

Experimental warming alters spring phenology of certain plant functional groups in an early successional forest community

CHRISTINE R. ROLLINSON* and MARGOT W. KAYE*†

*Ecology IGDP, The Pennsylvania State University, University Park, PA 16802, USA, †School of Forest Resources, The Pennsylvania State University, University Park, PA 16802, USA

Abstract

Experimental study of the effects of projected climate change on plant phenology allows us to isolate effects of warming on life-history events such as leaf out. We simulated a 2 °C temperature increase and 20% precipitation increase in a recently harvested temperate deciduous forest community in central Pennsylvania, USA, and observed the leaf out phenology of all species in 2009 and 2010. Over 130 plant species were monitored weekly in study plots, but due to high variability in species composition among plots, species were grouped into five functional groups: short forbs, tall forbs, shrubs, small trees, and large trees. Tall forbs and large trees, which usually emerge in the late spring, advanced leaf out 14–18 days in response to warming. Short forbs, shrubs, and small trees emerge early in spring and did not alter their phenology in response to warming or increased precipitation treatments. Earlier leaf out of tall forbs and large trees coincided with almost 3 weeks of increased community-level leaf area index, indicating greater competition and a condensed spring green-up period. While phenology of large trees and tall forbs appears to be strongly influenced by temperature-based growth cues, our results suggest that photoperiod and chilling cues more strongly influence the leaf out of other functional groups. Reduced freeze events and warmer temperatures from predicted climate change will interact with nontemperature growth cues to have cascading consequences throughout the ecosystem.

Keywords: climate experiment, forest harvest, forests, freeze patterns, leaf out, phenology, precipitation, warming

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Introduction

Phenology of both plants and animals has been altered by climate warming over the past 50 years and may be an important mechanism behind ecosystem response to global change in the future (Morissette *et al.*, 2009). Earlier spring green-up and dates of last frost have been observed in many systems across the globe and can alter the temporal availability of resources such as light, water, and nutrients (Cooter & Leduc, 1995; Menzel *et al.*, 2006; Schwartz *et al.*, 2006; Gordo & Sanz, 2010; Jeong *et al.*, 2011). In the eastern United States, spring leaf emergence has advanced at an average rate of 1.2 days per decade since 1955 and appears to be driven by a concurrent increase in spring and winter temperatures of as much as 0.6 °C per decade (Schwartz *et al.*, 2006). Temperatures are projected by climate models to continue rising at similar rates, with increases of 1.5–5.8 °C as well as 0–20% increased precipitation predicted by the end of this century in the eastern US (Intergovernmental Panel on Climate Change, 2007). While many groups of animals have

shifted their migratory or breeding phenology in response to changing food or habitat availability from warming temperatures, plants are sessile and cannot rapidly migrate to respond to changing environmental conditions (Hodgson *et al.*, 2011; Moyes *et al.*, 2011). Consequently, many plant taxa have phenological plasticity and sensitivity to environmental cues such as temperature to control the timing of leaf out (Schlichting, 1986).

Phenology of plants and animals is controlled by many cues and mechanisms, making it unlikely that species, communities, and ecosystems will respond uniformly to climate change or avoid the effects of altered phenology of some species. Winter chilling, photoperiod, and temperature are considered to be the most important cues controlling plant phenology, but exact mechanisms and cues vary by species (Lechowicz, 1984; Chuine & Cour 1999, van der Meer *et al.*, 2002; Durant *et al.*, 2007; Korner & Basler, 2010). Furthermore, climate change may alter the timing and reliability of these cues in the future and disrupt the temporal relationship of current phenology events (Reed *et al.*, 2010). Variation in species' ability to shift the timing of life-history events in response to changing environmental conditions could alter nutrient

Correspondence: Christine Rollinson, tel. + 440 935 4770, fax + 814 865 3725, e-mail: crr173@psu.edu

availability, biotic interactions, and community composition over time (Thompson & Naem, 1996). Advanced or delayed leaf out, flowering, and senescence of even a few plants could have cascading ecosystem effects by creating a mismatch between resource availability (e.g. pollen or fruit availability) and demand (Durant *et al.*, 2007; Kaiser *et al.*, 2010; Molinos & Donohue, 2010). Previous studies regarding the patterns or consequences of altered phenology have tended to focus either on a few selected species or on satellite imaging that aggregates entire communities (e.g. Schwartz *et al.*, 2006). However, the monitoring of all plant species within a community is a necessary step to continue to improve our understanding of species interactions and how systems as a whole may respond to climate change.

For long-lived organisms such as trees, the effects of climate change on forest community structure and function will likely be most pronounced early in succession, as the forest transitions between community states. Natural or anthropogenic disturbances, including timber harvesting, may help catalyze community response to climate change by creating a resource-rich environment that favors shifts in species dominance or establishment of new species (Oliver & Larson, 1996; Iverson *et al.*, 2004; Swanson *et al.*, 2010). Additionally, climate appears to affect species establishment strongly following disturbance due to the sensitivity of tree regeneration to climate variability (Jackson *et al.*, 2010). Furthermore, the biotic interactions between trees and nontree species are strong during the establishment phase and nontree species can act as an ecological filter that influences tree species' success (Gilliam & Roberts, 2003; Royo & Carson, 2006). This means that vegetation responses to climate change in the first few years following harvest may directly or indirectly impact forest development in the long term.

