the date of leaf out (hereafter "2012 GDD response"; Table 1). Differences in leaf out date and GDD at leaf out among years were tested for using Kruskal–Wallis one-way analysis of variance (ANOVA) on ranks (due to unequal variance among years) in Sigmaplot v. 13 (SYSTAT 2014). Standard one-way ANOVA was used to test for differences in leaf out date, 2012 leaf out response, and 2012 GDD response among species (with $n \geq 5$ individuals; total of 34 species), genera (with $n \geq 20$ individuals; total of 5 genera), leaf out requirement groups, wood anatomy groups, and successional categories. Individual group comparisons were made using the Holm–Sidak multiple comparison adjustment.

Table 1. Mean leaf out dates and difference in 2012 from mean date and growing degree day accumulation for the average years (2011, 2013, and 2014) for species (with *n* > 5), genera (with *n* > 20) and functional groups.

Genus/Species/Group	Count	Mean leaf out date†				2012 response	
		2011	2012	2013	2014	Days	GDD‡
Acer	22		107.2	122.0	130.5	19.0	151
Carya	25	125.0	111.9	131.8	134.4	18.7	116
Celtis	23		96.0	128.7	131.3	34.2	−114
Juglans	32	123.9	96.2	130.3	128.8	31.7	−80
Quercus	242	120.3	98.6	126.3	136.5	29.4	−105
Acer nigrum	8		114.5	124.5	132.9	14.2	215
Acer saccharum	8		110.3	120.0	132.9	16.2	194
Aesculus glabra	6		81.5	116.8	118.7	36.3	−74
Betula alleghaniensis	6		110.8	133.3	139.3	25.5	−47
Carya illinoinensis	13	130.5	101.8	134.0	136.8	32.0	−125
Carya ovata	5	113.8	126.2	131.2	133.8	0.1	434
Celtis laevigata	5		82.4	127.6	129.4	46.1	−318
Celtis occidentalis	13		96.3	130.8	129.6	34.4	−122
Celtis tenuifolia	5		109.0	124.2	137.2	21.7	114
Cercis canadensis	17		85.6	131.8	140.0	50.3	−460
Crataegus mollis	5		92.2	122.0	132.0	34.8	−103
Diospyros virginiana	5		100.6	130.4	140.5	33.5	−115
Gymnocladus dioicus	11		92.8	131.7	138.4	42.1	−231
Juglans ailantifolia	6	123.8	99.5	132.8	129.0	29.3	−15
Juglans mandshurica	10	119.6	80.7	125.6	122.0	41.7	−238
Juglans microcarpa	5	124.3	101.4	132.6	135.0	30.2	−81
Juglans nigra	6	128.6	107.0	131.7	131.7	23.6	56
Nyssa sylvatica	6		119.5	134.2	141.4	18.5	84
Platanus occidentalis	8		90.3	130.1	133.0	41.3	−205
Ptelea trifoliata	7		100.6	134.0	140.8	36.7	−157
Quercus acutissima	6	117.8	90.5	126.0	145.7	39.3	−369
Quercus alba	8	117.9	98.3	125.0	134.0	27.4	−60
Quercus bicolor	8	114.1	101.1	125.9	134.9	23.8	−40
Quercus ellipsoidalis	6	119.3	87.0	124.7	132.8	38.6	−227
Quercus imbricaria	5	119.7	101.2	125.8	135.4	27.4	−45
Quercus macrocarpa	22	114.8	89.2	125.7	135.9	36.6	−254
Quercus marilandica	9	123.2	96.4	126.0	135.6	31.8	−117
Quercus michauxii	6	121.2	94.3	128.7	142.2	36.3	−277
Quercus mongolica	6	111.5	87.0	126.0	125.8	34.1	−132
Quercus montana	10	122.3	99.4	124.9	136.8	28.6	−89
Quercus muhlenbergii	8	120.3	95.6	124.5	138.4	32.1	−159
Quercus palustris	9	112.1	93.9	124.8	133.2	29.5	−125
Quercus prinoides	9	114.2	108.1	129.1	141.8	20.3	−13
Quercus robur	9	129.4	106.9	126.2	134.0	23.0	66
Quercus rubra	5	121.4	105.6	124.4	132.6	20.5	57
Quercus shumardii	10	120.0	87.4	125.5	134.0	39.1	−257
Quercus stellata	5	121.8	95.6	127.4	141.0	34.5	−196
Quercus variabilis	9	131.0	109.2	129.0	144.9	25.7	−95
Quercus wutaishanica	12	119.0	95.0	125.3	130.5	29.9	−59
Quercus x bebbiana	5	119.8	105.6	126.0	135.4	21.5	22
Quercus x deamii	6	119.8	106.3	126.0	135.2	20.7	53
Quercus x jackiana	6	110.5	98.3	126.0	134.0	25.2	−63
Tilia americana	7		99.7	128.0	131.1	29.9	−17
Mild chilling	8		102.3	125.0	132.0	29.4	−2
Moderate chilling	19	119.2	99.4	124.8	131.2	26.3	−16
Strong chilling	42	126.9	107.8	126.3	132.2	21.2	123

Table 1. Continued.

