Forest phenology and a warmer climate – growing season extension in relation to climatic provenance

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Abstract

Predicting forest responses to warming climates relies on assumptions about niche and temperature sensitivity that remain largely untested. Observational studies have related current and historical temperatures to phenological shifts, but experimental evidence is sparse, particularly for autumn responses. A 4 year field experiment exposed four deciduous forest species from contrasting climates (*Liquidambar styraciflua, Quercus rubra, Populus grandidentata,* and *Betula alleghaniensis*) to air temperatures 2 and 4 °C above ambient controls, using temperature-controlled open top chambers. Impacts of year-round warming on bud burst (BB), senescence, and abscission were evaluated in relation to thermal provenance. Leaves emerged earlier in all species by an average of 4–9 days at +2 °C and 6–14 days at +4 °C. Magnitude of advance varied with species and year, but was larger for the first 2 °C increment than for the second. Effect of warming increased with early BB, favoring *Liquidambar*, but even BB of northern species advanced, despite temperatures exceeding those of the realized niche. Treatment differences in BB were inadequately explained by temperature sums alone. In autumn, chlorophyll was retained an average of 4 and 7 days longer in +2 and +4 °C treatments, respectively, and abscission delayed by 8 and 13 days. Growing seasons in the warmer atmospheres averaged 5–18 days (E2) and 6–28 days (E4) longer, according to species, with the least impact in *Quercus*. Results are compared with a 16 years record of canopy onset and offset in a nearby upland deciduous forest, where BB showed similar responsiveness to spring temperatures (2–4 days °C^{-1}). Offset dates in the stand tracked August–September temperatures, except when late summer drought caused premature senescence. The common garden-like experiment provides evidence that warming alone extends the growing season, at both ends, even if stand-level impacts may be complicated by variation in other environmental factors.

Keywords: autumn, *Betula alleghaniensis*, bigtooth aspen, climate change, forest, *Liquidambar styraciflua*, phenology, *Populus grandidentata*, *Quercus rubra*, red oak, spring, sweetgum, trees, warming, yellow birch

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Introduction

As atmospheric concentrations of CO_2 continue to rise, predictions of a warming climate (Christensen *et al.*, 2007) have increased scientific focus on the basic temperature responses of plants as they relate to both function and distribution (Sykes *et al.*, 1996; Chuine, 2000, 2010; Kirschbaum, 2000; Saxe *et al.*, 2001; Sage & Kubien, 2007). Because temperature is one of the major factors controlling productivity and species distribution (Woodward, 1988; Chuine & Beaubien, 2001; Saxe *et al.*, 2001), the predicted warming of 2–6 °C by 2100 in north temperate forest regions (Christensen *et al.*, 2007) could have substantial impacts on growth and species composition.

A known effect of higher temperatures is to accelerate bud burst (BB), flowering, and stem elongation in spring, and thus extend the growing season, potentially increasing growth and productivity (Grace, 1988; Saxe *et al.*, 2001; Badeck *et al.*, 2004; Vitasse *et al.*, 2009; Richardson *et al.*, 2010). Optimal temperatures for metabolism, growth, and phenological responses are the product of long-term adaptation to local conditions (Berry & Björkman, 1980; Carter, 1996; Chuine, 2010), even when imperfectly matched to local climate (Rehfeldt *et al.*, 1999; Savolainen *et al.*, 2007). While many factors combine to define range boundaries (Sykes *et al.*, 1996; Loehle, 1998; Chuine, 2010), global patterns of species distribution indicate that temperature sensitivity influences both the potential and realized niche of plants (Woodward, 1988; Iverson & Prasad, 2002; Thomas *et al.*, 2004; McKenney *et al.*, 2011). Because plant phenology has adapted to optimize the timing of growth and reproduction to the local environment,

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phenological fitness, and plasticity may be key to species distribution, and to competitive success (Kramer, 1995; Brooker, 2006; Chuine, 2010; Vitasse *et al.*, 2010). Climate-driven changes in phenology, physiology, productivity, and reproductive fitness thus have the potential to alter resource allocation, range limits, community structure, function, and diversity (Sykes *et al.*, 1996; Rehfeldt *et al.*, 1999; Iverson & Prasad, 2001; Thomas *et al.*, 2004; Brooker, 2006), but accurate predictions require an increased understanding of the mechanisms and component responses.

To test the relative impacts of atmospheric warming in relation to distribution, we designed an experiment to examine the impacts of year-round warming on four species distributed across the eastern deciduous forest biome. *Liquidambar styraciflua* and *Quercus rubra* are present in the local eastern Tennessee (TN, USA) environment and are presumably adapted to local conditions. *Betula alleghaniensis* and *Populus grandidentata* have a more northerly distribution, adapted to the cooler climates of their realized niches. Given their native habitats, conditions at the TN field site would represent an environment several degrees warmer than the ones to which the two northern species were adapted (Table 1). Further warming in the heated chambers was hypothesized to be particularly detrimental for northern species, disrupting interactions with other phenological cues, or exceeding the limits of a positive response to warming. This design allowed us to assess and compare the impacts of warmer temperatures on phenology and physiology in relation to the climate of origin. Physiological responses (Vollmar & Gunderson, 2006; Gunderson *et al.*, 2010) and growth are discussed elsewhere.

The primary objective of this experiment was to quantify and compare the impacts of warming on phenology, both in spring, when vegetative and flower buds would likely open earlier (Murray *et al.*, 1989; Badeck *et al.*, 2004; Ibáñez *et al.*, 2010), and in autumn, when the relationships appear more complex, and photoperiod control may dominate (Menzel, 2002; White & Nemani, 2003; Menzel *et al.*, 2006; Richardson *et al.*, 2006). A second objective was to evaluate any differences in sensitivity in relation to climatic and latitudinal origins of each species, as well as to species differences in the relative timing of spring and autumn phenological events, and in leaf production patterns.

The potential impact of global warming on phenology remains difficult to parameterize in ecosystem models (White *et al.*, 1997; Richardson *et al.*, 2006), even in spring, when accumulated thermal sums have long been used to predict BB, because of apparent interactions with accumulated chilling time, day length, and other factors (Cannell & Smith, 1983; Chuine, 2000;

Table 1 Comparison of habitat and site temperatures by temperature sum and mean annual temperatures (MAT)

	Across species' range		At source[†] or site[§]
	GDD[*]	MAT[‡] (°C)	MAT[†] (°C)
Betula alleghaniensis	1100–2500[*]	1–16	8.6
Populus grandidentata	1100–3169[*]	2–13	9.4
Quercus rubra	1100–4571[*]	1–18	12.3
Liquidambar styraciflua	2660–5993[*]	10–22	14.9
Oak Ridge, TN (field site)	2915–4177[§]	na	14.2[§]

*Growing day degrees (GDD) per year, using a base of 5.56 °C; from Pastor & Post (1985).
[†]30 years average of mean annual temperatures at source of plant material, from: http://www.ncdc.noaa.gov/oa/climate-research.html (accessed on 11 May 2010).
[‡]Mean annual temperatures across the range of the species, estimated from niche maps in Prasad *et al.* (2007-ongoing) (accessed 19 November 2010).
[§]Mean annual temperature (30 years) for Oak Ridge TN, Walker Branch Watershed records.

Schaber & Badeck, 2003). A third objective was therefore to examine the relative influence of various environmental drivers on phenology, and to characterize and quantify responses by species and climatic provenance for both spring and autumn relationships. A final objective was to compare results from the experiment with patterns of canopy phenology in a nearby deciduous forest to evaluate the whether bud and leaf responses of individual saplings are relevant to predicting the temperature responses of canopy onset and offset at the stand level.

Hypotheses being tested were that warmer temperatures would extend the growing season by hastening BB and canopy development in spring, and by extending the physiologically active period later into autumn. Null hypotheses were that growing season would not be extended on either end by warming, being constrained by other factors, such as chilling or photoperiod requirements, soil moisture, etc., or that BB would be earlier in spring, but that there would be no difference in autumn phenology, when other factors would dominate.

Materials and methods

Field site and chambers

The experiment was conducted at the Global Change Field Research Site on the Oak Ridge National Environmental Research Park, Oak Ridge, TN, USA (35°54′N, 84°20′W, elevation 230 m). The site has a Captina silt loam soil, with a relatively

high water table (Edwards & Norby, 1999). The experiment was conducted in nine temperature-controlled open-top chambers (OTCs), consisting of aluminum-framed cylinders, 3.0 m diameter × 2.3 m height, and covered with clear poly-vinyl chloride panels. In 2004 chamber height was extended to 3.4 m to accommodate sapling growth. Double-walled lower panels had holes in the inner wall, 2.5 cm in diameter, permitting continuous airflow into the chamber at 0.6 m³ s⁻¹ (Norby et al., 1997). Incoming air passed through an evaporative cooling system to provide cooling as needed on sunny days. Each OTC also had a 240 volt electric resistance heater between the evaporative cooler and the chamber (Norby et al., 1997). Heaters operated throughout the year, but the evaporative cooling system was drained over winter to prevent ice damage.

