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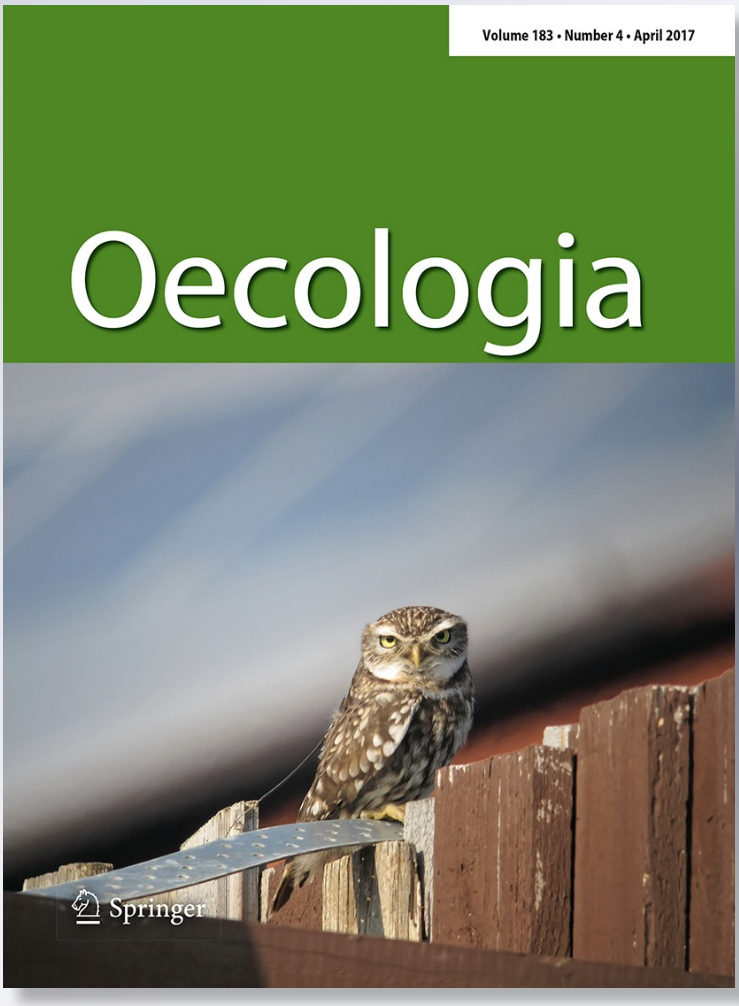

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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Warmest extreme year in U.S. history alters thermal requirements for tree phenology

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Abstract The frequency of extreme warm years is increasing across the majority of the planet. Shifts in plant phenology in response to extreme years can influence plant survival, productivity, and synchrony with pollinators/herbivores. Despite extensive work on plant phenological responses to climate change, little is known about responses to extreme warm years, particularly at the intraspecific level. Here we investigate 43 populations of white ash trees (*Fraxinus americana*) from throughout the species range that were all grown in a common garden. We compared the timing of leaf emergence during the warmest year in U.S. history (2012) with relatively non-extreme years. We show that (a) leaf emergence among white ash populations was accelerated by 21 days on average during the extreme warm year of 2012 relative to non-extreme years; (b) rank order for the timing of leaf emergence was maintained among populations across extreme and non-extreme years, with southern populations emerging earlier than northern populations; (c) greater amounts of warming units accumulated prior to leaf emergence during the extreme warm year relative to non-extreme years, and this constrained the potential for even earlier leaf emergence by an average of 9 days among populations; and (d) the extreme warm year reduced the reliability of a relevant phenological model for white ash by producing a consistent bias toward earlier predicted leaf emergence relative to observations. These results demonstrate a critical need to better understand how extreme warm years will impact tree phenology, particularly at the intraspecific level.

Keywords Bud break · Climate change · Extreme years · *Fraxinus* · Global change · Leaf emergence · Phenology · Thermal models · White ash

Introduction

Since the industrial revolution began (≈200 years ago), atmospheric [CO_2] has increased from 270 to 406 ppm, and average global temperatures have increased by 0.85 °C (IPCC 2012). In addition, extreme warm years have become more common, whereby the past 30 years constitute the warmest conditions in the past 1700 years (Donat et al. 2013; Weaver et al. 2014; Chang et al. 2015). Furthermore, in the United States, higher temperatures during recent decades (1979–2012) were most extreme during spring relative to other seasons (Mutiibwa et al. 2015), producing major implications for plants since many thermal cues for phenology occur during this period.

Shifts in plant phenology can have major impacts on ecosystem processes and may influence plant survival (Augspurger 2013), productivity (Chang et al. 2013), and

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synchrony with pollinators/herbivores (Forrest 2015). Little is known about phenological responses to extreme warm years, although the few studies that have been conducted report unprecedented accelerations in phenology. For example, Rutishauser and colleagues (Rutishauser et al. 2008) found that flowering time of cherry trees advanced by 28 days during the extreme year of 2007 compared with the long-term mean (1702–2007). Friedl and colleagues (Friedl et al. 2014) reported that leaf emergence was accelerated by as much as 14 days relative to long-term averages among tree species at Harvard Forest during the extreme years of 2010 and 2012. Fahey (2016) found even more advancement in the Midwestern U.S., where 96 species in an Illinois common garden showed an average acceleration of 31 days in leaf emergence during the extreme warm spring of 2012 (Fahey 2016). Furthermore, Ellwood and colleagues (Ellwood et al. 2013) observed the earliest flowering times among 32 species in Massachusetts, USA, during the extreme years of 2010 and 2012 relative to records dating back to the nineteenth century, with some species advancing flowering time by as much as 6 weeks during 2012. They also showed that during extreme years, shifts in phenology across species can be predicted from historical relationships between flowering time and mean spring temperature (Ellwood et al. 2013) although others have cautioned against further extrapolation into future conditions (Morin et al. 2009). Despite this, little is known about the intraspecific responses of plants to extreme warm years and whether thermal requirements for phenological cues during average years can be extrapolated to extreme years within individuals and populations. Such knowledge is critical for determining how plants will respond to extreme warm years as they gradually become the climate norms of the future (Hansen et al. 2012; IPCC 2012).

Leaf emergence is a major phenological event in the temperate zone because it marks the beginning of the majority of photosynthetic carbon assimilation during the growing season. The timing of leaf emergence is heritable in temperate trees (Polgar and Primack 2011) although the genetic mechanisms that control this process are not well understood (Cooke et al. 2012; Yordanov et al. 2014). Furthermore, shifts in the timing of leaf emergence in response to temperature extremes can have long-term implications for ecosystem functioning and carbon sequestration. For example, warmer temperatures in early spring have been linked to accelerated phenology that may initially enhance carbon uptake, but may make trees more susceptible to frost damage, ultimately reducing carbon gain and tree survival (Augspurger 2013).