Genus/Species/Group	Count	Mean leaf out date†				2012 response	
		2011	2012	2013	2014	Days	GDD‡
Early successional	63	119.7	93.7	126.6	135.8	34.5	−173
Mid successional	136	121.1	100.0	127.5	132.8	28.4	−51
Late successional	42	111.5	105.9	126.7	133.6	23.9	46
Diffuse porous	104		95.2	126.8	132.5	34.5	−127
Semi-ring porous	37	123.9	96.8	130.3	130.1	31.9	−87
Ring porous	329	120.7	99.4	127.2	135.9	29.6	−99
Total	479	121.0	98.3	127.4	134.7	30.8	−104

† For reference, ordinal date of 80 = March 21, 91 = April 1, 121 = May 1, and 152 = June 1.
‡ GDD, growing degrees base 30°F.

The relationships between leaf out variables (average overall leaf out date, date in each individual year, average leaf out date in the "average" years, 2012 leaf out date response, and 2012 GDD response) and location variables (species range center latitude, species northern and southern range limit latitude, species range breadth, individual accession latitude, latitude difference, and mean annual and spring temperature at the accession location) were tested using simple linear regression. The relationship of 2012 leaf out response with accession location and latitude difference was also assessed within major genera ($n \geq 20$), and species requirement groups. Where significant linear relationships were found between leaf out response and location variables, analysis of covariance (ANCOVA) was used to test for equality of slopes.

RESULTS

Spring temperatures differed greatly in 2012 relative to the other years in the data set (2011, 2013, and 2014) and the mean for the decade (Fig. 1a). For example, across the entire data set, the average GDD at leaf out for all individuals in all years was 860; this level was reached on April 10, 2012, but not until May 1 on average for the other years in the decade (Fig. 1a). Chilling day accumulation also differed greatly in 2012, plateauing at 106 days in 2012 vs. 140 days in the other years in the data set (Fig. 1b).

Mean leaf out date for all plants was significantly earlier in 2012 than in the more average years of 2011, 2013, or 2014 (April 8 vs. May 1, May 7, and May 15; Fig. 2) and differed significantly
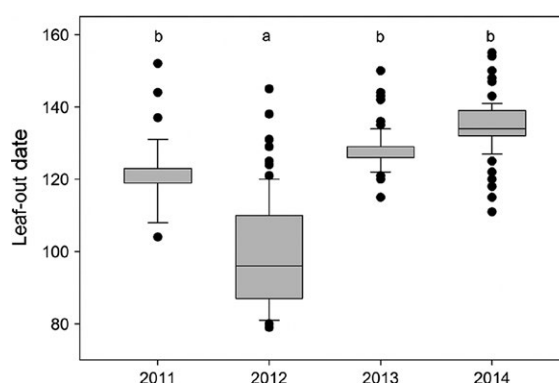

Fig. 2. Comparison of leaf out dates among years across all individuals. Kruskal–Wallis ANOVA indicated differences among years ($H = 1140.1$, df = 3, $P < 0.001$)—pairwise comparisons (with Dunn's multiple comparison method) indicated by letters above bars.