Research on forest responses to climate change has thus far centered on tree species, but the responses of herbaceous and nontree species characteristic of early successional forests is a critical area in need of study when considering the impacts of climate change on forest development. Observational studies (e.g. Walther *et al.*, 2005; Beckage *et al.*, 2008; Woodall *et al.*, 2009), models (e.g. Pacala *et al.*, 1996; McKenney-Easterling *et al.*, 2000; Iverson & Prasad, 2001), and field experiments (e.g. Gunderson *et al.*, 2010; Kardol *et al.*, 2010b) have provided valuable information on how trees respond to climate change but typically do not include analysis of the nontree community. In contrast, many field climate change experiments that address community patterns have been conducted on grass- and shrubland communities that function differently from forest ecosystems (e.g. Price & Waser, 2000; Wan *et al.*, 2002;

Sherry *et al.*, 2008; Kardol *et al.*, 2010a). While valuable information has been gained from these separate approaches, herbaceous and woody plants in early successional forest systems merit consideration due to their relatively brief but important influence on tree regeneration (Duffy & Meier, 1992; Gilliam & Roberts, 2003; Royo & Carson, 2006; Gilliam, 2007).

We used a field experiment to investigate the effects of warming and increased precipitation on the phenology of an early successional temperate deciduous forest in central Pennsylvania. Our research tests the hypothesis that predicted changes in climate affect the spring phenology of plant species in an early successional eastern forest community. Historical observations of phenology in this region led us to expect warming to advance spring leaf out through earlier warming cues while increasing precipitation would have no effect on phenology as it has not been linked to phenology in eastern forests (Schwartz *et al.*, 2006; Morin *et al.*, 2009; Korner & Basler, 2010). We expected earlier leaf out of plants in response to warming to be accompanied by temporal changes in competition for resources such as light that could be observed as increased leaf area index (LAI). Finally, we examined if altered freeze patterns from warming could affect the long-term reliability of warming-based growth cues. To test our hypotheses, we collected data from a simulated climate change experiment that mimicked a moderate warming scenario of 2 °C and +20% precipitation. We examined the relationship between date of leaf out and spring patterns of freeze-free days (FFD) in an attempt to isolate temperature cues from other potential controls of functional group leaf out. Temperature-based growth cues are commonly represented by growing degree days (GDD); however, we chose to represent spring warming cues with freeze-free days (FFD) because it captures similar spring warming patterns as GDD but also represents early spring chilling cues that often regulate bud burst (Lechowicz, 1984; Korner & Basler, 2010). Finally, we complemented our experimental results by comparing spring freeze patterns from our experiment to those from a long-term (117 years) temperature record to gain insight into how reduced freeze events and temperature-linked growth cues may interact and affect community phenology over a longer time frame than could be tested experimentally.

Materials and methods

An *in situ* climate manipulation experiment was established in two hectares of a central Pennsylvania oak-hickory forest (40°41'N, 77°54'W) that was whole-tree harvested prior to installing the experiment. Forest harvesting is common throughout the eastern U.S. and has been recognized as an

important consideration for understanding forest response to climate change (Jackson *et al.*, 2010). Prior to harvest, the dominant tree species in the second-growth forest were *Quercus rubra*, *Q. alba*, *Q. velutina*, *Carya tomentosa*, *Fraxinus americana*, and *Acer rubrum*. The site was whole-tree harvested in August 2007 and enclosed with a 2 m tall large-mammal exclosure fence, which is a common practice in central Pennsylvania to protect forest regeneration from deer browsing (Horsley *et al.*, 2003). The site is situated on a southeast-facing aspect with a slope of 10% and average elevation of 281 m. Average annual mean temperature in the area is 9 °C, with an average daily maximum of 15 °C and minimum of 4 °C throughout the year. Mean annual precipitation is ca. 100 cm and is distributed throughout the year. Soils in the site are Berks series with shale, siltstone, and fine grain sandstone origins.

Naturally regenerating postharvest vegetation communities in sixteen 2 × 2 m plots were the experimental units for our study. The experimental design was a two-factorial randomized complete block design consisting of four blocks containing one plot of each of the following treatments: warming only, precipitation only, warming + precipitation, and ambient. Plots received experimental treatments from May 2008 through August 2010 and were spaced a minimum of 10 m apart to minimize the effects of neighboring treatments or the probability of shared stump sprouting. In warming treatments, our targeted temperature increase above ambient were 1.5 °C during the day and 3 °C at night. We warmed plots with suspended infrared heaters, which have been used effectively in grassland and alpine climate change simulation experiments (Price & Waser, 2000; Wan *et al.*, 2002, 2005; Kimball, 2005). One 240 V infrared heater was suspended 1.5 m above each plot. A real-time proportional-integrative-derivative feedback system controlled warming through infrared radiometer (IRR) monitoring of surface temperatures in warmed and not warmed plots. Over the course of the experiment, hourly temperatures were raised by 1.8 °C (SE 0.6) above ambient in warming only plots and 1.7 °C (SE 0.21) in the warming + precipitation treatment. Precipitation slightly depressed average hourly temperatures by 0.3 °C (SE 0.08) over the course of the entire experiment. Daily minimum temperatures were more affected by warming due to the greater warming programmed for nighttime temperatures. Warming and warming + precipitation both raised daily minimum temperatures 2.3 °C (SE 0.2), while precipitation slightly lowered minimum temperature by 0.2 °C (SE 0.02). Ambient and precipitation only plots that did not receive warming treatments had heater replicas to replicate shading and drip-line effects of the lamp structures in warmed plots.

Plots receiving precipitation treatments had weekly additions of collected rainwater or snow that equaled 20% of the 1882–2005 monthly mean historical record from State College, PA (US Historical Climatology Data Network, Easterling *et al.*, 1996). April through December precipitation treatments were added in the form of water collected in a series of rainwater catchments distributed throughout the site. In winter months (December–March), precipitation was collected in a series of open topped plastic bins and distributed as water, ice, or snow, depending on the state at time of application. Volume

of weekly precipitation treatment additions were recorded and converted to precipitation depth equivalent. Ambient precipitation was recorded using a tipping-bucket rain gauge and effective precipitation treatment was calculated by dividing the weekly added precipitation treatment amount by the weekly ambient precipitation. The weekly addition of water resulted in a 23% increase in precipitation above ambient over the course of the experiment.