Temperature is the most dominant factor influencing phenology in the temperate zone, including the timing of leaf emergence (Polgar and Primack 2011). Temperature effects on leaf emergence are generally separated into two main components for predictive modeling purposes with trees requiring both chilling and warming requirements (Fig. 1). First, such trees require a specific number of chilling degree units (CDUs) in winter for buds to break dormancy. Once dormancy is broken, trees begin a second phase by tracking warming temperatures (growing degree units, GDUs) until thermal requirements are met (Fig. 1). At this point, bud break and subsequent leaf emergence can occur, assuming other constraints are overcome such as photoperiodic requirements and construction and/or activation of xylem conduits (Polgar and Primack 2011). In addition, there is evidence for interactions between chilling and warming requirements such that more GDUs may be required for leaf emergence if CDUs are not met during winter months (Vihera-Aarnio et al. 2014). Thus, extreme annual and seasonal temperatures can alter the interplay between CDU and GDU requirements, with major implications for phenological responses.

Common assumptions when modeling leaf emergence are that CDU and GDU requirements are met independently and sequentially and that they remain constant within species and across years [(Chuine et al. 2003; Luedeling et al. 2009); but see (Marchin et al. 2015)]. These assumptions are oversimplifications of how environmental factors cue leaf emergence, although models underlain with these assumptions have been used with relative success for over 50 years [see Chuine et al. (2003), Table 4.1-1 and references therein]. Unfortunately, however, it is not clear if thermal requirements will be similar during extreme warm years and if these requirements remain stable across populations through time.

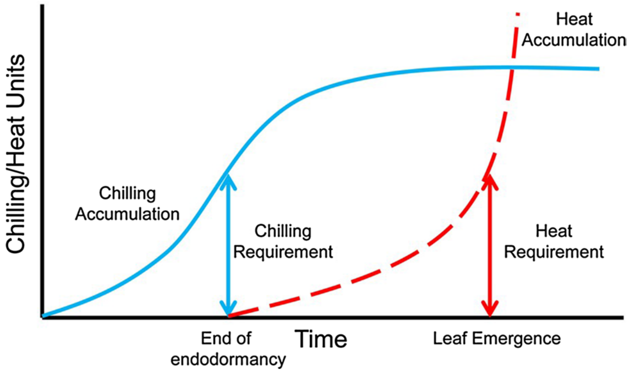

Fig. 1 Theoretical framework for predicting the timing of leaf emergence in response to temperature. Chilling is ineffective during the time in which heating accumulates and vice versa. Thus, the accumulation of both heating and chilling occurs in two distinct periods, and requirements are assumed to be fulfilled sequentially. This represents a common theoretical framework that has been used to successfully predict the timing of leaf emergence in many cases, although further molecular/physiological work is needed to better explain the specific mechanisms that underlie leaf emergence (adapted from Fig. 1 of (Luedeling et al. 2009))

Here we compared the timing of leaf emergence among 43 populations of *Fraxinus americana* L. (white ash) during the warmest extreme year in recorded U.S. history (NOAA 2012) with relatively non-extreme years (2005, 2010, 2011, 2013, 2014, 2015). Note that 2016 was warmer on a global basis, but 2012 remains the warmest year in U.S. history. We incorporated population-level variation from across the species range and investigated extreme year effects in a common garden at the University of Kansas Field Station (Lawrence, KS; Fig. 2). According to long-term records, 2012 was also the warmest year on record in this local area according to weather stations in Topeka (45 km away) and Leavenworth (55 km away) dating back approximately 130 years (National Weather Service 2014; United States Weather Bureau 1942). Leaf emergence of white ash is known to be highly affected by temperature, and has both chilling (CDU) and warming (GDU) requirements (Fig. 1) (Jeong et al. 2012; Polgar et al. 2013), making it an ideal species to investigate the effects of extreme years on phenology, and leaf emergence in particular. During 2012, average winter (November–February of 2011–2012) and spring (March–May of 2012) temperatures at the common garden were 4.5 and 17.6 °C, respectively, which were 3.9 and 6.1 °C warmer than average non-extreme years (Fig. 3). In addition, the common garden is located at the westernmost edge of the species range, and, therefore, is relatively warmer than many white ash habitats (Fig. 2). Thus, many of the populations were operating outside of the thermal environments to which they were adapted, much like is expected under climate change scenarios. Therefore, the anomalously warm year of 2012 allowed us the rare opportunity to test whether phenological predictions based on

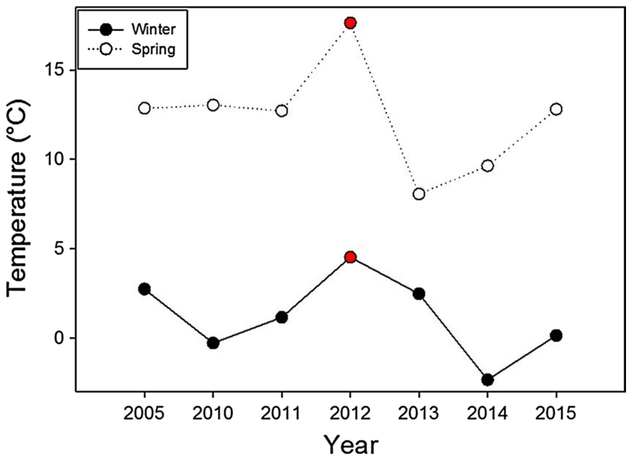

Fig. 3 The average winter (November–December of the previous year, and January–February of the named year) and spring (March–May of the named year) temperatures for the years 2005, 2010, 2011, 2012, 2013, 2014, and 2015 at the common garden located in Lawrence, KS, USA. The average winter and spring temperatures during the extreme warm year of 2012, the warmest year in U.S. recorded history, are highlighted in *red*

Fig. 2 Current range of white ash (*gray area*) and locations where experimental populations originated from (*black circles*). All populations of trees were grown and measured in a common garden at the University of Kansas Field Station (Lawrence, KS, *red star*). Trees have been growing at this common garden for approximately 40 years, with 45 populations represented with 25 trees planted per population (although long-term mortality has reduced that number) Adapted from (Marchin et al. 2008) and USDA Forest Service (www.na.fs.fed.us)

thermal requirements during non-extreme years are maintained during an extreme year. Moreover, our study provides insights into how increasing extreme warm years in the future will affect our current ability to forecast phenology responses at the intraspecific level. We addressed the following questions: (1) how does an extreme year affect the timing of leaf emergence at the intra-specific level in white ash, (2) how do populations originating from a wide range of locations vary in thermal requirements for leaf emergence across extreme and non-extreme years, and (3) how does an extreme year affect our ability to predict leaf emergence using a phenology model (spring warming model of Migliavacca et al. 2012) that was previously shown to be predictive for white ash.