among years (Kruskal–Wallis: $H = 1140.1$, df = 3, $P < 0.001$) and for 2012 vs. all other years following Dunn's adjustment for multiple comparisons: 2011 ($Q = 11.7$, $P < 0.01$), 2013 ($Q = 21.8$, $P < 0.01$), and 2014 ($Q = 32.8$, $P < 0.01$). Leaf out timing across years was not strongly correlated either in terms of date or rank (all $r < 0.35$; Fig. 3a, Appendix D). Leaf out response in 2012 was not correlated with timing of leaf out in average years ($r = 0.08$, $P = 0.416$), illustrating that there was no systematic difference between early and late leafing species in their ability to respond to anomalous spring onset (Fig. 3b). GDD accumulation at leaf out was much lower overall in 2012 than in average years (mean of −104 degrees difference), and differed significantly among years (Kruskal–Wallis: $H = 134.1$, df = 3, $P < 0.001$).
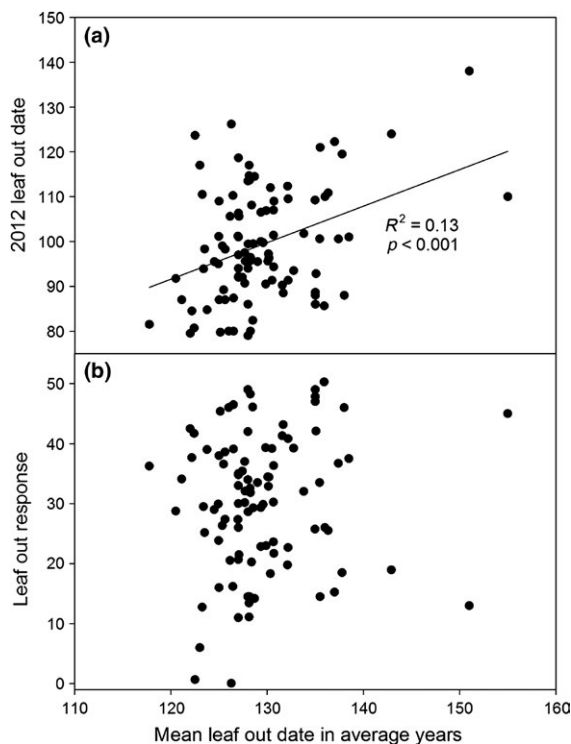
Fig. 3. Relationship of species mean leaf out date in average years (2011, 2013, and 2014) with (a) leaf out date in 2012 and (b) leaf out response in 2012 vs. average years. Leaf out response was not correlated with leaf out date in average years ($r = 0.08$, $P = 0.416$) illustrating the lack of a relationship between leaf out timing and responsiveness in leaf out timing.

Mean leaf out date also differed significantly among major genera (those with ≥20 individuals, $F_{4,333} = 5.58$, $P < 0.001$; Table 1) as did GDD at leaf out ($F_{4,333} = 11.17$, $P < 0.001$). Earliest leaf out occurred for *Celtis* (April 28) and latest for *Carya* (May 5). Leaf out date also differed among species ($F_{82,374} = 8.04$, $P < 0.001$) as did GDD at leaf out ($F_{82,374} = 4.86$, $P < 0.001$). Earliest leaf out (among species with $n ≥ 5$) occurred for *Aesculus glabra* (mean date April 16) and latest for *Nyssa sylvatica* (May 11; Appendix A). Species' mean leaf out date was later for species with strong chilling requirement relative to those with mild or moderate requirement ($F_{3, 113} = 4.54$, $P = 0.005$; Table 1). Mean leaf out date across all years did not differ among successional status categories ($F_{2, 238} = 2.79$, $P = 0.64$; Table 1).

Leaf out response (the difference in leaf out date in 2012 vs. the average for the other 3 years)

varied significantly among genera (with $n ≥ 20$; $F_{4,332} = 8.82$, $P < 0.001$) with *Celtis* and *Juglans* most responsive and *Acer* and *Carya* least responsive overall (Fig. 4a). Leaf out response also differed significantly among species ($F_{82,373} = 5.60$, $P < 0.001$). The most responsive species (with $n > 5$) was *Cercis canadensis* (50.3 days), while *Acer saccharum/nigrum* showed relatively little response (15.2 days; Table 1). Responsiveness varied among chilling requirement groups ($F_{2,61} = 3.22$, $P = 0.040$), but only differed significantly between species with strong vs. mild chilling requirement following adjustment for multiple comparisons (Fig. 4b). Responsiveness also varied among successional groups ($F_{2,238} = 8.46$, $P < 0.001$; Fig. 4c) as early-successional species were significantly more responsive than mid (3.00, $P = 0.006$) or, especially, late-successional species (3.97, $P < 0.001$). Responsiveness varied among wood anatomy types ($F_{2,466} = 5.22$, $P = 0.006$; Fig. 4d) with diffuse-porous species showing more response than ring-porous ($t = 3.19$, $P = 0.005$) species. Both late-successional and strong chilling requirement species leafed out at higher GDD in 2012 than in average years (mean 44 and 129 degrees higher, respectively; Table 1). GDD response differed among successional groups ($F_{2,238} = 11.12$, $P < 0.001$), marginally for chilling requirement ($F_{2,61} = 2.59$, $P = 0.083$), but not wood anatomy ($F_{2,467} = 0.59$, $P = 0.552$).