Phenology of all plant species was monitored in our research plots and analyzed on a functional group level to help account for plot and treatment-based differences in community composition. We identified over 130 species in our research plots between 2009 and 2010 with large block- and plot-level variation in species composition (see online supporting information). The use of functional groups in community-level analyses is common to allow comparisons in systems with high beta diversity and has been useful in predicting phenological responses in animals (Hobbs, 1997; Diamond *et al.*, 2011). The plant functional groups selected for our analyses were as follows and included 110 of the total species found at our site: short forbs with maximum height of 1 m (Rhoads & Block, 2007), tall forbs (max height >1 m), large trees that dominate the forest canopy at maturity, small trees that occupy the sub-canopy at maturity, and shrubs. The short forb functional group had 50 species and included 21 species that flower in the spring or early summer such as *Viola* spp. and *Potentilla canadensis*. In contrast, the tall forb functional group (26 species) generally flowered later in the season and included 11 species of goldenrod *s.l.* and aster *s.l.* *Acer* spp. and *Quercus* spp. are examples of the large tree functional group (17 species). *Cornus florida* was the most common small tree (total eight species), and *Rubus* spp. was the most common shrub (total nine species).

Phenology monitoring focused on leaf out started in mid-March of 2009 and 2010 and was conducted on a weekly basis through mid-June, at which point vegetation was monitored biweekly through senescence in November in 2009 and in 2010 to early August, when the experiment ended. Leaf out date by species was assigned to the date of first observation of at least one individual with at least three mature leaves expanded. While the use of first observation has been criticized as inaccurately representing population phenology (Miller-Rushing *et al.*, 2008), we relied on first observation for a species because it was not possible to identify and track individual plants to calculate an average leaf out date by species due to high density of plant stems in plots and the vegetative propagation of many species that makes identification of an 'individual' impossible. The leaf out date for a functional group for each plot was calculated by taking the mean first leaf out date of all species belonging to the functional group. Averaging the first date for several species also helped reduce first observation bias. Dates of leaf out for each functional group in all plots were standardized by subtracting the ambient treatment average for 2009 or 2010 from the value for each plot so that negative values indicate earlier leaf out. Standardization isolated treatment effects by removing natural interannual (2009 and 2010) variance in leaf out date. Bud burst of woody plants, defined by new growth emerged from at least

three bud scales, was also monitored and analyzed. Warming and precipitation effects were analyzed using repeated-measures two-way ANOVA using Proc Mixed in SAS 9.2 (SAS Institute, 2008, Cary, NC, USA) with block as a random effect and year as the repeated factor. All dates are presented as Julian date (day 1 = January 1) and results are significant at $\alpha = 0.05$ unless otherwise noted.

Leaf area index was measured every 1–2 weeks in full sun from March to November in 2009 and 2010 using an AccuPAR LP-80 PAR/LAI ceptometer (Decagon Devices, Inc., Pullman, WA, USA). The ceptometer averages light over a series of 80 photosynthetically active radiation (PAR) light sensors aligned on an 84 cm long wand and automatically calculates LAI using above and below canopy PAR, a leaf distribution constant, and the sun zenith. Two measurements per plot parallel to the slope and offset 0.5 m from the outside plot edges were averaged to gain a single LAI value per plot. LAI for each plot was standardized by subtracting the average ambient treatment LAI, and treatment effects were assessed using a two-way repeated-measures ANOVA using Proc Mixed in SAS 9.2 (SAS Institute, 2008), with date of measurement as the repeated factor and block as a random effect. As with leaf out dates, standardization to ambient was necessary to remove time-based differences in LAI resulting from community development that could confound treatment effects.

We used the number of freeze-free days (FFD) that occurred before average functional group leaf out as an indicator of warming effects on temperature-related growth cues. In preliminary analyses, we considered both FFD and the more common approach of GDD, but only present FFD because of similar effects of warming on GDD and FFD. Furthermore, the base temperature for GDD can vary greatly depending on what species is being examined.

Precipitation consistently had no effects on leaf out phenology, so treatments were aggregated as warmed and not warmed for temperature cue analyses. Plot-level IRR temperature data were used to determine the number of FFD ($T_{\min} > 0^{\circ}\text{C}$) that occurred between January 1 and the average leaf out date for each functional group. Daily minimum temperatures recorded by the IRR sensors (surface temperatures) in the ambient plots were slightly cooler than to the on-site measurements of minimum air temperatures but were tightly related ($T_{\text{IRR}} = 0.98 \times T_{\text{AIR}} - 1.16$, $R^2 = 0.91$). Linear regression and effects parameterized ANCOVA with random block and year effects in R (R Development Core Team, 2006) were used to compare the relationship between number of FFD before leaf out and day of leaf out among treatments. In these regressions, we focused on differences in the intercept to indicate functional group responses in the earliest day of leaf out to treatments.

Historical daily temperatures from State College, PA were used to put warming treatment effects on freeze patterns and potential growth cues reliability found in our experiment into context with past climate variability and estimates of future predictions of temperature increase. We used daily temperatures records from 1893 to 2009 from State College, PA (the closest continually running weather station, $40^{\circ}48'\text{N}$, $77^{\circ}52'\text{W}$) from the National Climate Data Center (NCDC) as the base

data set for our analyses. The State College NCDC weather station is located ~15 km to the south and 60 m higher elevation. Daily minimum temperatures from State College from 2008 and 2009 were compared with the corresponding recorded ambient treatment temperatures from our experiment site using linear regression to calculate equations that adjust State College records to represent our study site. State College minimum temperatures were adjusted with the linear equation: $T_{\min\text{ambient}} = 0.9561 \times T_{\min\text{StateCollege}} - 2.3249$ ($R^2 = 0.8986$). The adjusted 117 year daily data will herein be referred to as the long-term temperature record for the study site. Temperature increases predicted by climate models for our study site were modeled by adding a constant 2.8°C to daily minimum temperatures of the long-term temperature record. This level is slightly higher than the average level of warming achieved by the heaters in our experiment, but more closely reflects the target 3°C night time warming that would affect daily minimum temperatures. The $+2.8^{\circ}\text{C}$ modeled data will herein be referred to as the modeled warming data. The simple models of long-term historical and predicted temperature data were created to put our experimental treatments into the larger context of both past climate patterns and predictions of increased temperatures. We acknowledge that spatial and temporal trends in temperature are complex and are not likely to be linear, as we have assumed in our models. However, the historical data set encompasses more climate variability than we were able observe in our short-term experiment and helps us interpret our results in a larger climate context.