Materials and methods

Common garden conditions

The phenology of white ash is known to be strongly affected by warming (Jeong et al. 2011; Laube et al. 2014), making it an ideal species to test whether thermal requirements for leaf emergence are similar between extreme and non-extreme years and to better understand intraspecific responses to extreme warm years. White ash seeds originating from 45 populations from throughout the species range were collected by the U.S. Forest Service from open-pollinated native parent trees. Seeds were planted in 1976 in the common garden at the University of Kansas Field Station near Lawrence, KS (35.0°N, 95.1°W, 299 m; Fig. 2). Twenty-five replicate trees from each population were planted (1125 trees total), although long-term mortality reduced the number of living trees to ≈750. For the majority of analyses, we considered the timing of leaf emergence for 43 populations (two populations were not included as they only had one surviving tree). Additionally, for the modified two-parameter spring warming model described below (Migliavacca et al. 2012), we considered a set of 35 populations, eliminating populations with sample sizes of <10 surviving trees to minimize sampling error (as a result, $n = 10$–25 trees per population). From the beginning of the growing season, each tree was observed every 48 h until leaf emergence occurred.

The University of Kansas Field Station receives an average annual precipitation of ≈900 mm/year with more than 70% received during the growing season (April–September). Monthly average temperatures range from below −7 °C in January to 32 °C in July. For calculating thermal units, we considered the winter temperature for each year as the average of daily temperatures from November to December of the preceding year, along with January–February of the current year (the named year in all data sets). Spring temperature for each year was calculated as the average of daily temperatures of March–May. Hourly temperature data at the common garden are available from 2008-present from weather stations that are maintained by the University of Kansas Field Station staff. We used these hourly temperature data to calculate GDUs using the Utah Model (see the below section, "Calculation of thermal proxies").

Year 2012 was the warmest at the field station across all years in which leaf emergence was observed and across all years of local record keeping, as well as being the most extreme warm year in recorded U.S. history since 1895 (NOAA 2012). At the common garden, average winter and spring temperatures were 4.5 and 17.6 °C during 2012 (Fig. 3), respectively, which were 3.9 and 6.1 °C warmer than average tested non-extreme years. Total annual precipitation was lowest during the extreme year of 2012 (622 mm) relative to non-extreme years; however, we did not find a significant correlation between precipitation and timing of leaf emergence (likely because reductions in precipitation occurred after leaf emergence), and, therefore, this factor was not considered in our analyses.

Modeling approach

We carried out four different aspects of model analysis: (1) calculation of thermal proxies using three different thermal proxy models, the Utah model (Richardson et al. 1974), a forcing model from Migliavacca et al. (2012), and a forcing model from Jeong et al. (2012); (2) comparison of thermal proxy accumulation in extreme and non-extreme years; (3) model fitting for two phenological models, a two-parameter spring warming model from Migliavacca et al. (2012) and a three-parameter chilling/warming model from Jeong et al. (2012) that were previously shown to be effective at predicting leaf emergence of white ash (Jeong et al. 2012; Migliavacca et al. 2012); and (4) prediction of leaf emergence and consideration of prediction accuracy.

Calculation of thermal proxies

A number of models exist for calculating thermal proxies [see Table 2 in Rea and Eccel (2006)]. Of these, some require the use of additional fixed parameters estimated from experimental data for specific species (Anderson and Richardson 1986) or the use of a subset of leaf emergence data to fit model parameters (Vitasse et al. 2011; Jeong et al. 2012; Migliavacca et al. 2012). In the absence of such experimental estimates for *Fraxinus americana*, we initially chose a method for estimating thermal proxies that required no parameter estimation and then considered methods with fit parameters estimated from a subset of data. The Utah Model proposed by Richardson et al. (1974)

was used to calculate growing degree units (GDU) from available hourly temperature data. In addition, two forcing models that were previously shown to work well for white ash (Jeong et al. 2012; Migliavacca et al. 2012) were used to calculate accumulated forcing from daily mean temperature data.

The Utah model has been used extensively to calculate GDUs for a variety of species and has performed as well or better than other thermal proxy models depending on the species and location [see Table 4 in (Cesaraccio et al. 2004)]. In this study, we used this model to assess potential GDU requirement shifts during an extreme year versus a number of relatively non-extreme years. Growing degree units are calculated based on a linear forcing model with a fixed threshold [from the Utah model of (Richardson et al. 1974)],

$$\mathrm{GDU}\,(k) = \sum_{i=r}^{k} \sum_{h=1}^{24} \max[0, T_h\,(i) - T_\mathrm{b}] \tag{1}$$

for a given day k, where r is the day when the chilling requirement is fulfilled ($k > r$), $T_h\,(i)$ is the hourly mean temperature at hour h and day i, and T_b is the threshold (or base) temperature. The Utah model uses a base temperature of $T_\mathrm{b} = 4.4$ °C. Accumulating GDUs were calculated for each hour of the temperature record, with the beginning of the season set to November 1st.

The second method of calculating thermal proxies uses a forcing model defined by Jeong et al. (2012). This forcing model relies on calculating the accumulation of growing degree days (GDD). Under this forcing model, GDD is defined by:

$$\mathrm{GDD}\,(t) = \sum_{\mathrm{Jan}\,1}^{t} \max\left(T - 5\,^{\circ}\mathrm{C}, 0\right), \tag{2}$$

where T is the daily mean temperature and summation of GDD begins on January 1. This proxy for warming (GDDs) was used as part of a three-parameter chilling–warming model by Jeong et al. (2012) shown to be predictive of white ash leaf emergence. As with the Utah model, we do not use the forcing model of Jeong et al. (2012) to predict leaf emergence, but rather to assess potential shifts in GDD requirements across extreme and non-extreme years. However, we did assess the fit of the three-parameter chilling-warming model of Jeong et al. (2012) using daily mean temperature and leaf emergence data from the white ash common garden (see "Determination of model fit for leaf emergence model" below for further details).

The third method of calculating thermal proxies relies on a forcing model defined by Migliavacca et al. (2012). According to this model, forcing accumulates as a nonlinear function of daily mean temperature ($x\,(t)$):

$$R_\mathrm{f} = \frac{28.4}{1 + e^{-0.185(x(t) - 18.4)}}, \tag{3}$$

for $x\,(t) > 0$ °C. This forcing model was used as part of a two-parameter spring warming model to estimate leaf emergence of tree species in Migliavacca et al. (2012) that was shown to be most accurate at predicting white ash leaf emergence relative to other phenology models. We assessed the fit of a modified version of this two-parameter spring warming model using temperature and leaf emergence data specific to the white ash common garden (see "Determination of fit for leaf emergence model" below for further details).