Across all years there was not a significant relationship between species mean leaf out date and latitude of species range center ($r = -0.24$, Appendix E). However, for the average years (i.e., with 2012 removed), there was a slight negative relationship between leaf out and range center, meaning species with more northern ranges leafed out slightly earlier than more southern species ($r = -0.41$, $P < 0.001$, $n = 62$; Fig. 5a). Although statistically significant, this was a relatively weak relationship and there was no significant difference in slope among years (ANCOVA; $F = 1.52$, $P = 0.211$). There was no relationship between individual accession location and leaf out date (Fig. 5b). There was a weak positive relationship between latitude difference and leaf out date, (i.e., individuals accessioned from more northern locations with a species' range leafed out slightly later than those from southern parts of the range) for average years ($r = 0.22$, $P < 0.001$, $n = 246$; Fig. 5c), but not for 2012. There was not a
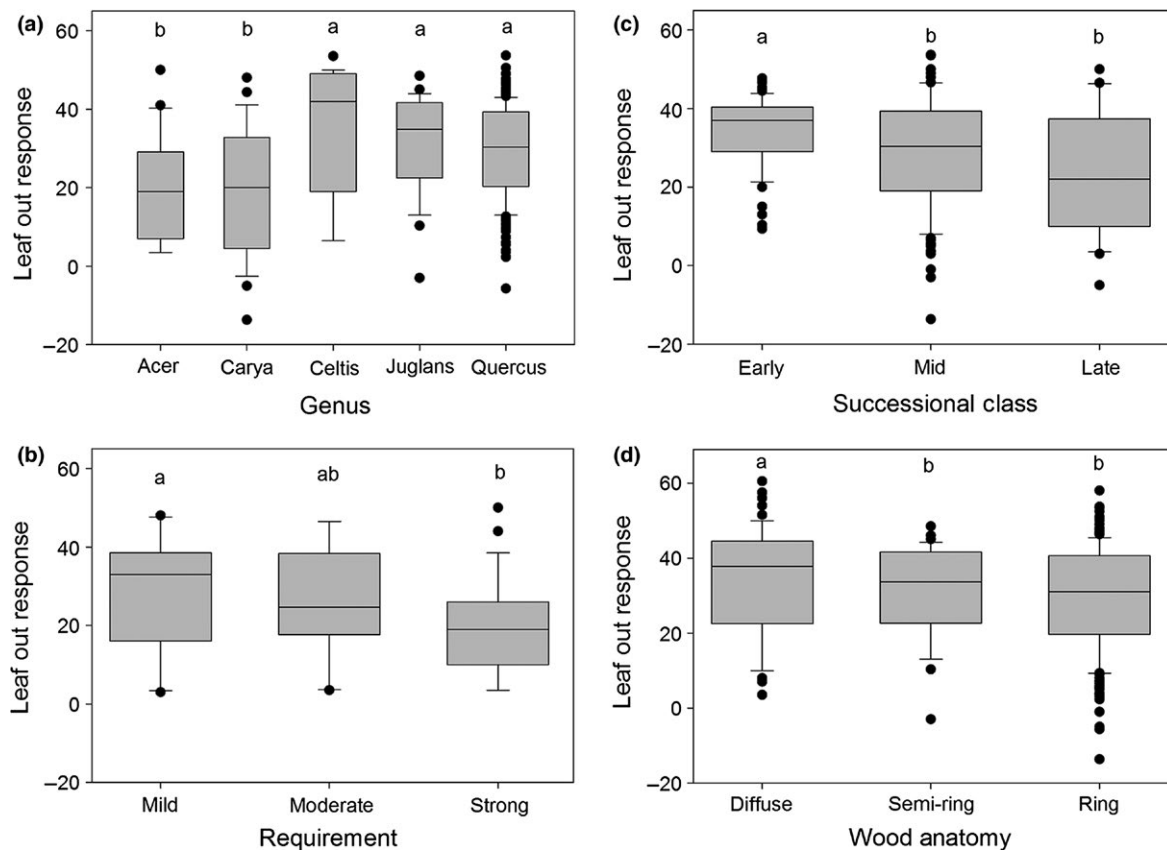
Fig. 4. Leaf out response (difference in leaf out date in 2012 from mean for 2011/2013/2014) for (a) all genera with at least 20 individuals (ANOVA: $F_{4,332}$ = 8.82, $P < 0.001$), (b) chilling requirement categories ($F_{2,61}$ = 3.22, P = 0.040), (c) successional categories ($F_{2,238}$ = 8.46, $P < 0.001$), and (d) wood anatomy groups ($F_{2,466}$ = 5.22, P = 0.006). Results of pairwise comparisons (with Holm–Sidak multiple comparison method) indicated by letters above bars.

significant difference among years in the slope of this relationship (ANCOVA; F = 1.95, P = 0.120). No other aspects of species range or individual accession locations were strongly related to leaf out date for all years together (all $r < 0.25$, $P > 0.05$), but accession latitude, northern range limit, southern range limit, and mean temperature at accession location were all somewhat related to leaf out date in average years (all $r > 0.25$, $P < 0.05$; Appendix E).