Volumetric soil water content was monitored at two depths per chamber (0–10 cm and 0–20 cm) by time domain reflectometry (TDR100, Campbell Scientific Inc., Logan, UT, USA), to determine whether warming treatments affected soil moisture. During summer, 2002, supplemental watering was provided as needed for seedling establishment, and to balance soil moisture across treatments. During the remainder of the experiment, the amount and timing of precipitation (totals 902, 733, and 549 mm, April–September in 2003, 2004, 2005) was adequate (cf a 30 years mean of 670 mm) to prevent moisture stress (Gunderson et al., 2010), although the 0–10 cm probes indicated small treatment differences.

Species selection

All four species are relatively common in the eastern deciduous forests of North America, but their distributions encompass a range of growing temperatures (Table 1). Two of the species, *Liquidambar styraciflua* (sweetgum) and *Quercus rubra* (northern red oak) are native to the Ridge and Valley Province of eastern Tennessee, where the experimental site is located. The range of *L. styraciflua,* a continuously flushing species, also extends much further southward, into warmer regions, where it is more abundant than it is locally (Burns & Honkala, 1990; Prasad et al., 2007-ongoing). In contrast, *Q. rubra*, with determinate leaf production, is more common in the cooler Appalachian mountain region than elsewhere in TN, and its range extends much further north, into New England, the upper plains states, and Canada, where it reaches a higher importance value (IV, based on frequency, density and dominance of the species) than in the southern part of its range (Prasad et al., 2007-ongoing). *Betula alleghaniensis* (yellow birch) is most common in the cooler climates of New England, Canada and the northern plains of the United States. In TN, it is limited to high elevations. The range of *Populus grandidentata* (bigtooth aspen) extends to northeastern and north-central United States and southeastern Canada, with highest IV in northern Michigan. It is found locally only in isolated portions of western North Carolina and northwestern TN (Burns & Honkala, 1990; Prasad et al., 2007-ongoing). Both northern species have indeterminate leaf production.

These four species were selected specifically because they are native to markedly different climates, and because their responses to warming might differ correspondingly. In empir-

ical habitat models (based on climate envelopes, or realized niches), the growth and relative importance of *L. styraciflua* is projected to improve in eastern TN with climatic warming, whereas *Q. rubra* would retreat northward and largely disappear from the region (Bugmann et al., 2001; Prasad et al., 2007-ongoing; Iverson et al., 2008). In the same models, *B. alleghaniensis* and *P. grandidentata* would not tolerate ambient temperatures at the experimental site (Tables 1 and 2), much less temperatures 2 or 4 °C warmer. Suitable habitats for those species are projected to shift poleward into Canada with warming (Solomon, 1986; Prasad et al., 2007-ongoing; Iverson et al., 2008).

Five individuals of each species were planted directly in the soil of each OTC in the spring of 2002. Species were segregated by quadrant, with faster-growing species planted to the north to reduce shading. Three of the four species (*Liquidambar styraciflua, Quercus rubra,* and *Betula alleghaniensis*) were planted in the chambers as bare-root seedlings, through holes in a weed barrier

Table 2 Temperature metrics in open top chambers, 2002–2005, and mean differences for each metric (treatment–control (A) chambers)

	[*]GDD	[†]MAT (°C)	July Avg. Max[‡] (°C)	January Avg. Min[¶] (°C)	May[**]–Sept Mean[¶] (°C)
OTC (2002)					
A	na	na	33.3	na	23.9[*]
E2	na	na	34.6	na	25.7[*]
E4	na	na	37.7	na	27.6[*]
OTC (2003)					
A	3796	14.3	32.1	−5.1	19.6
E2	4335	16.3	33.5	−3.1	21.5
E4	4785	17.9	34.9	−1.1	22.9
OTC (2004)					
A	3886	15.1	33.0	−3.3	22.4
E2	4347	16.9	34.1	−1.0	24.0
E4	4874	18.4	35.4	−0.02	25.8
OTC (2005)					
A	3808	14.6	31.9	0.0	22.5
E2	4204	16.0	33.2	1.7	24.0
E4	4844	17.9	35.6	3.2	26.1
Mean increase over A					
E2	465	1.8 °C	1.3 °C	2.0 °C	1.7 °C
E4	1004	3.4 °C	3.3 °C	3.5 °C	3.5 °C

[*]GDD, accumulated growing day degrees above 5.56 °C, January 1 through December 31;
[†]MAT, mean annual temperature;
[‡]July avg. max; mean of 31 maximum daily temperatures in July;
[§]January avg. min, mean of 31 minimum daily temperatures in January;
[¶]May-Sept, mean of all hourly temperatures (day and night) May through September, or
[**]for 2002, June through September.

cloth. *Populus grandidentata* were propagated from root segments that were collected near Ann Arbor, Michigan, during late autumn. Roots were stored at 5 °C for up to two months, then allowed to form sprouts in greenhouse sand beds. Sprouts were then detached from the root, dipped in rooting powder (0.1% indole-3-butyric acid, Schultz, Bridgeton, MO, USA), and rooted in peat pots. The peat pots were maintained in a mist bed until rooted and then placed into the soil of the OTCs.

Warming treatments

The experiment consisted of nine OTCs, with three replicates of each of three temperature treatments. Targets for control of air temperatures (T) were based on ambient T measured outside the chambers. The treatments were designated ambient (A), ambient +2 °C (E2), and ambient +4 °C (E4). Warming was provided day and night, and throughout the year. These treatments were chosen to provide information on two possible warming scenarios, both within the range of current general circulation model (GCM) projections for the eastern United States (Christensen *et al.*, 2007). By actively tracking ambient T, the treatments incorporated natural variability within and among years. The experiment itself was thus analogous to a series of common garden experiments for the four species. The ambient control chambers (A) formed a replicated set of "gardens" comparable to the local environment. Likewise, the two warmer treatments (E2 and E4) functioned as common gardens for potential future conditions, providing a thermal challenge for all species, but without the photoperiod differences of a latitudinal gradient.

Temperature control and monitoring were provided via three current/voltage output modules (model SDM-CV04, Campbell Scientific) programed to control chamber temperatures, and a data-logger (CR10X, Campbell Scientific). Air temperatures in E2 and E4 chambers averaged 2.3 and 4.0 °C above prevailing T at the site, but the ambient chambers (A), despite evaporative cooling in the summer, averaged 0.58 °C above site T. Air in the E2 and E4 chambers thus averaged 1.8 and 3.5 °C warmer than air in A chambers, respectively, over the course of the experiment (Table 2).

Phenology

Spring phenology was assessed by repeated observations of all seedlings, during the spring of 2003, 2004, and 2005. BB and leaf emergence were assessed for each individual, expressed as a single composite score for the tree. A scale from 1 (no bud activity) to 6 (leaves flat and expanded) was used, adapted from the phenological stages of maple in Norby *et al.* (2003). At stage 2, buds were swollen; at 3, buds were just open and leaf tips were beginning to emerge. At stage 4, leaves had fully emerged from the buds, but were still folded, crinkled, or for *Quercus*, pendant. At stage 5, leaves were unfolded but not expanded. Species and treatment comparisons were made using dates of BB (stage 4 leaf emergence), estimated by interpolation from graphs of mean bud stage as a function of time for each species and treatment.

A variety of potential environmental cues were evaluated for their relationship to the timing of spring leaf emergence, including date, which (at a single site) corresponds to photoperiod, and accumulated growing day degrees (GDD, also "growing degree days"), beginning either on January 1 or March 1. A thermal sum calculation, GDD is the accumulated sum of the daily mean T, after subtracting an arbitrary threshold or base temperature, in this case, 5.56 °C (after Pastor & Post, 1985). A daily mean of 5.56 °C or lower provides zero GDD. GDD are accumulated between time zero (January or March, here) and the event of interest, e.g., BB, which inherently assumes a linear developmental response to GDD (Hunter & Lechowicz, 1992). Other measures of T were also evaluated, including T on the date of BB, mean T for the preceding 10 days period, and minimum T over the five preceding days.

Autumn phenology was assessed in 2002–2005 with two methods. The most straightforward method was the periodic collection of leaf litter from the ground in each chamber, at 5 to 18 days intervals. Litter was separated by species as it was collected from the chamber, and dried to constant mass. Fraction of total litter mass for each species- collection date- chamber was determined after all leaf litter had been collected, and means by species-treatment combination were plotted against time. Comparisons across species, treatments and years were made using the readily interpolated date when 60% of leaves had fallen.

The second method was to monitor the chlorophyll remaining in individual trees, based on a pre-selected subsample of leaves and supplemented by a random sampling of leaves chosen at intervals throughout each crown. Fallen leaves were recorded as zero color. As trees grew and the number of leaves increased, adequately representing the canopy required sampling more leaves, and precision of the estimates likely decreased. For *Populus*, estimates were possible only in 2004, because during the other years, too many of the leaves were damaged by insects, mites or disease, to obtain a representative sample.