We analyzed the effects of modeled warming on spring temperature cues with three metrics: the long-term mean of the date of last freeze (LF, last day $T < 0^{\circ}\text{C}$), the number of freeze events before date of last frost for each year, and the number of days without freeze (freeze-free days, FFD) before last frost for each year. All three metrics we use have been tied to spring plant phenology and survival (Morin *et al.*, 2009; Reed *et al.*, 2010). Last frost is a common metric used to describe the growing season for plants, as freezing temperatures can damage plant growth and date of last frost is highly variable from year to year. While warming necessarily advances the day of last frost and reduces the number of freeze events experienced between January 1 and that date, the number of days without frost before the last frost may increase or decrease with warming depending how far the LF advanced. The values presented for both number of freeze events or days without freeze are the sum of events between January 1 and the date of LF. Analysis of freeze patterns in long-term data was performed using paired *t*-tests, while experimental data was analyzed for heat effects using one-way repeated measures ANOVA with year as the repeated factor and random block effects. Both analyses were performed in SAS 9.2.

Results

Response of leaf out phenology to experimental warming

Tall forbs and large trees were the only functional groups to leaf out earlier in response to ca. 2°C

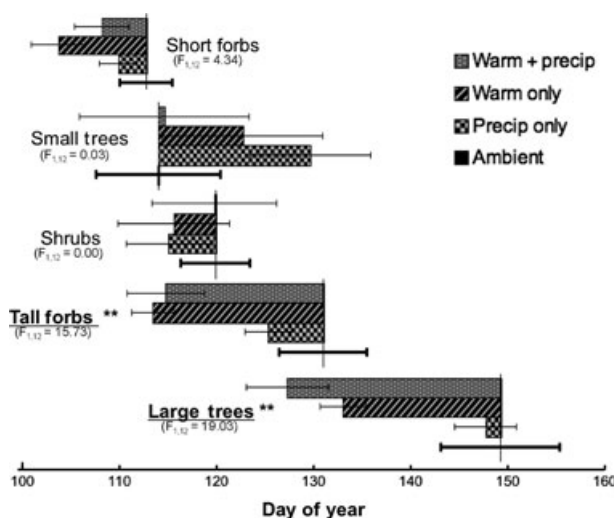


Fig. 1 Average functional group leaf out dates (2009 and 2010) in response to experimental warming ($\sim 2^\circ\text{C}$) and precipitation increase ($\sim 20\%$) of an early successional forest community. Leaf out in each plot was standardized to the average ambient leaf out for each functional group (vertical lines). Bars indicate ± 1 standard error, $n = 4$ for each bar, and ** indicates $P < 0.01$.

experimental warming, and no functional groups responded to $+23\%$ precipitation (Fig. 1). Tall forb leaf out advanced 14 days and shifted from an average day 128 (SE 3.2) in nonwarmed plots to day 114 (SE 1.2) in warmed plots ($F_{1,12} = 15.73$, $P < 0.01$). Large tree leaf out in warmed treatments was 18 days earlier in warmed plots (day 130, SE 2.5) than not warmed plots (day 148, SE 3.8, $F_{1,12} = 19.03$, $P < 0.01$). Short forbs, small trees, and shrubs tended to leaf out earlier in the growing season (days 113 SE 2.9, 114 SE 7.7, and 119 SE 4.6 days, respectively in the ambient treatments) but did not significantly change timing of leaf out in response to warming or increased precipitation. Short forbs displayed a greater trend towards advanced leaf out in 2010 than in 2009 (data not shown), but earlier leaf out from warming remained a statistically weak trend over the course of the 2 years ($F_{1,12} = 4.34$, $P = 0.06$). Bud burst in woody functional groups was not affected by warming or increased precipitation (data not shown). Overall, the duration of spring green up between short forb leaf out and large tree leaf out was shortened 15 days by warming ($F_{1,12} = 4.94$, $P = 0.046$).

Leaf area index was similar in all treatments at the beginning of the growing season, diverged among the treatments during the course of the spring, and returned to similar levels in the middle and end of the growing season (Fig. 2). Earlier leaf out of tall forb and large trees coincided with a period of increased LAI in

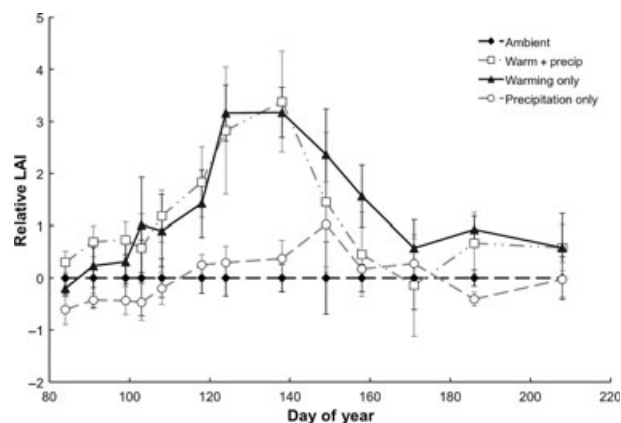


Fig. 2 Average (2009 and 2010) leaf area index (LAI) in response to experimental warming ($\sim 2^\circ\text{C}$) and precipitation increase ($\sim 20\%$) of an early successional forest community. LAI by treatment was standardized to ambient for the spring growing season. Bars indicate ± 1 standard error, $n = 4$ for each point.

warmed plots (Fig. 2). A significant warming \times day interaction occurred in both 2009 and 2010 ($F_{21,250} = 2.63$, $P < 0.01$) and shows that warming increased LAI during the period of rapid community green up during leaf out. This period of increased LAI occurs when tall forbs and large trees are leafing out in warmed plots and persists through days 106–226 in 2009 and days 108–149 in 2010.