There was no significant overall relationship between 2012 leaf out response or GDD response and species range center, individual accession location, or latitude difference (all $r < 0.2$, $P > 0.05$; Appendix E). However, there were some strong within-genus relationships. Individuals from more northern locations were much less

responsive in *Acer* and *Carya* (Fig. 6a, b), while there was no significant relationship for the other genera (all $P > 0.1$). Individuals that were accessioned from areas north of their species range center were more responsive in *Celtis* and *Carya*, but less responsive in *Acer* (Appendix A). There was no significant relationship for *Quercus* or *Juglans* ($P > 0.1$). This relationship also varied greatly among species, both in direction and strength (Appendix A), and was most positive (northern individuals more responsive) for *Quercus bicolor* (r = 0.82, $P < 0.01$, n = 8) and most negative (southern individuals more responsive) for *Betula alleghaniensis* (r = −0.89, $P < 0.01$, n = 6). The relationship between leaf out responsiveness and accession latitude also varied among chilling requirement groups (Fig. 7). For species with mild
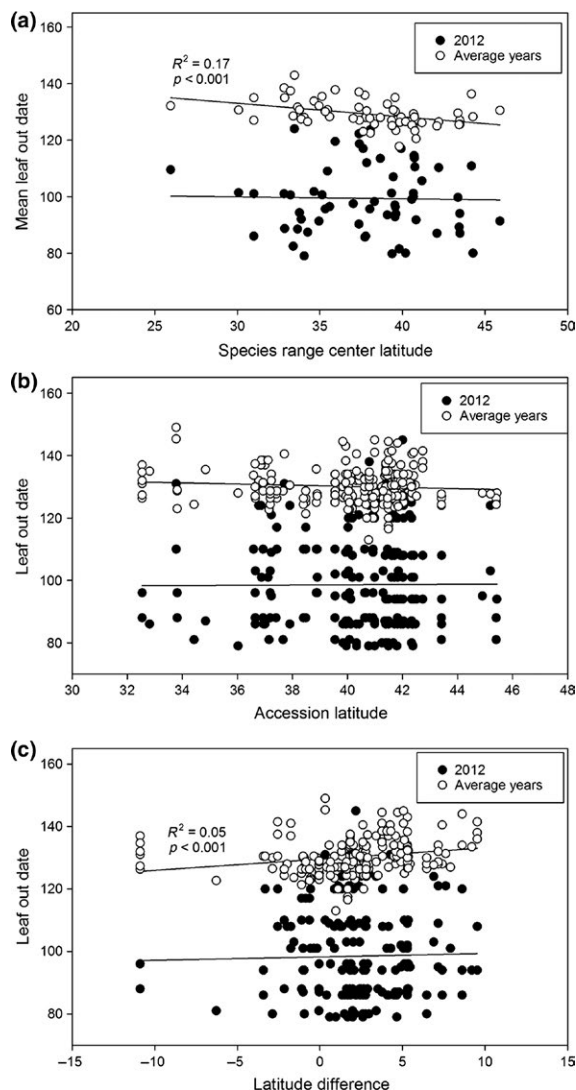
Fig. 5. Relationship of leaf out date for each year (2011, 2012, 2013, and 2014) with (a) latitude of species range center, (b) accession location for individual trees, and (c) latitude difference (difference between individual tree accession location and range center for the species).

chilling requirement, responsiveness was greater in northern individuals ($r = 0.71$, $P = 0.02$, $n = 8$), for those with moderate requirement, there was not a significant relationship, and for those with a strong requirement, southern individuals were more responsive ($r = -0.69$, $P = 0.01$, $n = 14$). Slopes of this relationship were found to be significantly different among chilling requirement groups (ANCOVA; $F = 3.54$, $P = 0.021$).

DISCUSSION

Anomalous spring warming had a very strong impact on leaf out phenology across a large suite of woody plant species. Mean leaf out date in 2012 was advanced approximately 31 days across all individuals, and every species in the data set showed a positive response to early spring warming. As a result of this advancement, the mean leaf out date in 2012 for all but two species was earlier than the beginning of the entire leaf out period (i.e., the date on which the first plant leafed out) in an average year. These findings support previous results indicating that phenology can be highly responsive to early onset of spring warming (Ellwood et al. 2013). However, the magnitude and universality of the response was somewhat surprising, as many studies have indicated a lack of responsiveness of phenology due to unmet chilling or photoperiod requirements (Körner and Basler 2010, Polgar and Primack 2011, Way and Montgomery 2014). The results of this study indicate that extreme spring warming may overcome such limitations in many woody plants, which could have important implications for projecting their response to climate change (Körner and Basler 2010). To further illustrate the extremity of the response, in 2012 all individuals of *Cercis canadensis* (the most responsive species) had leafed out by April 4, while in the other years the earliest leaf out date for any individual was May 7 and the earliest initial budbreak did not occur until April 24.