Comparison of thermal proxy accumulation in extreme and non-extreme years

To determine if accumulated GDUs [from Eq. (1) using the Utah model] were similar between the extreme year of 2012 and non-extreme years, we plotted accumulated GDUs at leaf emergence from the Utah model for each population. We compared these points to a hypothetical one-to-one line representing a hypothesis of fixed GDU requirements between years. We also conducted the same analysis using accumulated GDD as calculated from the forcing model of Jeong et al. (2012); see Eq. (2). We regressed these points between years using a general linear model (SAS 9.2, Cary, North Carolina, USA).

Determination of fit for leaf emergence models

In this study, we assessed the fit and prediction of leaf emergence across two phenological models: (1) a two-parameter spring warming model (Migliavacca et al. 2012), and (2) a three-parameter model incorporating both chilling and warming (Jeong et al. 2012). We used these models to test whether phenological predictions based on thermal requirements are maintained during extreme and non-extreme years. These two models were identified as providing the best fit for white ash in previous studies comparing the performance of phenological models across tree species for prediction of leaf emergence.

The phenology model of Migliavacca et al. (2012) is a two-parameter spring warming model where leaf emergence is predicted to occur when accumulated forcing from the date where accumulation of warming begins (t_2) exceeds the fit parameter F^*, such that $\sum_{t_2}^{t} R_\mathrm{f}(x\,(t)) > F^*$ (Chuine et al. 2003; Migliavacca et al. 2012). To reduce the number of fit parameters, a modified version of this model was considered, with a fixed value for t_2 (date where accumulation of warming begins, set to January 1); this is the same start date as for the simple spring warming or GDD model described in Jeong et al. (2012). Assessment of model fit for this modified spring warming model involved three important aspects: (1) calculation of thermal proxies (R_f) requiring only daily temperature data rather than hourly, which was available for all 6 non-extreme years and the extreme year of 2012, (2) estimation of a fit parameter, F^*, the forcing state at which leaf emergence occurs [see Chuine et al. (1998) and "Materials and methods"], and (3) use of only non-extreme year data to assess model fit. Five years of data were used for parameter estimation, reserving 2012 and one additional non-extreme year to test model prediction. All possible subsets of five non-extreme years from the overall set of six non-extreme years were considered. Model run refers to a run of the model utilizing one of these six subsets of non-extreme years. Fit for the spring warming model was determined using a least squares method after Chuine and colleagues (Chuine et al. 1998), minimizing $\sum_i \left(\mathrm{dExp}_i - \mathrm{dObs}_i\right)^2$ for the parameters of the model, where dObs_i gives the average observed date of leaf emergence for year i and dExp_i gives the predicted date from the model. Since the modified model has only a single fit parameter (F^*, the forcing state at which the transition from quiescence to bud-burst occurs), the least squares minimization was carried out across all possible values of F^*, which can be found by considering the sum of forcing from day 1 to 365 for each year. The fit parameter F^* was estimated both separately for each individual population, and using combined data for the entire set of 35 populations, using the average dObs_i across all individuals and all populations. Graphs of minimum least squares found by the model as a function of the fit parameter F^* for individual populations showed distinct differences in F^* across populations, indicating that there was considerable population-level variation in the response of leaf emergence to forcing accumulation (results not shown). Therefore, we focused on the population level analysis rather than the combined data.

The chilling–warming model of Jeong et al. (2012) is a three-parameter model that incorporates both the effect of chilling and warming in estimating timing of leaf emergence. For the fitting of this model, we carried out joint estimation of the three fit parameters using daily average temperature data and observed dates of leaf emergence, using a simulated annealing minimization routine (amebsa, Press et al. 1992). However, with only 5 years of data (and thus 5 dObs_i), the data provide only 4 degrees of freedom with which to estimate the 3 parameters. Thus it is not surprising that the minimization surface was almost completely flat with regard to the three model parameters, and the corresponding interval estimates essentially spanned the entire range considered. Additionally, calculation of a small sample corrected Akaike Information Criterion [AICc; Burnham and Anderson 2002; (Migliavacca et al. 2012)] for this model with a sample of $n = 5$ years of data and $p = 3$ fit parameters for a randomly sampled population gave AICc = 36.28. The same calculation for the spring warming model with only a single fit parameter [(Migliavacca et al. 2012), see "Calculation of thermal proxies", above] gives AICc = 9.213. The ΔAICc >27 indicates that using the more highly parameterized model is not justified in this case since the gain in the goodness-of-fit (model explanatory power) is overwhelmed by the increase in model complexity (number of fit parameters). The combination of a flat likelihood surface for the model parameters and the large ΔAICc indicated that use of the Jeong et al. model (Jeong et al. 2012) is not justified for our data. Therefore, only the modified version of the two-parameter spring warming model from Migliavacca et al. (2012) was used for all further analyses.

Prediction of leaf emergence and consideration of prediction accuracy

The predicted date of leaf emergence for the two-parameter spring warming model of Migliavacca et al. (2012) was calculated as the date when accumulated forcing from t_2 (set to January 1 for our modified model) exceeded the fit parameter F^*, such that $\sum_{t_2}^{t} R_{\mathrm{f}}(x(t))F^*$, as described above (Chuine et al. 1998; Migliavacca et al. 2012). To consider prediction accuracy, we calculated the root mean square error (RMSE) of leaf emergence for each year, using $\mathrm{RMSE} = \sqrt{\sum_{i=1}^{n} \left(\mathrm{dExp}_i - \mathrm{dObs}_i\right)^2/n}$, where the summation i is over all populations, n gives the number of populations, and dExp_i and dObs_i give the expected and observed dates of leaf emergence for population i for that year. To indicate the direction of error, we calculated the relative error, using $\left(\mathrm{dExp}_i - \mathrm{dObs}_i\right)/\mathrm{dObs}_i$.

Statistical analyses

To assess the effect of the extreme year on the timing of leaf emergence, we used a general linear model. A mixed model was used to assess the effect of population on timing of leaf emergence with year included as a random effect to account for repeated measures within the design. To test the internal reliability of rank among populations across years, a Cronbach's alpha internal reliability measure was calculated. We used a simple regression calculation to compare accumulated GDU and accumulated GDD at leaf emergence for each population between extreme (2012) and non-extreme years. We also used regression to consider between-population variation in model fit as functions of both population size and latitude of origin. All statistical analyses were carried out in SAS 9.2 (Cary, North Carolina, USA).