Foliar chlorophyll concentrations were estimated at similar intervals using a portable chlorophyll meter (SPAD-502, Konica Minolta Sensing, Inc., Osaka, Japan), a non-destructive method based on light absorption (optical density difference) at two wavelengths. Unitless SPAD values were converted to chlorophyll concentrations using a calibration established from a subsample of leaves of each species. For calibration, leaf tissue was incubated in 90% ethanol for 48 h in the dark. Extracts were measured with a multi-wavelength spectrophotometer and total chlorophyll calculated according to Lichtenthaler & Wellburn (1983). The relationship ($R^2 = 0.83$) between SPAD value and total chlorophyll in mg m^{-2} was:

$$\text{Chlorophyll} = 0.784 \times \text{SPAD} \tag{1}$$

As with BB and litter mass data, a mid-process date (50% of initial chlorophyll) was estimated by interpolation from plots of mean chlorophyll content as a function of date.

Forest stand data

Canopy phenology records for a nearby forest stand were obtained over a 16 years period, as part of a water manipulation study, although the treatments had no effect on phenology

(Hanson *et al.*, 2003a). *Quercus*, *Carya*, and *Acer* species, along with *Nyssa sylvatica*, *Liriodendron tulipifera*, and *Cornus florida* were common on the plots (Hanson *et al.*, 2003a). Relative leaf area index (LAI) was calculated using daily sums of photosynthetically active radiation above and below the canopy (Hanson *et al.*, 2003a). Day of year when the canopy achieved 30%, 50%, and 70% of maximum LAI was interpolated from the annual plots of relative LAI.

Statistics

Response variables (dates of defined phenological stages and days of advancement or delay) were evaluated for differences by one-way analysis of variance for treatment differences within species and by two or three-way ANOVA for species, treatment, and sometimes year interactions, using chamber as the unit ($n = 3$). Quantitative relationships between BB and specific T variables were evaluated by linear regression and multiple linear regression, using maximum R^2 improvement (MaxR) for model selection within Proc Reg (SAS), minimizing Mallow's C(p). All analyses were performed using SAS software (SAS Institute, Cary, NC).

Results

Spring BB and leaf expansion

Trees in the warmed E2 and E4 chambers reached each stage of bud swell, leaf emergence, and leaf expansion earlier than the trees in the ambient (control) chambers (A), and trees in the E4 chambers were ahead of those in E2 (Fig. 1). This treatment pattern was significant ($P < 0.01$) and consistent across species and years, despite within- and between-chamber variation. The absolute dates of BB, that is, stage 4 leaf emergence (BB date, *y*-axes Fig. 2a, b) also varied by species and from year to year (both $P < 0.01$). *Liquidambar* was the first species to break bud, followed by *Betula* and *Populus*, and lastly, *Quercus*, which was later than *Liquidambar* by 20–30 days. Across treatments and years, date of BB varied within a species by 17–37 days (Fig. 2, *y*-axes). For each species and year, however, BB was earlier ($P < 0.01$) in the warmer chambers.

The extent to which BB was advanced by warming also varied by species (Fig. 3), although the species differences were significant only at the $P = 0.11$ and $P = 0.07$ level for the advance at 2 and 4 °C warming, respectively. This is related to the high intra-species variation in *Populus* and *Liquidambar*; in fact, year-to-year differences were significant at the 6% level ($P = 0.06$) in the E4 treatment. *Liquidambar* leaves emerged an average of 9 and 14 days earlier in E2 and E4 treatments, respectively, than in the A chambers (Fig. 3), despite the smaller responses in 2005 (4 and 6 days advancement). The effects of warming were
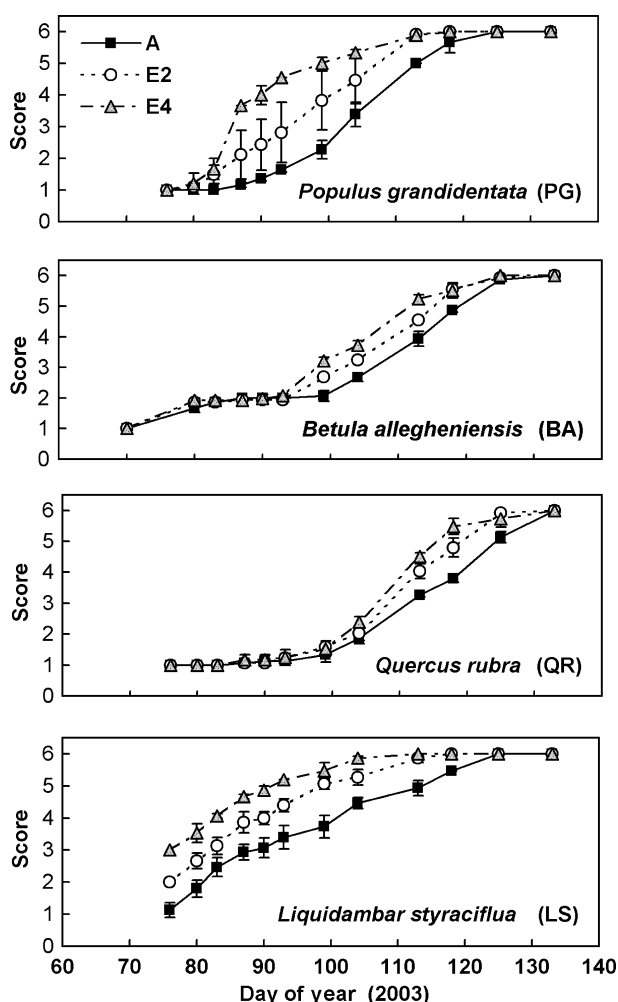

Fig. 1 Mean score for leaf emergence in a representative year, spring of 2003. Individual trees were assessed (see text) and averaged within a chamber to obtain a chamber score for each species. Points and bars represent the mean and standard error of $n = 3$ chamber scores. Species are *Betula alleghaniensis* (BA), *Populus grandidentata* (PG), *Liquidambar styraciflua* (LS) and *Quercus rubra* (QR). Target treatments were A, tracking ambient temperatures; E2, Ambient +2 °C; and E4, Ambient +4 °C.

smaller, but still pronounced, in the other species. The E4 treatment hastened BB by 11, 7, and 6 days in *Populus*, *Betula*, and *Quercus*, respectively. Dates of BB in E2 were intermediate between dates in A and E4 (Fig. 3).

In general, the earlier trees began to leaf out, the larger the effect of the imposed warming treatment on hastening BB. This was true for year-to-year differences within a species ($R^2 = 0.57–0.95$) and across all species and years ($R^2 = 0.7$; $P < 0.01$, Fig. 4). For example, *Liquidambar,* the earliest species to break bud, usually showed the greatest treatment effect, but the acceleration was shorter in 2005 when BB began later in the spring. Similarly, *Quercus* and *Betula*, with typically late
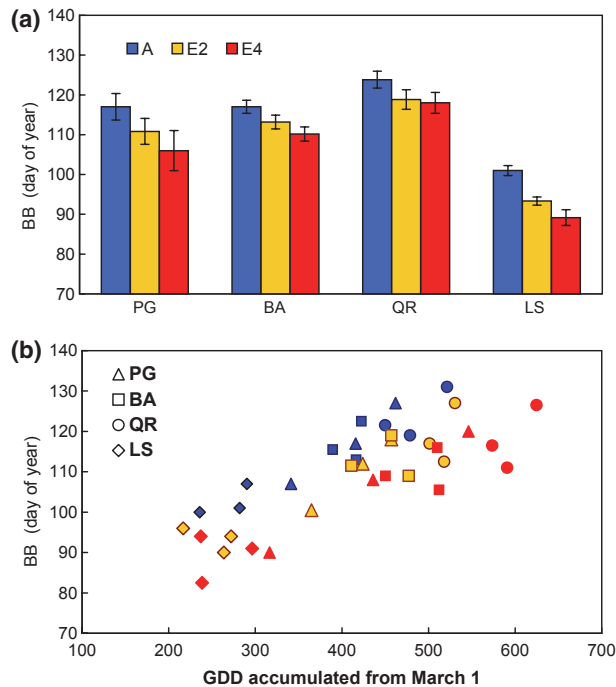
(a)

(b)

Fig. 2 Date of stage-four leaf emergence (bud burst, BB, see text) (a) Mean BB dates by species. Bars are standard error of $n = 3$ years. (b) BB date in each species, treatment, and year of the experiment. BB dates are plotted as a function of growing day degrees accumulated beginning March 1. Species (indicated by shape of symbols) are abbreviated as in Fig. 1. Color represents the treatment: Blue = A; Yellow = E2; Red = E4, defined as in Fig. 1. Symbols of matching shape (species) and color (treatment) represent BB in different years. Each symbol is the mean of $n = 3$ chambers.
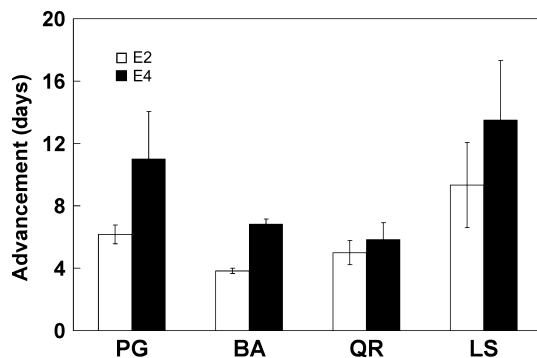
Fig. 3 Advancement of bud burst (BB) by warming treatments, relative to ambient leaf emergence. Species and treatments abbreviated as in Fig. 1. Mean and standard error of 3 years.