However, there was also high variability among genera and species in leaf out timing and responsiveness to anomalous spring warming. The primary genera that were included in the study varied in their timing as well as in responsiveness, with *Acer* and *Carya* showing less response than the other major genera (*Quercus*, *Celtis*, and *Juglans*). There was also strong variation among species within most genera, for example in *Quercus* mean leaf out response was 29.4 days, but varied between 6 days for *Q. coccinea* and 47 days for *Q. phellos*. Variation in leaf out timing among species was somewhat related to species origin (in terms of latitude of range center); with northern species leafing out slightly earlier on average than southern species. These
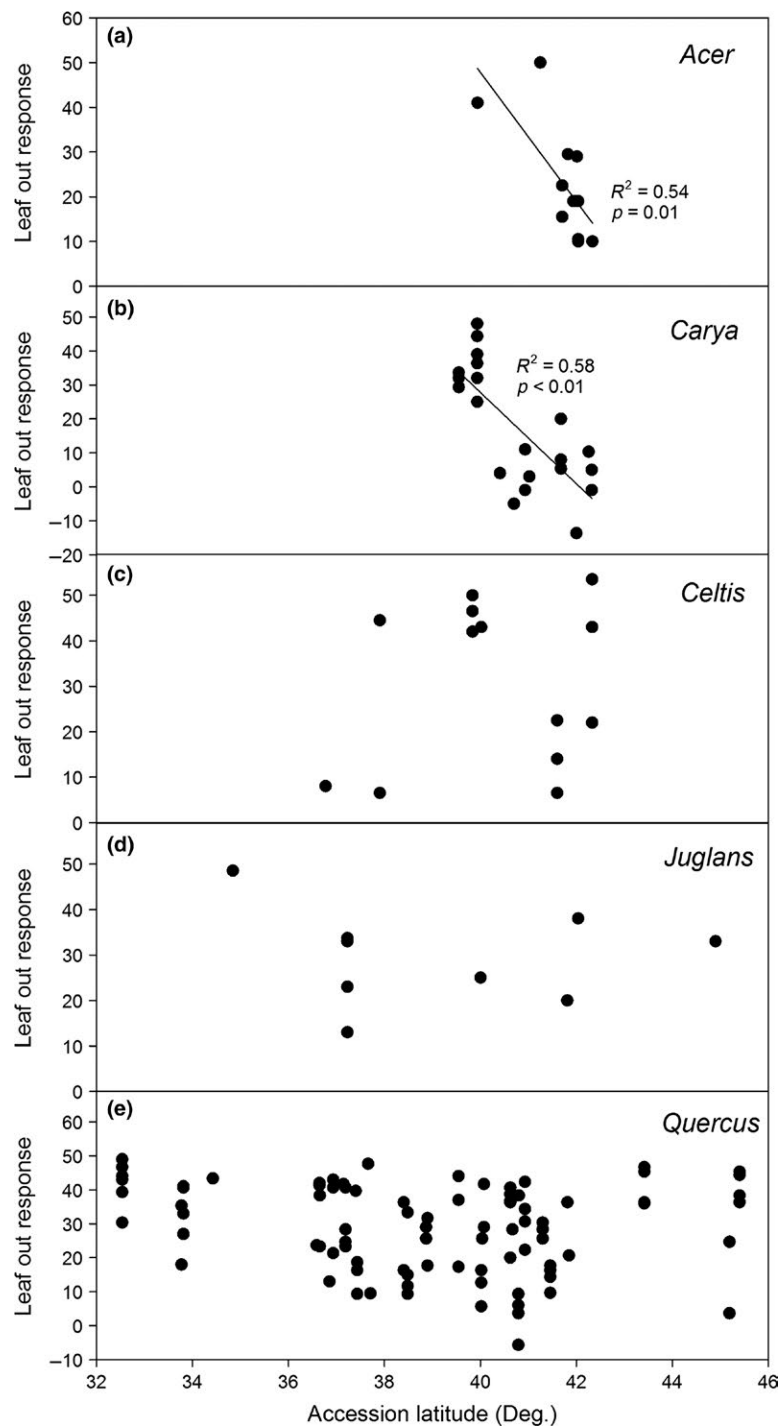
Fig. 6. Leaf out response (difference in leaf out date in 2012 from mean for 2011/2013/2014) for five most common genera (all with n > 20) vs. individual tree accession location with individual regression results (where significant).