Results

We examined 43 white ash populations by comparing leaf emergence responses during extreme and non-extreme years in a common garden at the University of Kansas Field Station (Figs. 2, 3). Overall, we show that (a) leaf emergence among white ash populations was accelerated by 21 days on average during the extreme warm year of 2012 relative to non-extreme years; (b) rank order for the timing of leaf emergence was maintained among populations across extreme and non-extreme years, with southern populations emerging earlier than northern populations; (c) greater amounts of warming units accumulated prior to leaf emergence during the extreme warm year relative to non-extreme years, and this constrained the potential for even earlier leaf emergence by an average of 9 days among populations; and (d) the extreme warm year reduced the reliability of a relevant phenological model for white ash by producing a consistent bias toward earlier predicted leaf emergence relative to observations.

Timing of leaf emergence during the warmest year in U.S. history

Average leaf emergence occurred significantly earlier by 21 days in extreme year 2012 compared with non-extreme years ($p < 0.0001$), with population responses ranging from 16 days (Onondaga, NY) to 25 days earlier (Overton, TN) (Fig. 4). Such accelerations are consistent with other reported phenology responses during extreme years with

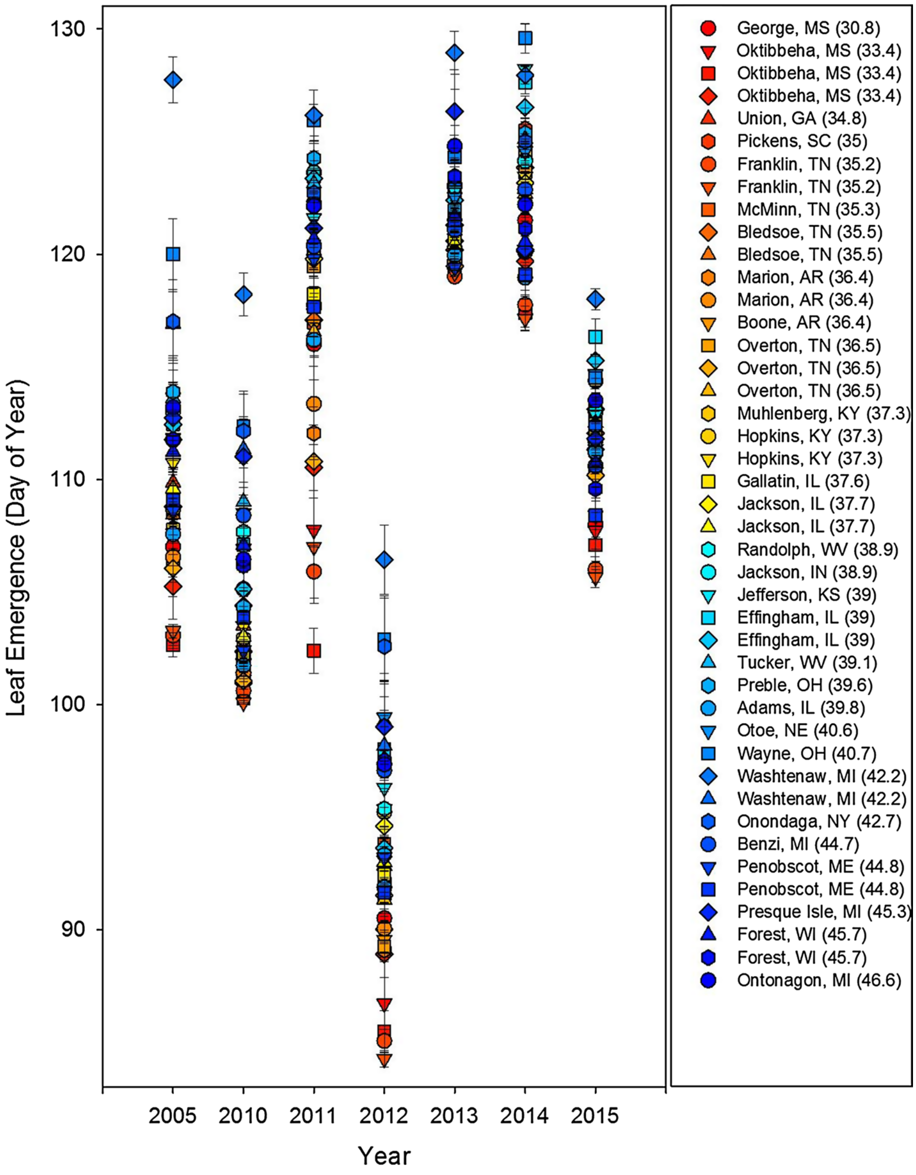

Fig. 4 Timing of leaf emergence among 43 populations of white ash grown in a common garden (University of Kansas Field Station). *Symbols* are mean leaf emergence times ±1 SE. The total number of trees observed each year ranges from 700 to 763, and sample sizes within populations range from 2 to 25 trees depending on long-time survivorship in the common garden. Populations with <10 trees were not used in modeling analyses, although they are shown here. *Symbols* indicate seed source locations for each population. *Symbols* of more southern latitudes are in warmer colors (*red-yellow*) and more northern latitudes are in cooler colors (*cyan-dark blue*)

multiple species (Luterbacher et al. 2007; Rutishauser et al. 2008; Ellwood et al. 2013; Friedl et al. 2014), although in this case we documented similar absolute responses at the intraspecific level.

Population-level leaf emergence and rank order across extreme and non-extreme years

Interestingly, we found that the 43 white ash populations maintained rank order for leaf emergence across extreme and non-extreme years in the common garden (Cronbach's alpha >0.9), with populations originating from lower latitudes consistently showing earlier leaf emergence than those from higher latitudes (Fig. 4). More specifically, leaf emergence for populations originating from lower latitudes (lower than 39°N) occurred on average 4 days earlier relative to populations originating from higher latitudes (above 39°N) across all years of observation. During the extreme year of 2012, the average timing of leaf emergence for populations originating from lower latitudes (below 39°N) occurred 6 days earlier relative to populations originating from higher latitudes (above 39°N; $p = 0.0003$).