BB, showed the least effect of warming on BB (Fig. 3, 4). Dates of BB in *Populus* were most variable, ranging from day 90 to 120 in the E4 chambers, with the largest advancement (17 days) observed in 2003, the year of earliest BB.
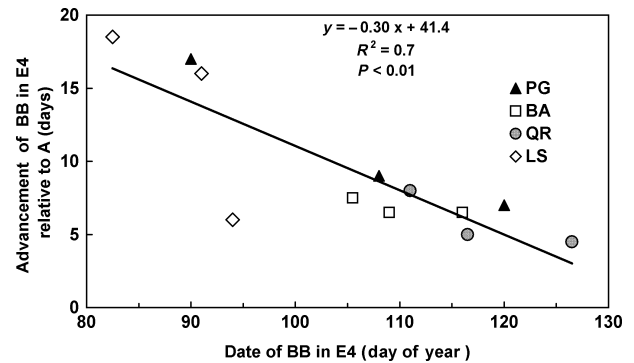

Fig. 4 Days of advancement of bud burst (BB) in E4 relative to A, as a function of the date when E4 trees reached BB (stage 4, see text). Each point represents a species-year combination (mean from 3 chambers). Species indicated by symbols, abbreviated as in Fig. 1.

Environmental drivers

Because BB did not occur at a constant photoperiod (i.e., date) for a species, but varied significantly with treatment and year (both $P < 0.01$, Table 3), several temperature-related parameters were explored to explain the variation, including a traditional fixed GDD trigger. As expected, species differed from one another, but the GDD accumulated between January 1 and BB was highly variable, even within a species. In fact, GDD_{JAN} sums differed by as much as 180 to 430 GDD within a single species, related to both treatment and year ($P = 0.01$, Table 3). In all cases, trees in E2 and E4 treatments accumulated successively more GDD_{JAN} at BB than did trees in A, even though the dates of BB were earlier in warmed chambers. Accumulating thermal sums starting on March 1 (GDD_{MAR}) reduced the inter-annual and treatment variability within a species (Table 3) by approximately one-half, but in *Betula* and *Quercus*, GDD_{MAR} at BB still increased consistently with warming treatment (*x*-axis, Fig. 2). A species' mean GDD_{MAR} could predict BB within 3 days for 50% of the observations, but error in the remaining predictions extended from 12 days early to 9 days late. Mean absolute error in prediction was 3.5 days. The short-term (10 days) average T before BB was not a particularly good indicator, either, as it tended to vary with treatment such that the 10 days before BB were successively warmer from A to E2 to E4 chambers for eight of 12 species-year combinations (*ns* at the 5% level). The coefficient of variation of T_{avg} was lower than that of GDD_{MAR} only for *Populus* (Table 3). Minimum T (5 days) and T on the day of BB were less effective and more variable (Table 3).

Because none of the temperature parameters fully explained the variability in BB date, multiple linear

Table 3 Environmental parameters associated with budburst (BB) in four species and three temperature treatments over 3 years. Mean and coefficient of variation (CV) and significance probabilities for differences associated with year and warming treatment (Trt)

	Betula alleghaniensis				*Liquidambar styraciflua*				*Populus grandidentata*				*Quercus rubra*			
	Mean	CV (%)	Year	Trt	Mean	CV (%)	Year	Trt	Mean	CV (%)	Year	Trt	Mean	CV (%)	Year	Trt
Day of year	113	5	<0.01	<0.01	95	7		<0.01	111	10	<0.05	<0.01	120	6	<0.01	<0.01
GDD_{JAN}	588	18	<0.01	<0.01	397	14		<0.01	556	24	<0.01	<0.05	669	18	<0.01	<0.01
GDD_{Mar}	450	10	0.01	<0.01	259	11	0.01	0.03	418	17	0.01		532	10	0.01	<0.01
10 days T_{avg} (°C)	15.6	14			15.2	13			15.1	10			17.7	13		
T_{date} at BB (°C)	17.1	28	0.02		14.7	25			15.2	24			19.5	16		
5 days T_{min} (°C)	7.8	37			8.2	33			7.4	40			10.3	36		

Day of Year, day that leaves reached stage 4 budburst (BB, see text); GDD_{JAN}, Growing day degrees (GDD) accumulated from January 1 until BB; GDD_{MAR}, GDD accumulated from March 1 until BB; 10 days T_{avg}, mean of average daily temperature (T) for the 10 days preceding BB; T_{date}, average T on the date of BB; 5 days T_{min}, mean of daily minimum temperatures for the 5 days preceding BB.

regression was performed. Although individual models could explain 67–95% of within-species variation, none of the combinations were useful for all of the species. The number of parameters contributing significant improvement to the models also varied by species, and although none of the (correlated) parameters emerged as universally the most useful, each explained a significant portion of variability for at least one species.

Autumn senescence and leaf abscission

Comparisons of senescence across species, years, and treatments were based on date of 50% foliar chlorophyll loss, determined by interpolation (e.g., Fig. 5). This date varied by species and by year, as well as with treatment (all $P < 0.01$). *Populus*, then *Betula*, were earliest to lose chlorophyll, followed by *Liquidambar*, whereas *Quercus*
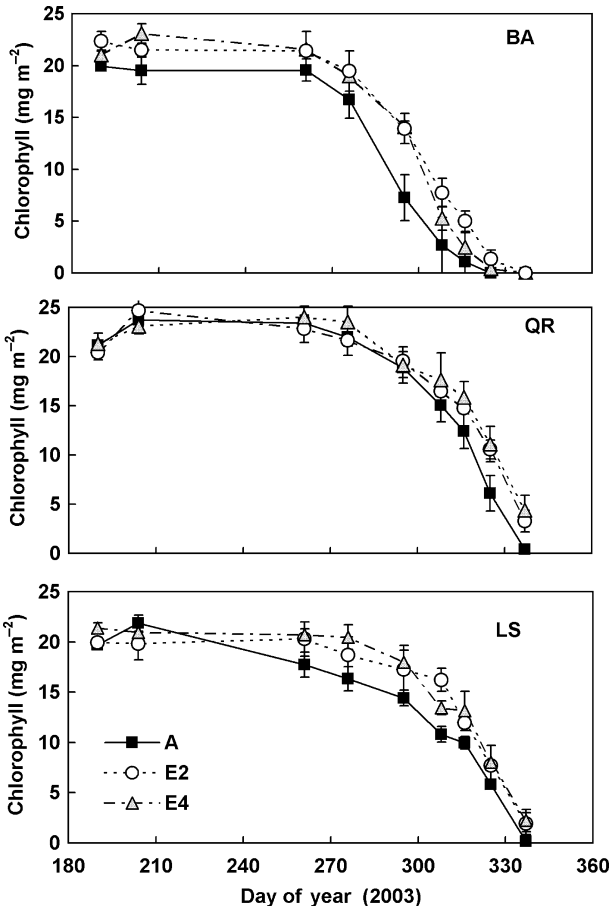

Fig. 5 Chlorophyll content, on an area basis, for a representative year, 2003, in July and during autumn, in leaves of *B. alleghaniensis* (BA), *L. styraciflua* (LS), and *Q. rubra* (QR) seedlings. Symbols represent means and their standard errors. Foliar chlorophyll was estimated with a SPAD meter (unitless) and converted using Eqn (1). Leaves of *P. grandidentata* suffered extensive mite damage and could not be assessed in 2003.

retained its pigments 20–30 days longer than did *Populus*. Color was retained the longest in 2002, the year of planting, in fact, into December, which is very unusual.

Leaves in the warmer chambers retained their green color and chlorophyll content up to 16 days longer than did leaves in A chambers, but in some cases the delay was negligible, e.g., for *Quercus* in 2003, Fig. 5). The average delay in pigment loss was 4.6 and 7.5 days in E2 and E4 chambers, respectively, or approximately 2 days $°C^{-1}$, but the extent of the delay varied somewhat by year ($P < 0.02$ in E2; $P = 0.12$ in E4) and by species ($P = 0.12$ in E2; $P < 0.04$ in E4). Four-year average delays for the species (Fig. 6a) varied from 3 to 10 days in E2, and from 4 to 16 days in E4. The largest delay was in E4 *Populus* in 2004 (Fig. 6a), the only year that color in *Populus* leaves could be monitored effectively, because of extensive mite damage in other years. The largest consistent difference with warming was in *Betula* (Fig. 5, 6a), but visible differences were most striking in *Liquidambar*, as foliage in the A chambers changed to yellow and deep red, while trees in the warmer E2 and E4 chambers retained progressively more green color.