findings indicate some role of species origin in the timing of leaf out, matching results of other work (Zohner and Renner 2014), but this effect was not consistent across genera. Responsiveness to anomalous spring warming was not strongly related to species range characteristics.
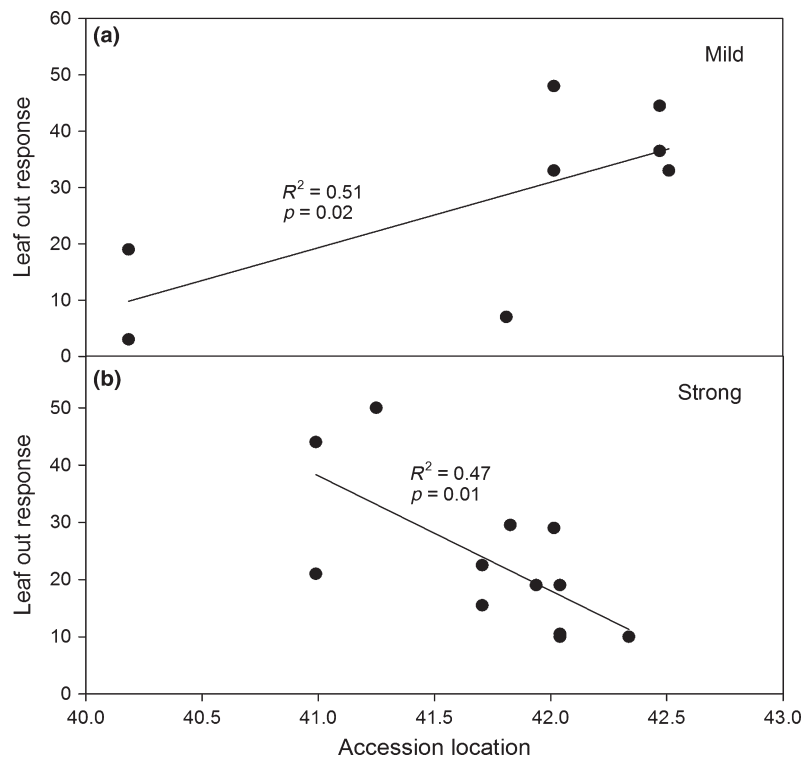
Fig. 7. Leaf out response (difference in leaf out date in 2012 from mean for 2011/2013/2014) vs. individual tree accession location for (a) strong (n = 14) and (b) mild (n = 8) chilling requirement groups. Moderate chilling group is not pictured because regression was nonsignificant (R^2 = 0.09, P = 0.418). Slopes differ significantly among groups (ANCOVA; F = 3.54, P = 0.021).

This contrasts the modeling of Morin et al. (2009), which indicated a stronger response of southern species to climate warming. Also, the lack of a stronger response among southern species does not support the idea that southern species will fill an early-season niche in northern forests under future climate conditions (Polgar et al. 2014).

One primary factor in the lack of a consistent relationship of leaf out timing and responsiveness with geographic origin is the role of leaf out requirements (i.e., chilling and photoperiod). These requirements have evolved over long time periods, and therefore are not necessarily strongly associated with a species' current geographic range (Zohner and Renner 2014). In this study, species with a strong chilling requirement (Polgar et al. 2014) were less responsive to anomalous spring warming (Fig. 4b). In average years this chilling threshold was generally exceeded in early March, but in 2012 this threshold was never reached (Fig. 1b). However, even species

with very high chilling requirement did show a positive response to intense early spring warmth, suggesting that heat accumulation eventually overrode this requirement.

Successional status also appeared to affect timing and responsiveness of leaf out, as late- and mid-successional species were less responsive to anomalous spring warming than early-successional ones. Many late-successional species have high chilling requirements and opportunistic early-successional species have been shown to respond more readily to forcing (Caffarra and Donnelly 2011, Basler and Körner 2012). Long-lived, late-successional species appear to have a more conservative response to high early spring temperatures than opportunistic species. This pattern is probably related to the tradeoff between rapid spring growth and potential frost damage, which is likely also associated with growth form, shade tolerance, and wood anatomy (Panchen et al. 2014). For example, small,

relatively shade intolerant understory trees *Cercis canadensis*, *Prunus angustifolia*, and *P. virginiana* were especially responsive, and would also likely benefit most from leafing out before the upper canopy layer.