The relationship of freeze-free days and date of leaf out provides insight into the onset of functional group leaf out in response to temperature cues (Fig. 3). All functional groups showed heat lowering the intercept ($P < 0.01$), which indicates earlier first observations of leaf out in warmed plots. However, lower intercept (Fig. 3) does not correspond to earlier average date of leaf out (Fig. 1) for most functional groups. For example, the earliest observation of short forb leaf out in both treatments was tightly grouped around roughly 20 FFD, but most leaf out observations occurred ca. day 110 in both warmed and not warmed treatments, leading to no difference in average date of leaf out. In contrast, the first observations of small tree and shrub leaf out appear to be more tied to a day of the year (ca. day 90) than the number of freeze-free days experienced. These two functional groups also displayed a few instances where the latest leaf out in warmed plots was later than not warmed. Leaf out for tall forbs and large trees in warmed plots started after more FFD had occurred, but at an earlier date than in not warmed plots (Fig. 3). Interestingly, these two functional groups were the only two that advanced their average day of leaf out in response to warming.

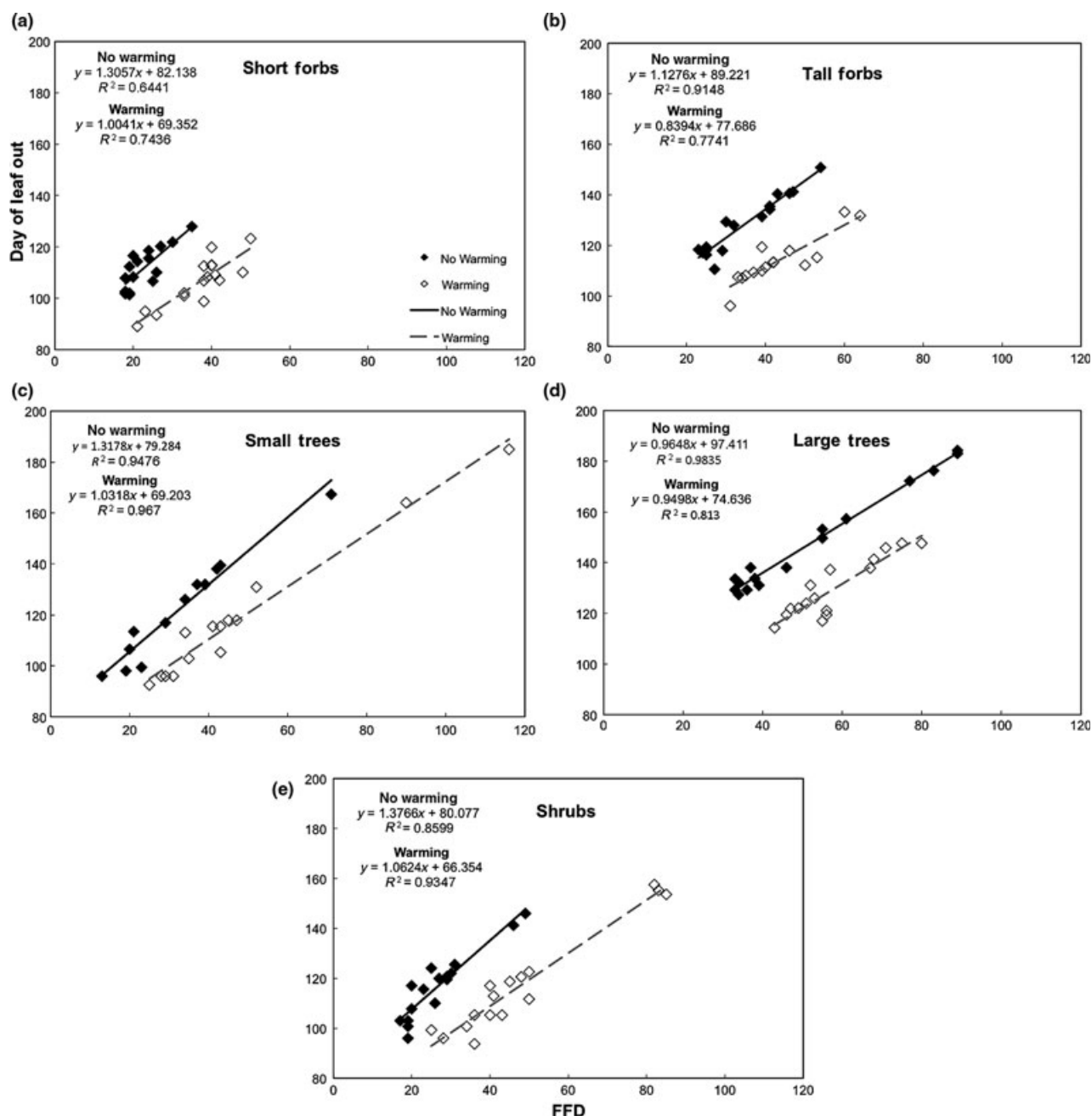


Fig. 3 Linear regression and correlation between number of freeze free days (FFD, days without frost between January 1 and date of leaf out) and date of leaf out from 2009 to 2010 in plots receiving warming treatments ($\sim 2^\circ\text{C}$) or not ($n = 16$ for each) for (a) short forbs, (b) tall forbs, (c) small trees, (d) large trees, and (e) shrubs.