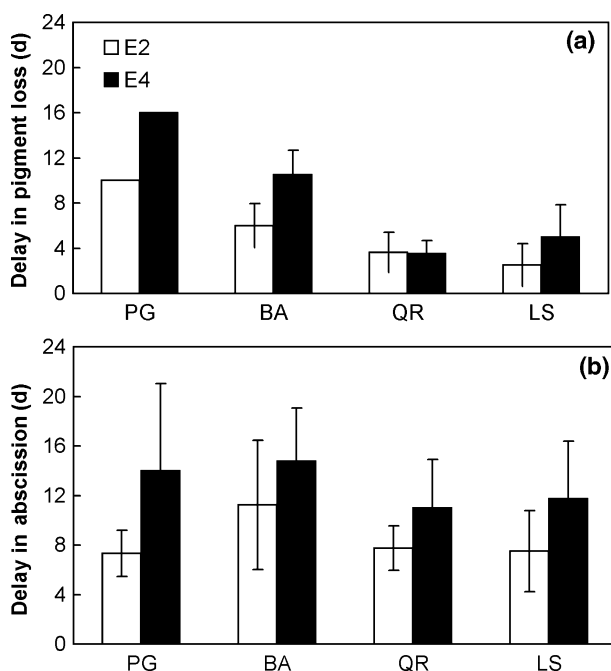Although the treatment delays demonstrated that later chlorophyll loss was related to warmer chambers, neither the 10-day or 20-day average T before date of half-color loss was positively correlated with that date. The T variable that did relate later chlorophyll loss to warmer air T (within species) was the mean August–September T (2003–2005). The relationship held for year-to-year and treatment-year variation, but was significant only in *Betula* ($P = 0.04$). Timing of chlorophyll loss was not positively correlated with T means over other time periods (September alone, September-October, or September-October).

Trees in the warmer chambers also *retained* their leaves longer than did those in the ambient chambers, with abscission later in E4 chambers than in E2 (Fig. 6b, 7). Dates for 60% leaf loss, even in A chambers, varied by year and by species (both $P < 0.01$), but they were clearly delayed by the warming treatments ($P < 0.01$). Abscission date in ambient (A) chambers ranged from day 286 (*Betula*, 2003) to day 361 (*Liquidambar*, 2002). As with chlorophyll loss, the best correlate for abscission date was mean August–September T. The *delay* in date of abscission with warming treatment ($P < 0.01$) was also variable, ranging from delays of a day or two (*Betula*, *Liquidambar*, 2005) to a 29-day delay (*Populus*, 2004) in E4 relative to A. Year-to-year differences in length of the delays were marginally significant ($0.05 < P < 0.10$), and were larger than species differences (e.g., mean delays by year in E4 chambers (across species) ranged from 3.3 days in 2005 to 20 days in 2004). Species differences were inconsistent from year to year, and 4 years means (Fig. 6b), from 11.8 days (*Liquidambar*) to 14.8 days (*Betula*) were not significantly different among species ($P = 0.4$).

The magnitude of the delay in abscission was also correlated with the calendar date of leaf-loss in A. In general, earlier leaf-loss (in ambient conditions) was associated with a greater time difference between abscission in A and in the warmed chambers. In E4, where the relationship was strongest, across all species and years,

$$\text{Delay in E4} = -0.283 \times DOY_A + 101.5 \ (P = 0.03), \quad (2)$$

where DOY_A is day of year when trees in A had lost 60% of leaves. This was similar to the relationship between earlier BB and a longer time span between BB in E4 and BB in A. Without the unusually late 2002 leaf-fall, relationships within species were extremely tight ($R^2 = 0.74$–0.99; $P < 0.01$ to $P = 0.3$), with slopes between -1 and -1.83.

Fig. 6 Autumnal extension of the growing season by warming in E2 and E4 treatments compared to unheated (A) controls. Means of four autumns, 2002–2005. (a) Delay in senescence, evaluated using the date of 50% loss of chlorophyll. *Populus* values are from 2004 only. (b) Delay in leaf abscission, measured by date when 60% of the leaf litter had fallen. *Populus* leaf litter was collected in 2003–2005. Bars are ± 1 SEM.

Length of growing season

The combination of earlier leaf emergence and later senescence resulted in a growing season (GS) longer by a mean of 14 and 23 days longer in E2 and E4, respectively
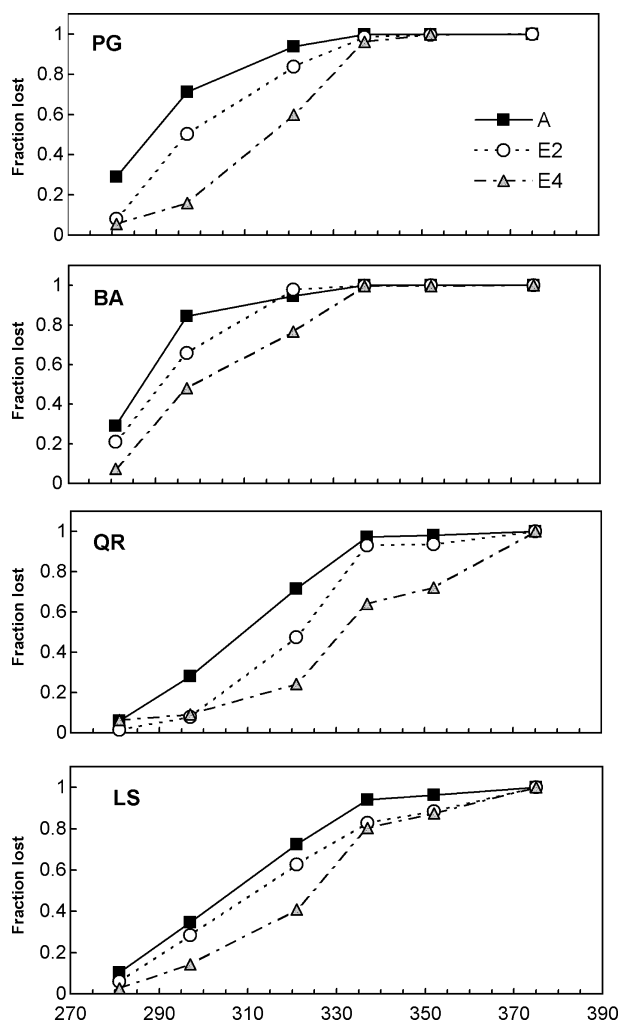
Fig. 7 Fraction of total leaves abscised, by species, in each treatment (*y*-axis), on various dates during a representative autumn (2004). Abbreviations as in Fig. 1. Symbols represent mean and standard error from three chambers per treatment.

Fig. 8 Mean extension of the growing season in E2 (+2 °C) and E4 (+4 °C) atmospheric warming based on observation of four autumns (one autumn in PG) shown as solid portion of the bar, and three springs, hatched portion. Error bars are standard error of the mean; abbreviations as in Fig. 1.

data, whether or not spring and fall phenology data could be paired. Data from three springs and four autumns suggest that a 2 °C warming might, on average, extend the GS by 9 days (*Quercus*) to 17 days (*Populus*), depending on species (Fig. 8). Likewise, a 4 °C warming might add from 9 to 27 days. Given that both spring and fall could be extended the maximum (or minimum) number of days in the same year, the potential impact of a + 4 °C warming could range from 5 to 33 more days in the GS.

DISCUSSION

Earlier leaf emergence in spring

The rate of BB and canopy development in temperate and boreal forests is generally accelerated by warmer temperatures (Wang, 1960; Murray *et al.*, 1989; Hunter & Lechowicz, 1992; White *et al.*, 1997; Menzel *et al.*, 2006). Consistent with that pattern, BB was hastened by E2 and E4 warming treatments in all four species, and in all years of the experiment, even in species growing well outside their native ranges. The advancement of BB varied by species and by year, from 4 to 13 days (mean 6.2 days) in E2, roughly 2–6 days per °C of warming, for a mean advance of 3.1 days °C^{-1}. In E4, BB was accelerated by 5–17 days (mean 9.3 days), or 1 to 4 days °C^{-1}, averaging 2.3 days °C^{-1}.

Responses were comparable to those of *Acer saccharum* and *A. rubrum* saplings grown at the same TN site, where BB was usually 4–12 days earlier in the +4 °C chambers, for an average advance of 2 days °C^{-1} (Norby *et al.*, 2003). In other field experiments, a range of tree species have responded to artificial warming (+1.5 to +5 °C warmer) with BB advanced by 6–27 days. In those studies, rates of BB advance varied from 1 to 9

(P < 0.01). Except for *Populus*, both spring and fall phenology data were available for three of the years (2003–2005). Actual GS lengths in those years, based on dates of BB and chlorophyll loss in spring and fall of the same year, differed with species, year, and treatment (P < 0.01 for all three factors), but there was not a significant interaction between species and warming treatment (P = 0.37). The number of days added to the GS in E2 and E4 chambers varied as much with year (P < 0.01, P = 0.07 for E2 and E4) as it did with species (*ns*, P = 0.2, 0.1). The days added by the E2 treatment ranged from 5 days (all species, 2005) to 18 days (*Liquidambar*, 2004). The E4 warming treatment added from 6 days (*Quercus*, 2005) to 28 days (*Liquidambar*, 2004).