Wood anatomy may also be an important factor in driving leaf out timing and response. Diffuse-porous species have been shown to leaf out earlier on average than ring-porous species (Panchen et al. 2014), but there was not a significant difference in timing in this study for the average years. However, there was a significant difference in responsiveness between wood anatomy groups, with diffuse-porous species exhibiting slightly greater responsiveness than ring and semiring-porous species. Species with diffuse-porous anatomy may be under less threat from embolisms resulting from freeze–thaw events and are more likely to retain functioning vessels from the previous season than ring-porous species (Michelot et al. 2012), both of which could allow them to be more responsive to early onset of spring warming.

There was strong variation among individuals within species in leaf out timing (average of ~9 days). Some of this variation appeared to be related to geographical origin, which could be indicative of potential ecotypic variation in leaf out timing (Vitasse et al. 2009a). However, the relationship between accession location and leaf out timing was not significant either in average years or 2012. The lack of any relationship could be related to the fact that this analysis combines a large number of species, but sample sizes were too small to assess individual species relationships. When location relative to species range was considered, southern individuals from within a species tended to leaf out slightly earlier in average years (Fig. 5c), but not in 2012. Responsiveness was also highly variable within species (difference in response among individuals averaged 18 days). Difference between the individual accession location and species range center was not significantly related to response across all individuals, but this appeared to obscure significant but opposing within-genus and species relationships (Fig. 6, Appendix A). Differences among genera and species in the relationship between responsiveness and geographic origin may, again, have been associated with chilling requirement patterns. Northern individuals of

species with a high chilling requirement were less responsive, suggesting that there may be some variation among individuals in chilling requirement for these species. However, this analysis had very low sample size ($n = 14$) and thus this result should be viewed primarily as an interesting pattern that may warrant further exploration. Previous work has indicated that southern ecotypes within a temperate species´ range can lose chilling requirements altogether (Borchert et al. 2005), and other work has indicated altitudinal variation in leaf out timing (Vitasse et al. 2009a).

The high responsiveness of leaf out to anomalous spring warming exhibited by almost all of the woody plants included in this study has important implications for climate change response and community dynamics. For example, these data indicate that most species and populations could be at risk of frost or freezing damage in years where spring warming occurs much earlier than usual (Hänninen 1991, Vitasse et al. 2014), which could lead to reduced growth or even mortality (Augspurger 2009). On the other hand, these individuals could also potentially benefit from a growing season that is likely to have been extended by weeks or even months (Menzel and Fabian 1999, Menzel et al. 2006, Gunderson et al. 2012). Although almost all species showed a positive response in leaf out date, the among-species differences illustrated here and elsewhere likely will affect competitive dynamics among species in natural ecosystems (Cleland et al. 2007). The most responsive species were generally opportunistic, early-successional species and these species may be at an advantage in the future (Körner and Basler 2010). None of the species in this study are recognized as invasive species, which have been shown to have highly responsive phenology (Wolkovich and Cleland 2010). However, some of the most responsive were opportunistic species growing outside their natural range and such phenological traits may be related to invasive potential (Fridley 2012).

Currently, chilling requirements may be limiting responsiveness to some extent, at least for species that have a very high chilling requirement. This pattern could be much more common and extend to many more species in the future as winters become shorter and more mild (Morin et al. 2009, Körner and Basler 2010). For this and other reasons, long-term responses for

most species are likely to be difficult to predict without detailed experimental and observational data (Chuine et al. 2010). Models that attempt to predict species responses will need to incorporate this balance of chilling and forcing to better assess likely species responses (Laube et al. 2014). The results of this study suggest also that models may need to incorporate variation among individuals within a species and some of this variation could be related to geographic origin (Ghelardini et al. 2006). However, these responses are likely to be species specific both in strength and direction of response (Vitasse et al. 2009b). Such variation is likely to play some role in the response of species to climate change, and may have implications for the potential utility of assisted migration of species and populations into locations that are expected to be more climatically suitable in the future (Gunderson et al. 2012).

Understanding leaf out response in species and populations to variation in spring onset could have important implications for forecasting the overall effects of climate change on ecosystems (Polgar and Primack 2011). The very large response seen in most of the woody plants studied here may not be tracked by the other components of the biota that depend on leaf out. For example, insect herbivore emergence may exhibit a different response to early spring warming than the leaves that they utilize as a food source, which could affect their total abundance or offset it from the arrival of spring migratory birds (Walther et al. 2002, Visser and Both 2005, van Asch and Visser 2007, Wood and Kellermann 2015). Changes to leaf phenology could also affect the spring herbaceous flora across the deciduous forest biome, as an advance of leaf out by weeks or months would almost certainly impact this important reservoir of plant biodiversity in deciduous forests (Walther et al. 2002).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/ doi/10.1002/ecs2.1209/supinfo