Climatic context of experimental treatments

Warming altered both number of spring freezes and the date of LF in both our modeled and experimental warming data. The mean Julian day of LF in the long-term data set was 131 (SE 1.2) and showed no significant advancement for the period 1893–2009 (data not shown). In the 2 years of our experiment, the date of LF

was slightly later than average in 2009 (day 139) and matched the long-term average in 2010 (day 131). Experimental warming caused last frost to occur 15 days (SE 3.5) earlier than in nonwarmed plots ($F_{1,14} = 17.51$, $P < 0.01$). Modeled long-term data showed a similar level of last frost advance, with the 2.8°C warming advancing average date of LF by 17 days (SE 1.2) to day 114 (SE 1.0, $T_{114} = 13.99$,

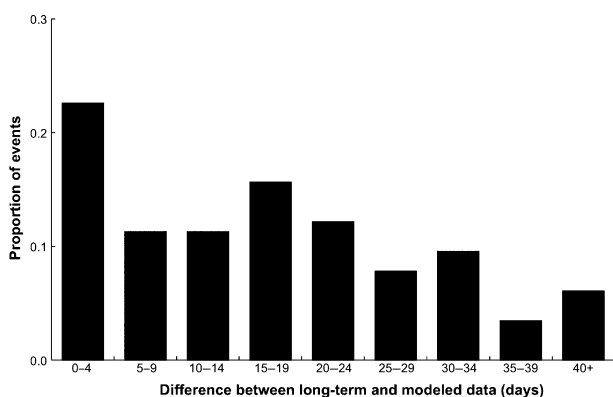


Fig. 4 Changes in freeze patterns as shown by the number of days earlier last frost occurred between January 1 and date of last freeze caused by modeled constant 2.8 °C warming in the long-term data set (117 years). Changes in date of last frost were calculated by subtracting the date of last frost with modeled warming from the last frost date without warming.

$P < 0.01$). However, the distribution of the number of days frost was advanced by warming was positively skewed (Fig. 4): many years showed little frost advancement (24% of years showed frost advanced 4 or fewer days). Modeled warming also produced several years in which the date of last frost advanced by over 30 days (Fig. 4). Modeled warming reduced the number of freeze events between January 1 and the last frost by 20 (SE 0.5) ($T_{113} = 41.2$, $P < 0.01$). Our experimental warming resulted in a similar reduction in freeze events (24 SE 1.5, $F_{1,14} = 280.16$, $P < 0.01$). In contrast, freeze-free days during the same time period displayed different patterns. Modeled warming caused three more FFD (SE 1.4) than the long-term data ($T_{113} = 1.95$, $P = 0.05$), but only 55% of years showed an increase in FFD while 45% of years showed reduced FFD. Our experimental warming increased FFD between January 1 and last frost by 9 (SE 3.4, $F_{1,14} = 6.91$, $P = 0.02$).

Discussion

Warming advanced leaf out for two of the five functional groups we examined in our study. Leaf out of tall forbs and large trees was sensitive to warming, while short forbs, small trees, and shrubs were unaffected. Functional groups that did not advance leaf out in response to warming tended to leaf out in the early spring. Similar patterns have been observed in other regions, suggesting that early season vegetation in some regions may be adapted to avoid early leaf out (Askeyev *et al.*, 2010). Because our warming treatments affected both spring warming and early spring chilling requirements, leaf out of functional groups that show no response to warming (e.g. short forbs, small trees, shrubs) are likely to be constrained at least in part by

photoperiod (Kramer, 1994; Li *et al.*, 2003; Korner & Basler, 2010). Even though most phenology research focuses on leaf out advance in response to warming, it is also possible for warming to delay leaf out (Yu *et al.*, 2010). Less frequent chilling early in the growing season could extend the time necessary for chilling cues to be met and is a particular concern for woody species (Korner & Basler, 2010; Yu *et al.*, 2010). While delayed spring phenology was a rare response within our study, we did observe a few instances of later leaf out for small tree and shrub functional groups in warmed plots. These two groups had the lowest species richness and would be most easily skewed by differences in species composition or an anomalous response of a single species.

Warming effects on freeze patterns in the long run may reduce the reliability of spring growth cues and affect temporal patterns of community leaf out. While simplistic, our long-term modeled warming analysis indicates that spring temperature-based cues will not simply occur earlier in the season, but will instead vary from year to year. For example, nearly 25% of the years we modeled showed little to no change in the date of last frost. However, we found that warming drove a 2-week advance in leaf out of tall forbs and large trees. A consistent advance in spring phenology combined with variable last frost timing could put newly emerged leaves at risk of frost damage more frequently (Morin *et al.*, 2009). Because warming does not cause FFD to consistently increase or decrease before last frost, it may be difficult for species to rely on similar warming-based temperature cues in the future (Reed *et al.*, 2010). Finally, photoperiod is a cue that will remain constant despite climate variability; however any shift in a spring climate will mean that the average climate conditions represented by a photoperiod in the future will be different than it is today. This means that functional groups such as short forbs that appear to be strongly influenced by photoperiod may be the most vulnerable to increased cue variability. The effects of our experimental warming on freeze patterns and warming-based cues matched warming conditions modeled from long-term climate data. This suggests that our experimental results of warming-based changes in leaf out represent how functional groups could respond to climate change over a longer time period.

Although many recent studies have emphasized the importance of multi-factor climate simulations for determining potential plant or ecosystem response to climate change (Matesanz *et al.*, 2009), most research involving the role of precipitation regimes in phenology has been centered on regions with strong seasonal patterns of precipitation (e.g. Matesanz *et al.*, 2009; Gordo & Sanz, 2010; Bradley *et al.*, 2011; Misson *et al.*, 2011). Our results suggest that in temperate regions

with relatively constant water availability, precipitation does not play a major role in controlling plant phenology. This supports conclusions from long-term observational studies that correlate spring phenology in the eastern US with warming temperatures without detecting any correlation with precipitation (e.g. Schwartz *et al.*, 2006; Morin *et al.*, 2009).