The range of potential GS responses for each species was also calculated using all BB and chlorophyll loss
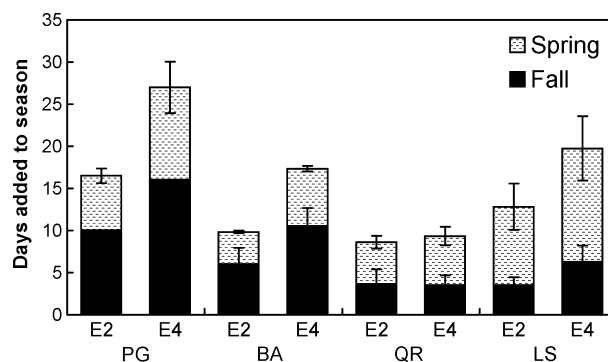
days °C^{-1}, with a median response of 4 days °C^{-1} (Repo *et al.*, 1996; Guak *et al.*, 1998; Norby *et al.*, 2003; Slaney *et al.*, 2007; Bronson *et al.*, 2009; Morin *et al.*, 2010). Significant year-to-year variation was also observed within studies as it was here.

Natural variation in BB reveals a similar pattern, e.g., over a 62 years period in a northern taiga forest, BB in *Betula* was earlier by 2.5 days °C^{-1}, based on mean T during March, April and May (Kozlov & Berlina, 2002). Over an approximately 50 years record in eastern Europe, BB in *Quercus* advanced 2.8 days °C^{-1} (Askeyev *et al.*, 2005) based on March and April T. In a 3 years study, four species in an elevational gradient showed an advance in BB of 2–7 days °C^{-1}, based on a 3 months mean T (Vitasse *et al.*, 2009). Using a combined leaf-unfolding index, Chmielewski (2002) identified a response of 6.7 days °C^{-1} in a 30 years record of BB in four European woody species. A meta-analysis using 160 long-term phenological time series, from 21 European countries, revealed a recent temperature-correlated advance in BB and flowering in many species, corresponding to an average of 2.5 days °C^{-1} for tree species (Menzel *et al.*, 2006). Similarly, long-term East Asian records revealed a mean response of 3–3.5 days °C^{-1} (Ibáñez *et al.*, 2010), and 2.9 days °C^{-1} in *Ginkgo* (Matsumoto *et al.*, 2003). Distinct species differences were identified in the long-term data sets, as they were in glasshouse and common garden studies (Murray *et al.*, 1989; Chuine & Cour, 1999). For species with earlier BB, there was more variability in date of BB, in conjunction with a higher temperature sensitivity (Bradley *et al.*, 1999; Sparks & Menzel, 2002), similar to our findings, e.g., Fig. 4.

Expressing the effects in days per °C suggests a linear relationship, as observed in altitudinal populations grown in common gardens (Vitasse *et al.*, 2010), and the only contradictory evidence from long-term records is at the cold end of the range, for flowering (Sparks & Menzel, 2002; Menzel *et al.*, 2005). There remains, however, a hesitancy to use a linear extrapolation of BB responses, especially beyond temperatures in the historic record (Sparks & Menzel, 2002; Menzel *et al.*, 2005; Ibáñez *et al.*, 2010; Man & Lu, 2010; Richardson *et al.*, 2010). Experimental studies with two levels of warming have reported a larger impact for the first warming increment (in days °C^{-1}) than for the second (Greer *et al.*, 2005; Morin *et al.*, 2010; this study). We found no evidence, however, for a shorter total advance of BB with greater warming, e.g., of BB in E2 preceding that in E4, as suggested by the chilling requirements of some models (Morin *et al.*, 2009). Further, BB response rates in the current study were not lower in *Populus* and *Betula* than in the southern species, even though mean annual temperatures (MAT) in A chambers were

already 5–7 °C warmer than MAT at their provenance, such that additional warming might have interfered with a chilling requirement.

Non-linear responses with increasing degrees of warming could indicate a diminishing effect on cellular processes, or a constraining interaction with photoperiod (Häkkinen *et al.*, 1998; Morin *et al.*, 2010) or chilling sum (Murray *et al.*, 1989; Guak *et al.*, 1998; Morin *et al.*, 2009) or both (Cannell & Smith, 1983). A diminishing effect of increasing warming on BB occurred even with identical chilling periods, however, in a root-warming study in *Malus* (apple; Greer *et al.*, 2005). Conversely, the effect of added warming sometimes appears larger under warmer background conditions; long-term phenological records revealed larger responses at warmer climate stations (Menzel *et al.*, 2005) and in warmer countries (Menzel *et al.*, 2006).

Environmental cues

Although the influence of spring temperature on BB has long been recognized, there is no consensus on the details of the relationship, judging by the array of different models used to predict BB (White *et al.*, 1997; Chuine, 2000). Some models, common in analyses of historic records, are based on a threshold T, or the mean, minimum, or maximum T over a particular time period (Primault, 1992; Askeyev *et al.*, 2005; Borchert *et al.*, 2005; Gordo & Sanz, 2005, 2009; Vitasse *et al.*, 2009; Pinto *et al.*, 2011). Many others predict BB using a critical thermal sum model, e.g., GDD accumulated above a threshold T, frequently 0 or 5 °C (Wang, 1960; White *et al.*, 1997; Rousi & Heinonen, 2007; Man & Lu, 2010), an approach dating from Réaumur's work in 1735 (Wang, 1960; Primault, 1992; White *et al.*, 1997). Originally, GDD models accumulated temperature sums from an arbitrary fixed date, often January 1, and for trees, often 5 °C (Murray *et al.*, 1989; Rousi & Heinonen, 2007), although dates from January 1 to April 10 and threshold T's ranging from −5° to +15 °C have been used effectively (Hunter & Lechowicz, 1992; Hänninen *et al.*, 2007; Man & Lu, 2010). Rather than use a fixed date, critical GDDs are sometimes modeled as varying with one or more other factors, such as accumulated chill time (Murray *et al.*, 1989; Hunter & Lechowicz, 1992; Chuine & Cour, 1999), photoperiod (Heide, 1993; Linkosalo *et al.*, 2000; Borchert *et al.*, 2005; Caffarra *et al.*, 2011a,b), or MAT (White *et al.*, 1997). Models of BB based on GDD and chilling units have also been interpreted as special cases of a more general model, with species-specific base temperatures and response slopes (Chuine, 2000).

Accumulated GDD from a fixed date is sometimes quite effective for predicting BB. For example, BB in

two *Acer* species in a warming experiment varied by only 20–37 GDD (under *most* conditions; Norby *et al.*, 2003). Median BB varied by 37 GDD over 9 years in mature *Fagus* (Rousi & Heinonen, 2007), and by 89 GDD in progeny trials of *Larix* buds (Gauchat & Paques, 2011). In the current experiment, however, GDD at BB was more variable, and when accumulated from January 1, varied by 180–430 GDD, depending on species. Within a treatment, inter-annual variation in accumulated GDD was correlated with date of BB. As in Rötzer *et al.* (2004), GDD_{JAN} values for a species were higher in years with later BB. Rötzer *et al.* (2004) concluded that the threshold GDD for BB rises as the year proceeds, though this conflicts conceptually with other models where long days reduce the GDD requirement (Heide, 1993).

Treatment-related differences were consistent; trees always accumulated more GDD_{JAN} in the warmed chambers, just as they did in warming experiments with *Picea abies* (Slaney *et al.*, 2007) and *Pseudotsuga menziesii* (Guak *et al.*, 1998). In growth chambers, GDD at BB also increased with treatment T in *Picea glauca* seedlings (Man & Lu, 2010). These experimental findings are consistent with a set of forest observations in the northeastern United States, where GDD values at BB were almost double at the more southerly (warmer) of two sites (Richardson *et al.*, 2006). Likewise, at a continental scale, White *et al.* (1997) found that GDD requirements were best modeled as increasing with MAT.

In this experiment, accumulating GDD beginning March 1 narrowed the within-species range by half or more, and eliminated the treatment bias in *Liquidambar* and *Populus*, giving better predictions than GDD_{JAN} or mean day-of-year. Slaney *et al.* (2007) similarly reduced the treatment discrepancies in *Picea* by starting on April 1, but ruled out a chilling constraint because of the boreal location. GDD models are also sometimes optimized with species-specific start dates or threshold temperatures (Heide, 1993; Chuine, 2000). In the same *Picea* experiment (Slaney *et al.*, 2007), Hänninen *et al.* (2007) found that a start date of either March 21 or April 10 satisfied a "best fit" optimization, although with markedly different GDD estimates. In this experiment, using GDD_{MAR} (Fig. 2) left a within-species variation from 80 to 230, a range of uncertainty similar to those accepted for model development (e.g., Richardson *et al.*, 2006).