GDU requirements during extreme versus non-extreme years

In order to test whether GDU requirements for populations were similar between extreme and non-extreme years, we compared average accumulated GDUs at leaf emergence between the extreme (2012) and non-extreme years. GDUs were calculated using the standard Utah model (see "Calculation of thermal proxies" for further detail on calculation) that utilizes hourly weather data (2005 was not included due to lack of hourly temperature data). Overall, we found that more GDUs accumulated at leaf emergence during the extreme warm year relative to non-extreme years (Fig. 5). More specifically, the average amount of GDUs accumulated at leaf emergence across all populations during 2012 was 16,275, whereas the average for non-extreme years was 13,270, with a range among non-extreme years of 11,041 (2010) to 14,945 (2011). If overall GDU accumulation at leaf emergence had been similar in 2012 as in non-extreme years, average leaf emergence would have occurred 30 days earlier in 2012 compared with the observed acceleration of 21 days, whereby the extra GDU requirements during the extreme year produced a partial buffering effect of 9 days. We also conducted a similar analysis using calculated GDDs (see "Calculation of thermal proxies" above for further detail on calculation) that were shown to be predictive for white ash leaf emergence in a previous study (Jeong et al. 2012). As with GDUs, we found that accumulation of GDDs at leaf emergence was higher during the extreme versus non-extreme years for the majority of populations (using daily rather than hourly temperature data as required for these calculations; Fig. S1).

The average accumulation of GDUs at leaf emergence varied across latitude of population origin. Across all years, the average accumulation of GDUs at leaf emergence was higher for populations originating from higher latitudes (14,173, above 39°N) relative to those originating from lower latitudes (13,246; below 39°N; Fig. 5). Additionally, the forcing parameter F^* for the modified two-parameter spring warming model of Migliavacca et al. (2012) increased significantly with increasing latitude of origin ($R^2 = 0.35$, $\beta = 6.56$, $p < 0.001$), implying that northern populations require more accumulated forcing prior to leaf emergence. During the extreme year, populations originating from higher latitudes (above 39°N) exhibited an average of 17,292 GDUs at leaf emergence, whereas populations originating from lower latitudes (below 39°N) had a lower accumulation of GDUs at leaf emergence (15,351 on average) (Fig. 5).

Model fitting

We fit a modified two-parameter spring warming phenological model described by Migliavacca et al. (2012) using local temperature and leaf emergence data at the white ash common garden. This model was fit using a least squares method after Chuine and colleagues (Chuine et al. 1998), and this method is more fully described in the "Materials and methods" (see "Determination of fit for leaf emergence models"). Substantial variation was seen across populations and across model runs within populations for model fit (Table S1). Population sample size did not explain the differences observed across populations in model fit ($R^2 = 0.04$, NS). However, latitude of population origin did explain some differences across populations in both average model fit (average minimum least squares, $R^2 = 0.36$, $\beta = 5.66$, $p < 0.001$) and in the variation in model fit across runs (SD for minimum least squares, $R^2 = 0.37$, $\beta = 2.91$, $p < 0.0001$). The model fit is diminished (indicated by increasing minimum least squares values) and more variable (indicated by higher SD for minimum least squares) for northern populations. The model fit parameter F^* also showed substantial variation across populations and across model runs (Table S1). Differences observed between the populations for the variation in parameter estimation across model runs (SD for F^*) are not explained by either population sample size or latitude and may reflect unidentified differences in temperature sensitivity (or other variables) across these populations.

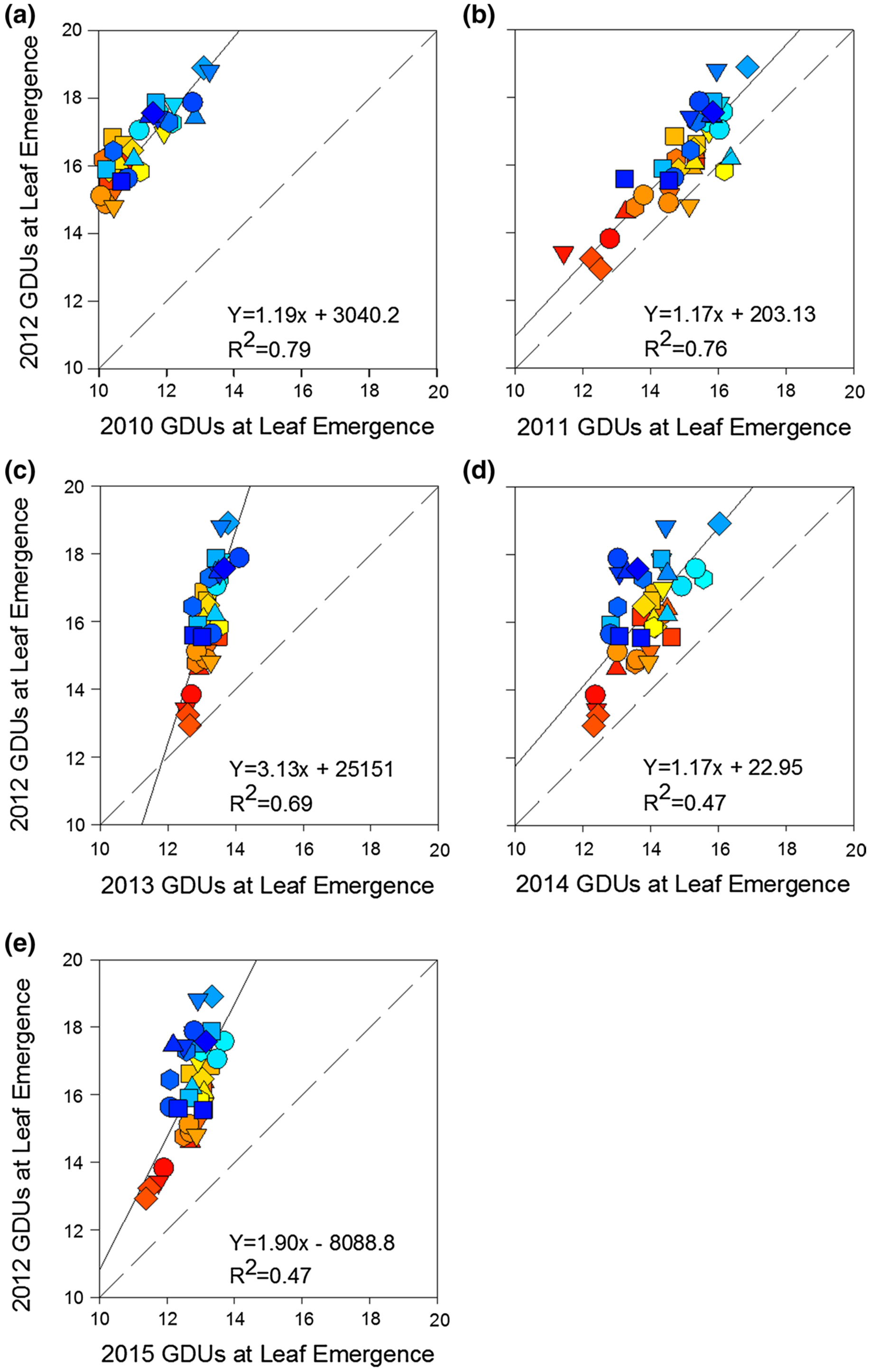

Fig. 5 Average growing degree units (via the Utah model that uses hourly temperature data), in thousands, accumulated at leaf emergence for 43 white ash populations regressed between the extreme year of 2012 and tested non-extreme years, 2010, 2011, 2013, 2014 and 2015 (panels **a**–**e**, respectively). The one-to-one line (*dashed*) is a hypothetical line indicating no difference in required GDUs between 2012 and the non-extreme year. The *solid line* shows a linear regression of the actual data with regression equation and R^2 value. Populations are represented by the same *symbols* and *colors* as in Fig. 4. We conducted this same analysis using growing degree days (GDD) that are calculated using daily mean temperature data, a thermal proxy that has been shown to be relevant for prediction of leaf emergence in white ash. We find similar results for GDDs as shown here for GDUs (see Fig. S1)