Earlier leaf out of only a few functional groups can affect community dynamics and have cascading effects throughout the ecosystem. Earlier leaf out of tall forbs and large trees likely drove increased spring leaf area. However, increased LAI could also be the result of increased leaf growth from other functional groups, which would not be captured by our analysis focused on first observation of leaf out (Miller-Rushing *et al.*, 2008). Regardless of the mechanism, increased spring leaf area in response to warming indicates higher competition for resources such as light earlier in the growing season. If early season and often low-stature functional groups such as short forbs do not advance their phenology in proportion to large trees and tall forbs, they will likely lose their competitive niche as their current window of high resource availability and low competition disappears. Altered competition success at the species or functional group level in the spring could drive changes in community composition as the community develops (Morissette *et al.*, 2009; Forrest *et al.*, 2010; Dijkstra *et al.*, 2011). In the most extreme case, sensitive species that are unable to compete for resources in the altered spring climate may experience localized extinction, lowering community biodiversity. Both loss of species and increased leaf area at the community level can alter system-wide carbon dynamics and nutrient cycling (Dragoni *et al.*, 2011). Altered nutrient cycling can then have cascading effects throughout the ecosystem and affect a variety of biological taxa (Kaiser *et al.*, 2010).

Our experimental approach to studying functional group and community-level spring phenology provides a perspective on forest response to climate change that complements long-term observational studies. The use of controlled experimental manipulations isolates the influence of temperature and precipitation on phenology and monitors the response of intact, naturally assembled communities (Thuiller, 2007; Kimball, 2011). In our experiment, the differing responses of functional group phenology to warming emphasize the need for intensive, full community phenology studies to complement current large-scale and long-term research. Because trees are the dominant, most persistent component of a regenerating forest, it is tempting to focus solely on them, but altered phenology of any woody or herbaceous group has feedback cycles that may influence biotic interactions and the general successional

trajectory of the forest. For example, earlier leaf out of tall forbs and large trees is likely to impact other functional groups negatively such as short forbs and shrubs that appear less able to shift their phenology to maintain their temporal niches. While these functional groups have only a fleeting influence on mature trees, they contribute to ecosystem biodiversity, can be important ecological filters early in succession, and can affect the species composition and rate of development of regenerating seedlings (Gilliam, 2007). Future migration of tree species in response to climate change, as predicted by climate envelope models (e.g. Prasad *et al.*, 2007-ongoing), will be affected by early successional herbaceous and woody plant dynamics during the establishment phase, thereby altering future forest composition.

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References

- Askeyev OV, Sparks TH, Askeyev IV, Tishin DV, Tryjanowski P (2010) East versus West: contrasts in phenological patterns? *Global Ecology and Biogeography*, **19**, 783–793.
- Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *PNAS*, **105**, 4197–4202.
- Bradley AV, Gerard FF, Barbier N *et al.* (2011) Relationships between phenology, radiation, and precipitation in the Amazon region. *Global Change Biology*, **17**, 2245–2260.
- Chaine I, Cour P (1999) Climatic determinants of budburst seasonality in four temperate-zone tree species. *New Phytologist*, **143**, 339–349.
- Cooter EJ, Leduc SK (1995) Recent frost date trends in the north-eastern USA. *International Journal of Climatology*, **15**, 65–75.
- Diamond S, Frame A, Martin R, Buckley L (2011) Species' traits predict phenological responses to climate change in butterflies. *Ecology*, **92**, 1005–1012.
- Dijkstra JA, Westerman EL, Harris LG (2011) The effects of climate change on species composition, succession and phenology: a case study. *Global Change Biology*, **17**, 2360–2369.
- Dragoni D, Schmid HP, Wayson CA, Potters H, Grimmond CSB, Randolph JC (2011) Evidence of increased net ecosystem productivity associated with a longer vegetated season in a deciduous forest in south-central Indiana, USA. *Global Change Biology*, **17**, 886–897.
- Duffy DC, Meier AJ (1992) Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biology*, **6**, 196–201.
- Durant JM, Hjermandt DO, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.
- Easterling DR, Peterson TC, Karl TR (1996) On the development and use of homogenized climate datasets. *Journal of Climate*, **9**, 1429–1434.
- Forrest J, Inouye DW, Thomson JD (2010) Flowering phenology in subalpine meadows: does climate variation influence community co-flowering patterns? *Ecology*, **91**, 431–440.
- Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience*, **57**, 845–858.
- Gilliam FS, Roberts MR (2003) Interactions between the herbaceous layer and overstory canopy of eastern forests: a mechanism for linkage. In: *The Herbaceous Layer*