Whatever the constraint, better performance of GDD with later start dates indicates that above-freezing temperatures in mid-winter months do not promote BB. This has been attributed to an unfulfilled requirement for chilling, or "rest completion" (Murray *et al.*, 1989; Hunter & Lechowicz, 1992; Guak *et al.*, 1998; Hänninen *et al.*, 2007; Morin *et al.*, 2009) or to a photoperiod

constraint (White *et al.*, 1997; Caffarra *et al.*, 2011a,b). In our experiment, GDD_{MAR} at BB still increased with warming treatment in *Quercus* and *Betula*, potentially because of a chilling restraint. Some additional evidence for a chill time interaction was inadvertently provided while forcing *Populus* roots in the greenhouse for the field study. Roots that had remained longer at cold room temperatures required less time in the greenhouse for sprouts to form, i.e., longer chilling seemed to hasten the BB of dormant root buds, as found in a controlled study with *Betula* budsticks (Caffarra *et al.*, 2011a). A chilling co-requirement might account for a higher GDD accumulation under elevated temperatures, but the accumulation of more GDD_{JAN} in E2 and E4 was similar in all species, even though chilling requirements vary by species (Murray *et al.*, 1989; Schaber & Badeck, 2003); adding a chilling interaction improved BB modeling for only half of 26 temperate species (Hunter & Lechowicz, 1992). Photoperiod thresholds have also been useful in modeling BB, but only in late-flushing species (Hunter & Lechowicz, 1992; Schaber & Badeck, 2003). Consistent with those results, the later BB of *Quercus* and *Betula* was less affected by warming treatments, and effects of treatment were smaller when all species flushed late (i.e., when days were longer). Photoperiod was not an overriding factor here, however, as BB date varied by 17–20 days even in *Betula* and *Quercus*, and BB was always earlier in warmer chambers. The two constraints might also interact, e.g., the critical photoperiod for BB could decrease with chilling exposure. (Caffarra *et al.*, 2011a)

This experiment provided a unique combination of four species (early-and late- leafing, of northern and southern origin) growing for 4 years at three temperature levels, under otherwise common conditions. This eliminated differences in such factors as precipitation, photoperiod, or total solar radiation which can confound interpretations of gradient studies and long-term data sets. It is nonetheless impossible to distinguish between chilling and photoperiod requirements even in an experiment, because of the inherent correlations (Hunter & Lechowicz, 1992; Morin *et al.*, 2010). Several empirical models could prove equally effective, yet not be indicative of the underlying mechanisms (Hunter & Lechowicz, 1992; Schaber & Badeck, 2003). Because the many empirical models are based on largely theoretical relationships, e.g., with chilling or photoperiod, differences among models may seem arbitrary, but may arise from real species differences in sensitivity. More complex models, however, are not always more accurate, and simple regression models, using readily available meteorological data may be adequate to identify key climatic factors or describe species differences (Gordo & Sanz, 2009). Yet without a mechanistic basis, all models

should be applied with some caution to future climate projections.

Autumn phenology

There is far less consensus on the environmental cues for leaf coloring and abscission in autumn, partly because the pool of ground observations is much smaller, and events (e.g., percentage of color) may be more difficult to quantify (Sparks & Menzel, 2002; Estrella & Menzel, 2006; Menzel *et al.*, 2006; Richardson *et al.*, 2006; Delpierre *et al.*, 2009; Vitasse *et al.*, 2009; Gordo & Sanz, 2010). Observations of growth cessation, bud set, senescence, abscission, and cold-hardiness represent different aspects of "autumn syndrome" (Heide & Prestrud, 2005), mediated through an array of signaling pathways (Taylor & Whitelaw, 2001). These pathways likely respond to different cues, yet the limited pool of autumn observations includes them all. At larger scales, autumn observations may rely on ground- or satellite-based estimations of color change; abscission dates may be based on light transmission through the canopy or leaf-litter collections, even though leaf fall can be induced prematurely by extreme temperatures, drought, insects, or pathogens, and may respond to a single episode of high wind, rain, or frost (Taylor & Whitelaw, 2001; Sparks & Menzel, 2002; Delpierre *et al.*, 2009;).

Because photoperiod is a generally accepted autumnal trigger, the potential impact of warming on the end of the GS is sometimes ignored or dismissed (e.g., White *et al.*, 1999; Saxe *et al.*, 2001; Schaber & Badeck, 2003), yet inter-annual differences beg an explanation (Estrella & Menzel, 2006; Delpierre *et al.*, 2009). Although sensitivity may differ with species, a relationship between leaf coloration and a threshold temperature was postulated by 1955 (Dittmar & Elling, 2006). A temperature component is also supported by the phenological record. For example, in long-term data from four species, Estrella & Menzel (2006) calculated correlations ($0.39 \leq r \leq 0.63$) between onset of leaf color and occurrence of a threshold low T. They found similar correlations ($0.45 \leq r \leq 0.56$) with mean September and August temperatures, but only for regionally pooled data. In a shorter time series, autumn temperatures were the primary cue for senescence in two *Quercus* species (delayed 3.3 days °C^{-1}), while in *Fagus* (delayed by 2.2 days °C^{-1}), photoperiod appeared to play a role as well (Delpierre *et al.*, 2009).

There is also experimental evidence of a role for temperature. In *Populus*, although senescence was triggered by long nights, lower T accelerated chlorophyll degradation (Fracheboud *et al.*, 2009). Conversely, senescence in *Malus* and *Pyrus* was induced by low T, and insensitive

to photoperiod (Heide & Prestrud, 2005). The leaves in our study remained green much later than normal in the year of planting, apparently insensitive to the long nights of late autumn, but responsive to differences in T treatment. Warming delayed autumn phenophases in all four species, regardless of differences in photoperiod between source and field site. Species rankings for senescence responses were unrelated to latitude or climate of origin. Delays in leaf abscission were more pronounced than delays in chlorophyll loss, but all four species responded similarly.

Long-term records suggest that the end of the GS is occurring later over time, in correlation with increasing atmospheric temperatures (Sparks & Menzel, 2002; Ibáñez *et al.*, 2010). Leaf coloring was delayed on the order of 1 or 2 days °C^{-1} in European records (Menzel *et al.*, 2006), and leaf fall in Mediterranean species was significantly delayed in warmer autumns, but with low regression coefficients (Gordo & Sanz, 2010). In East Asian species, however, autumn changes were more pronounced than those in spring, with delays of 3.6–5.4 days °C^{-1} (Ibáñez *et al.*, 2010), and in *Ginkgo*, 4.4 days °C^{-1} (Matsumoto *et al.*, 2003). As further confirmation of species differences, no trends with T were identified in populations of *Fraxinus* or *Acer* along an altitudinal gradient, but in *Quercus* and *Fagus*, senescence was delayed by warmer August-November temperatures, by 5–6 days °C^{-1} (Vitasse *et al.*, 2009). In contrast with these studies that correlate delays in leaf coloring and abscission with higher temperatures, Kramer (1995) noted that in some species in his study, abscission was earlier, not later, at warmer sites. This apparent anomaly may relate to characterizing the sites by mean T for May through September, whereas temperature-related delays in other studies were specifically associated with higher autumn temperatures, e.g., the 85 days preceding leaf fall (Matsumoto *et al.*, 2003). Similarly, later leaf coloring correlated with warmer August and September T, but higher T in May and June was associated with earlier leaf color and fall (Estrella & Menzel, 2006).

Experimental warming studies, like the one reported here, provide platforms where photoperiod, rainfall, and other relevant factors are consistent across treatments. Such studies, though still rare, have been done in several different biomes, with a variety of species, not all deciduous. Both the warming techniques and the amount of warming applied have also varied, with understandably mixed results. Leaf coloring was delayed by 10–15 days in one *Quercus* species warmed by infrared lamps, yet it was slightly earlier in another (Morin *et al.*, 2010). Passive (daytime) warming had no impact on leaf yellowing in dwarf arctic willow (Jones *et al.*, 1997). In contrast, two temperate deciduous

maple species exposed to continuously warmed air, as in our study, showed significant delays in abscission for each of three autumns (Norby *et al.*, 2003), ranging from 4 to 22 days later in +4 °C chambers (1–5.5 days °C^{-1}), comparable to the average delay of 1–4 days °C^{-1} for the species in this experiment.

Scaling to the forest: inferences, caveats, and an example

From the present experiment as well as others, we conclude that a warming climate can extend canopy duration in the temperate deciduous forest, at both ends of the season, by 5–30 days for a + 4 °C warming. Most species are responsive to temperature, despite any complex and species-specific interactions with photoperiod and chilling. Our findings also support the observation that the impact on early spring events will likely be more pronounced than on later phenophases.