Leaf emergence prediction accuracy

Using data from only the non-extreme years as described above, we considered the ability of the modified two-parameter spring warming model of Migliavacca et al. (2012), that was previously shown to be predictive for white ash, to accurately predict leaf emergence in both the extreme year and an additional non-extreme year (using all years in turn). We observed a consistent bias in predicted leaf emergence towards earlier emergence dates for the extreme year of 2012. The spring warming model consistently predicted an earlier than observed date of leaf emergence during the extreme warm year of 2012 for all populations and for all model runs, with relative errors ranging from −0.062 to −0.093. The RMSE values for 2012 ranged from 6.85 to 9.27 for the six model runs. Published values of RMSE from phenological models for many leaf emergence studies give values <7 (Rea and Eccel 2006; Morin et al. 2009; Vitasse et al. 2011), although some studies give much wider ranges, depending on the model used and the species under study [RMSE = 3–51, (Cesaraccio et al. 2004); RMSE = 5–28, (Fu et al. 2013)]. For three of our model runs, the non-extreme year used for estimation (2005, 2014, and 2015) showed good model fit, with RMSE values of 2.80, 3.47, and 3.76 (RE = 0.001, −0.022, and −0.024), respectively. For the remaining three model runs, the non-extreme years (2010, 2011, and 2013) showed fits as poor (or worse) as the extreme year, with RMSE values of 10.93, 12.35, and 8.77 (RE = 0.103, −0.098, and 0.069), respectively. Thus, although this modeling approach was previously shown to perform best in estimating leaf emergence of white ash relative to other phenological models (Migliavacca et al. 2012), we found variability in its ability to predict non-extreme years. Nonetheless, no combination of available non-extreme years for model fitting allowed this approach to accurately predict leaf emergence for the extreme year.

Discussion

Overall response to the extreme warm year

Leaf emergence of white ash occurred on average 21 days earlier in the extreme warm year of 2012 relative to non-extreme years (Fig. 4). Recent evidence suggests that trees that are able to accelerate leaf emergence in response to warming may have a competitive advantage, in that this extends their growing season, providing a longer period for carbon accumulation (Cleland et al. 2012). However, the potential for white ash to utilize an extended growing season during extreme warm years will also depend on other factors such as hydraulic and leaf damage and mortality due to enhanced vulnerability to frost (Augspurger 2013), drought effects that are predicted to increase over much of the species range (IPCC 2013), and mortality following introduction of the emerald ash borer beetle (Poland and McCullough 2006).

We found that more GDUs (and GDDs) accumulated at leaf emergence during the extreme year versus non-extreme years based on modeled threshold temperatures (Fig. 5). If overall GDU accumulation at leaf emergence had been similar in 2012 as in non-extreme years, average leaf emergence would have occurred 30 days earlier in 2012 compared with the observed acceleration of 21 days. This buffering effect of 9 days may have been driven by a number of factors. First, GDU requirements may have increased in response to the extreme warm year and this would have constrained further accelerations in phenology. In a second, but related factor, modified temperature thresholds may have produced leaf emergence at the same GDUs during the extreme year, but at a different rate of accumulation. Clonal studies with other species indicate that threshold temperatures in trees are genetically determined (Rousi and Pusenius 2005; Sanz-Pérez et al. 2009), suggesting a greater likelihood for the former (more GDUs) rather than the latter (changing temperature thresholds). Also, unfulfilled CDU requirements may have constrained the advancement of leaf emergence during the extreme year. In support of this, the winter preceding leaf emergence in 2012 was 3.9 °C warmer on average than non-extreme years at the common garden (Fig. 3), and, therefore, it is possible that chilling requirements (CDUs) were not fully met during 2012. This phenomenon has been observed in other species in the U.S. (Morin et al. 2009; Cook et al. 2012), Europe (Pletsers et al. 2015), and on the Tibetan Plateau (Yu et al. 2010). Last, other biological factors may have played a role in driving higher accumulation of GDUs during the extreme warm year such as avoidance of xylem embolism and responses to photoperiodic cues (discussed below).

Population-level responses to the extreme warm year

The rank order of leaf emergence was maintained among 43 populations of white ash across both extreme and non-extreme years. This maintenance of rank order suggests that we can expect a similar relative "line-up" in the timing of leaf emergence among white ash populations, even during the most extreme warm years. This finding is key for forecasting phenological responses as southern populations migrate to more northern areas with climate warming, and as distant populations are intentionally introduced into new areas through transplant approaches in forest management. The maintenance of rank order may be driven by a number of factors, including the sensitivity of freeze–thaw xylem embolism in ring-porous species such as white ash, a potentially strong genetic basis for temperature thresholds, as well as the possibility of photoperiodic responses and their interactions with population-level responses (described below).

Our results suggest that the evolutionary history of white ash, namely that it is a ring-porous species, plays a key role in determining latitudinal patterns for leaf emergence. From a meta-analysis, as well as other studies (Salk 2011; Zohner and Renner 2014), it was found that northern populations of temperate tree species most commonly exhibit earlier leaf emergence than southern populations in common garden studies. However, here we find the opposite response for white ash (Fig. 4), and although this is less common overall, this trend has been observed in all ring-porous species studied to date, including white ash (Salk 2011; Liang 2015). This pattern is likely due to a conservative strategy involving extensive warming requirements for ring-porous species that generally show later leaf emergence than other species, and one that is particularly evident in northern and/or cold-adapted populations. For example, Dantec and colleagues (Dantec et al. 2014) found that in ring-porous oak, cold-adapted genotypes (from high elevations) exhibited later leaf emergence than warm-adapted genotypes (from low elevations), due to greater degree-day requirements that were calculated in controlled growth environments. This pattern did not occur in diffuse-porous beech that showed no differences in leaf emergence and degree-day requirements between cold and warm-adapted genotypes. Such responses were further supported in our study with white ash where we found that the accumulation of GDUs at leaf emergence were significantly higher among northern populations than southern populations (Fig. 5). Additionally, from responses occurring during non-extreme years, we found that the forcing parameter F^* (calculated according to Migliavacca et al., 2012) increased significantly with increasing latitude of origin ($R^2 = 0.35$, $\beta = 6.56$, $p < 0.001$), indicating that northern populations require more accumulated forcing prior to leaf emergence. These results may explain why populations from more northern latitudes consistently show later leaf emergence than southern populations in the common garden. Relatively later leaf emergence would reduce the likelihood of frost damage, which would be highly adaptive in the native northern range, since the larger spring xylem vessels of ring-porous species (including white ash) are particularly vulnerable to freeze–thaw embolism that disrupts hydraulic conductance (Wang et al. 1992). On the other hand, for southern populations, relatively earlier leaf emergence in northern locations may extend the growing season as it did by several days/weeks in our study (Fig. 4), although the potential for early frost exposure increases.