- in *Forests of Eastern North America* (eds Gilliam FS, Roberts MR), pp. 198–223. Oxford University Press, Oxford.
- Gordo O, Sanz JJ (2010) Impact of climate change on plant phenology in Mediterranean ecosystems. *Global Change Biology*, **16**, 1082–1106.
- Gunderson CA, O'Hara KH, Campion CM, Walker AV, Edwards NT (2010) Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. *Global Change Biology*, **16**, 2272–2286.
- Hobbs RJ (1997) Can we use plant functional types to describe and predict responses to environmental change? In: *Plant Functional Types* (eds Smith TM, Shugart HH, Woodward FI), pp. 66–90. Cambridge University Press, Cambridge, UK.
- Hodgson JA, Thomas CD, Oliver TH, Anderson BJ, Bereton TM, Crone EE (2011) Predicting insect phenology across space and time. *Global Change Biology*, **17**, 1289–1300.
- Horsley SB, Stout SL, DeCalesta DS (2003) White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications*, **13**, 98–118.
- Intergovernmental Panel on Climate Change (2007) Climate Change 2007: Synthesis Report.
- Iverson LR, Prasad AM (2001) Potential changes in tree species richness and forest community types following climate change. *Ecosystems*, **4**, 186–199.
- Iverson LR, Schwartz MW, Prasad AM (2004) How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology & Biogeography*, **13**, 209–219.
- Jackson ST, Betancourt JL, Booth RK, Gray ST (2010) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *PNAS*, **106**, 19685–19692.
- Jeong SC, Ho C, Gim H, Brown ME (2011) Phenology shifts at start versus end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982–2008. *Global Change Biology*, **17**, 2385–2399.
- Kaiser C, Fuchslueger L, Koranda M *et al.* (2010) Plants control the seasonal dynamic of microbial N cycling in a beech forest soil by belowground C allocation. *Ecology*, **92**, 1036–1051.
- Kardol P, Campy CE, Souza L, Norby RJ, Weltzin JF, Classen AT (2010a) Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Global Change Biology*, **16**, 2676–2687.
- Kardol P, Cregger MA, Campy CE, Classen AT (2010b) Soil ecosystem functioning under climate change: plant species and community effects. *Ecology*, **91**, 767–781.
- Kimball BA (2005) Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology*, **11**, 2041–2056.
- Kimball BA (2011) Comment on the comment by Amthor *et al.* on “appropriate experimental ecosystem warming methods” by Aronson and McNulty. *Agricultural and Forest Meteorology*, **151**, 420–424.
- Korner C, Basler D (2010) Phenology under global warming. *Science*, **327**, 1461–1462.
- Kramer K (1994) Selecting a model to predict the onset of growth of *Fagus sylvatica*. *Journal of Applied Ecology*, **31**, 172–181.
- Lechowicz MJ (1984) Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *American Naturalist*, **124**, 821–842.
- Li C, Juntilla O, Ernsten A, Heino P, Palva ET (2003) Photoperiodic control of growth, cold acclimation and dormancy development in silver birch (*Betula pedula*) ecotypes. *Physiologia Plantarum*, **117**, 206–212.
- Matesanz S, Escudero A, Valladares F (2009) Impact of three global change drivers on a Mediterranean shrub. *Ecology*, **90**, 2609–2621.
- McKenney-Easterling M, DeWalle D, Iverson L, Prasad A, Buda A (2000) The potential impacts of climate change and variability on forests and forestry in the mid-Atlantic region. *Climate Research*, **14**, 195–206.
- van der Meer PJ, Jorritsma ITM, Kramer K (2002) Assessing climate change effects on long-term forest development: adjusting growth, phenology, and seed production in a gap model. *Forest Ecology and Management*, **162**, 39–52.
- Menzel A, Sparks TH, Estrella N *et al.* (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976.
- Miller-Rushing AJ, Inouye DW, Primack RB (2008) How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *Journal of Ecology*, **96**, 1289–1296.
- Misson L, Degueldre D, Collin C, Rodriguez R, Rocheteau A, Ourcival J, Rambal S (2011) Phenological responses to extreme droughts in a Mediterranean forest. *Global Change Biology*, **17**, 1036–1048.
- Molinos JG, Donohue I (2010) Interactions among temporal patterns determine the effects of multiple stressors. *Ecological Applications*, **20**, 1794–1800.
- Morin X, Lechowicz MJ, Auspurgur C, O'Keefe J, Viner D, Chuine I (2009) Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology*, **15**, 961–975.
- Morisette JT, Richardson AD, Knapp AK *et al.* (2009) Tracking the rhythm of the seasons in the face of global climate change: phenological research in the 21st century. *Frontiers in Ecology and the Environment*, **7**, 253–260.
- Moyes K, Nussey DH, Clements MN *et al.* (2011) Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology*, **17**, 2455–2469.
- Oliver CD, Larson BC (1996) *Forest Stand Dynamics*. McGraw-Hill, Inc, New York.
- Pacala S, Canham C, Saponara J, Silander J, Kobe R, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*, **66**, 1–43.
- Prasad AM, Iverson LR, Matthews S, Peters M (2007–ongoing) A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States [database]. Available at: <http://www.nrs.fs.fed.us/atlas/tree> (accessed 25 November 2011), Northern Research Station, USDA Forest Service, Delaware, OH.
- Price MV, Waser NM (2000) Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications*, **10**, 811–823.
- R Development Core Team (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org> (accessed 25 November 2011).
- Reed TE, Waples RS, Schindler DE, Hard JJ, Kinnison MT (2010) Phenotypic plasticity and population viability: the importance of environmental predictability. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **277**, 3391.
- Rhoads AF, Block TA (2007) *The Plants of Pennsylvania*. University of Pennsylvania Press, Philadelphia, PA.
- Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research*, **36**, 1345.
- Schlichting CD (1986) The evolution of phenotypic plasticity in plants. *Annual Review in Ecology and Evolution*, **17**, 667–693.
- Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology*, **12**, 343–351.
- Sherry RE, Weng E, Arnone JA *et al.* (2008) Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Global Change Biology*, **14**, 2923–2936.
- Swanson ME, Franklin JF, Beschta RL *et al.* (2010) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, **9**, 117–125.
- Thompson LJ, Naeem S (1996) The effects of soil warming on plant recruitment. *Plant and Soil*, **182**, 229–242.
- Thuiller W (2007) Climate change and the ecologist. *Nature*, **448**, 550–552.
- Walther GR, Post E, Convey P *et al.* (2005) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wan S, Luo Y, Wallace LL (2002) Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Global Change Biology*, **8**, 754–768.
- Wan S, Hui DF, Wallace L, Luo Y (2005) Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. *Global Biogeochemical Cycles*, **19**, 1.
- Woodall CW, Oswalt CM, Westfall JA, Perry CH, Nelson MD, Finley AO (2009) An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management*, **357**, 1434–1444.
- Yu H, Luedeling E, Xu J (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *PNAS*, **107**, 22151–22156.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Species presence/absence by plot. X indicates leaf out observation was included in calculation of functional group leaf out in 2009 and/or 2010.

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