Model predictability during the extreme year

In our study, the modified two-parameter spring warming model of Migliavacca et al. (2012) was unable to accurately predict the timing of leaf emergence of white ash during the extreme year of 2012 due to a consistent bias towards earlier leaf emergence predictions relative to observations. These results could be explained by a number of factors including higher GDU requirements or altered temperature thresholds (described above), other biological constraints, altered temperature sensing by the trees, or an inability of this type of model to be predictive under extremely warm conditions, even though it was previously shown to be most useful for white ash.

Other biological factors

If photoperiod requirements are not met prior to thermal requirements, the timing of leaf emergence may potentially be delayed, particularly during extreme years when GDUs can accrue rapidly (Way and Montgomery 2014). While photoperiod may have constrained leaf emergence during the extreme warm year, it did not appear to be a major factor in our study. If this were the case, leaf emergence timing would have remained relatively constant across years within each population (since photoperiodic signals do not change from year to year), and this was not observed. In addition, trees most sensitive to photoperiod often exhibit a dampened response to temperature change for leaf emergence (Vitasse et al. 2014a, b), whereas we observed large overall shifts in the timing of leaf emergence with changing inter-annual temperature. Additionally, photoperiod did not affect the timing of leaf emergence in *Fraxinus excelsior* (same genus) under controlled experimental conditions (Basler and Körner 2012). Also, Way and Montgomery (2014) compiled results from studies that investigated photoperiodic sensitivity of leaf emergence and found that ash species were generally photoperiod insensitive (e.g., *Fraxinus chinensis, Fraxinus excelsior, and Fraxinus pennsylvanica*), as well as most other early successional species. In contrast, Hunter and Lechowicz (1992) suggested that leaf emergence of white ash may be sensitive to photoperiod as evidenced by a negative correlation between mean temperature 10 days before leaf emergence and photoperiod on the day of leaf emergence (Hunter and Lechowicz 1992). Across a number of models used to predict leaf emergence, these same authors found that a spring warming model (warming only) most accurately predicted white ash leaf emergence, with better outcomes than a photothermal model. Moreover, a major review concluded from studies using dormant twigs grown under controlled conditions that photoperiod requirements for leaf emergence may be less important than previously thought (Primack et al. 2015). Nonetheless, we cannot rule out the possibility that interactive effects of temperature and photoperiod influenced the timing of leaf emergence, as well as the influence of population, since little is known about the role of these potential two- and three-way interactions.

Other biological factors involved in water uptake, such as the timing of xylem construction, may have also constrained leaf emergence during the extreme year. Wang and colleagues (Wang et al. 1992) reported a nearly 100% loss in xylem conducting capacity by late winter in white ash trees. To support newly emerging leaves, white ash trees must first form new xylem each spring. Thus, the developmental timing of xylem formation in the spring may constrain further advancements in leaf emergence, even if GDU and CDU requirements are met. Vessel formation in ring-porous species is generally initiated 2–6 weeks prior to leaf emergence (Suzuki et al. 1996), and, therefore, this factor is not likely to be constraining leaf emergence under normal conditions. However, the extreme year may have created a scenario where the formation of xylem may have constrained the timing of leaf emergence since GDUs accumulated rapidly in our study.

Extreme temperatures may limit the performance of phenology models

The extreme year of 2012 may have also altered the temperature sensing mechanisms that underlie leaf emergence and this may have reduced model predictability. These mechanisms are not well understood in trees, and it is currently not possible to speculate how extreme warm years may alter such responses. Phenology models that only consider how one phenological state (leaf emergence) responds to temperature may result in imprecise predictions if aggregated variables (e.g., CDUs and GDUs) are not representative of chilling and warming sensitivity in the tree, particularly during extreme years. Along this line, Clark et al. (2014) suggested that uneven warming results in an interaction between phenological state and seasonality of warming, and this effect is likely to be amplified in extreme warm years, reducing the ability to predict phenological events using conventional models. Future models that incorporate multiple phenological states and that do not aggregate temperature time series into a cumulative sum or average value may be better able to deal with phenological responses to extreme warm years (Clark et al. 2014). Unfortunately, the drawback in these future models is that measurements at multiple states of leaf development are required, and the full sensing mechanisms to establish such parameters are often unknown. Furthermore, traditional degree-day models may not be predictive during extreme years since warm climates may alter underlying biological processes that are sensitive to temperature. Along this line, Luedeling and Brown (2011) and Borchert et al. (2005) pointed out that commonly used thermal proxy models (e.g., Utah model used to calculate GDUs and CDUs) are not as accurate in warmer regions (sub-tropical or tropical regions) compared to cooler temperate regions. It is possible that even in temperate regions, for which these models were designed, conditions may be getting too warm for accurate predictions of leaf emergence, particularly during extreme years.

Regardless of why the modeling approach of Migliavacca et al. (2012) failed to accurately predict leaf emergence in the extreme warm year, our data suggest that this phenological response may be fundamentally altered during the extreme year. This is evidenced by the fact that no combination of non-extreme year data for model fitting allowed for the accurate prediction of leaf emergence for the extreme year. Thus, we need to be cautious when applying common phenological models to project future shifts in phenology under climate change scenarios where extreme warm years are becoming more common. Moreover, these results demonstrate a critical need to better understand the underlying biology of how extreme warm years affect tree phenology, mainly because these years are predicted to become the climate norms of the next century.

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Author contribution statement JMC, MEO, RMM and JKW conceived and designed the experiments. JMC, LMG, JHS, RMM and JKW conducted field work, and MEO, JMC and JKW developed and performed modeling and statistical analyses. JMC, MEO, JN and JKW wrote the manuscript; all authors provided editorial advice.

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