With species differences largely undefined, and underlying mechanisms unresolved, regional and even stand-level scaling will remain challenging. There is a degree of uncoupling between experimental and historical phenology records, which are based on detailed species-specific observations, and the multi-species estimates of canopy duration derived from satellite "greenness" indices, or at a smaller scale, seasonal changes in atmospheric [CO$_2$] or canopy light transmission (White *et al.*, 1997; Botta *et al.*, 2000; Hanson *et al.*, 2003a; Jolly *et al.*, 2005; Richardson *et al.*, 2010). The various methods provide complementary, but qualitatively different, information (Badeck *et al.*, 2004). Even combining results from multiple ground-based studies is complicated by the array of specific stages evaluated for the same basic event. Some observers record first appearance (of a leaf, or leaf color), others use a descriptive definition, e.g., of BB stage, or a fractional change (i.e., % of canopy fill, leaf litter, color development). Only a few report more than one temperature metric, and they vary from mean (or extreme) T for various time periods to thermal sums (GDD), each calculated slightly differently.

Next, atypical weather patterns can introduce considerable noise, because plants respond not only to convenient summary variables, but also to short-term variation. A sudden brief but sharp cold period in the midst of a warm spring can delay BB as if resetting the signal (Norby *et al.*, 2003; Rousi & Heinonen, 2007), with minimal impact on mean T or GDD. The relationship with "temperature" in such a year would likely lie outside the normal pattern. In a short time series, one atypical year could alter or obscure the more general relationship with temperature.

Some of these scaling issues can be illustrated by comparing our experimental results with the 16 years record of canopy leaf-out and development from a nearby stand of mixed deciduous forest on Walker Branch Watershed (WBW; Hanson *et al.*, 2003a,b, 2005). Day of year when the canopy achieved 30%, 50%, and 70% of maximum LAI are plotted for spring (Fig. 9a) and fall (Fig. 9a). The average time between 30% and 70% canopy fill was 9 days, and relative leaf-out dates tended to track one another in most years (e.g. 1995 vs. 1996; Fig. 9a). There were notable exceptions, however, and the earlier in the year that canopy development began, the longer it took to finish (Fig. 10), presumably because periods of cool weather were likely to intervene. Canopy fill time (from 30% to 70% LAI) ranged from 4 days (1994, 2002) to 17 and 28 days (2003, 2007). In 2003 and 2007, BB and growth to 30% LAI were early, but further progress (to 50% and 70%) was slowed by cold weather, extremely so in 2007. Initial BB and leaf unfolding were unusually early in 2007, in response to record high temperatures, but several days of freezing T in early April killed newly formed leaves and shoots, across a wide geographic area, visible even in satellite images (Gu *et al.*, 2008; Augspurger, 2009). As a result, relative LAI on WBW declined from approximately 45% to 25% (Gu *et al.*, 2008). A slow recovery began after about 10 days, but the canopy never reached normal LAI in 2007. The delayed dates for 50% and 70% LAI (Fig. 9a) could thus appear in a long-term record as a delay "in response to" a warmer spring whereas in fact, BB itself was earlier in 2007.

Milder freeze-related delays have also been documented. In a native *Betula* population, Rousi & Heinonen (2007) observed that in one of 9 years, though many trees achieved BB at the usual GDD, 3 weeks of freezing temperatures intervened, nullifying the accumulated GDD for the remaining trees (cf Schaber & Badeck, 2003), which required a second accumulation of GDD for BB. Similarly, in one of three springs, sub-zero Ts reset the BB clock in an *Acer* OTC experiment, but only in the warmed chambers, where buds were already beginning to expand (Norby *et al.*, 2003). Thus date of BB and GDD may be decoupled by atypical weather patterns, which are almost certain to occur periodically in a long-term record.

Analyzed in terms of mean monthly temperatures, a metric frequently applied to long-term phenological records, the date of 30% canopy fill on WBW was best described as function of mean temperature in March ($R^2 = 0.47$; slope = −1.9 days °C^{-1}), but March T explained only 14% and 3% of the variation at 50% and 70% LAI, respectively. A stronger correlation was between 50% canopy fill and mean T in February–April ($R^2 = 0.59$, slope −3.5 days °C^{-1}; $P < 0.01$; Fig. 11), and it was the only relationship which explained the late BB in 1996, i.e., the 1996 point was far from the best-fit line
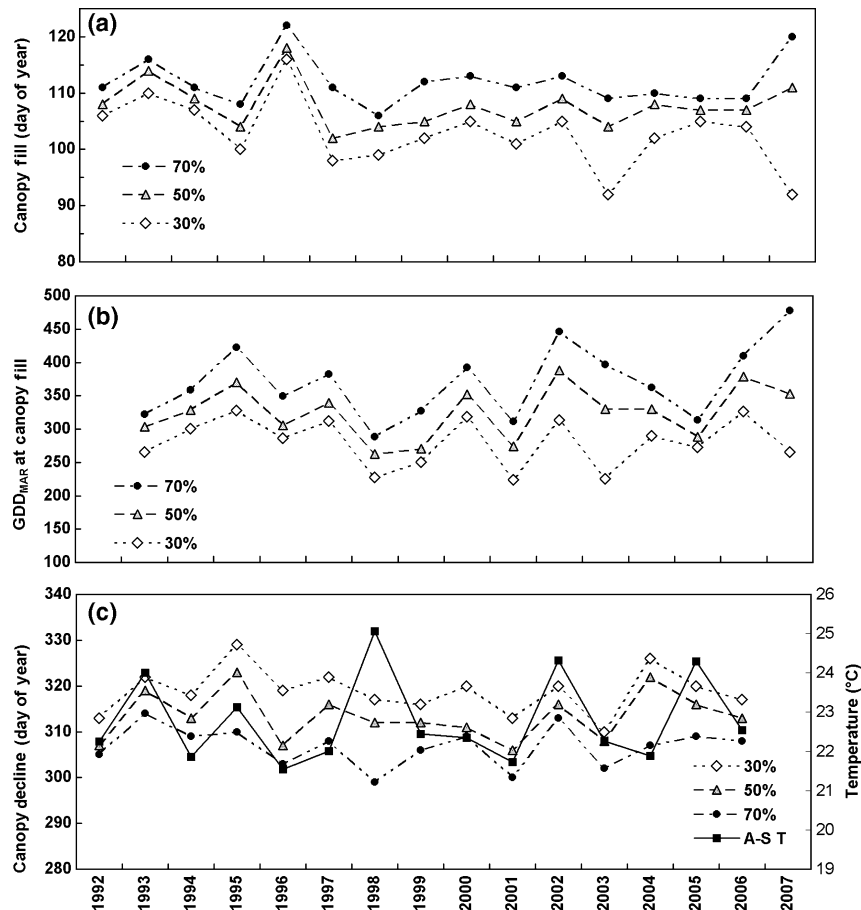
Fig. 9 Leaf phenology in a mixed upland deciduous forest in eastern TN, USA, by year, 1992 through 2007. (a) Dates of partial canopy fill: day of year at 30%, 50% and 70% of full canopy LAI (symbols on figure), based on light transmission through the canopy (Hanson *et al.*, 2003a). (b) Growing day degrees (GDD_{MAR}), accumulated from March 1, at each fractional level of LAI. (c) Dates of canopy decline (leaf abscission) when 70%, 50%, and 30% of the maximum LAI remained. A-S T (solid squares, connected by solid line) is the mean temperature during August-September of each year (second *y*-axis).

in other correlations. For 50% fill, the next best fits were February–March ($R^2 = 0.44$; $P = 0.03$), and January–April ($R^2 = 0.4$; $P < 0.03$) with slopes -2.2 and -3.0 days $°C^{-1}$, respectively (Fig. 11). Date of 70% fill was poorly explained at best; the best fit was with mean January-April T ($R^2 = 0.28$; slope = -2.6 days $°C^{-1}$). The expected advance in BB, based on WBW, could thus vary between 1.9 and 3.5 days $°C^{-1}$ of warming, depending on the stage of leaf onset evaluated and the time period considered "effective". These estimates (and uncertainties) are generally consistent with forest phenology responses calculated by the other methods described, and with results from warming experiments.

Buried within the response of the intact forest canopy, however, is the fact that species vary in apparent sensitivity to forcing temperatures, chilling temperatures, and photoperiod. The canopy on WBW, for example, is dominated by two late-flushing oak species
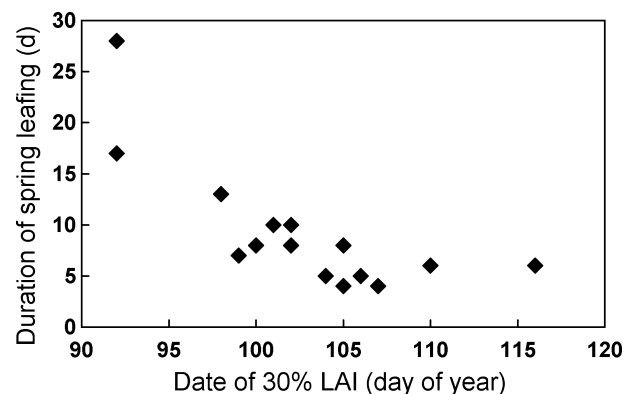

Fig. 10 Duration of spring canopy development in a mixed deciduous forest on Walker Branch Watershed, TN, USA. Number of days for canopy leaf area index (LAI) to increase from 30% to 70% of the maximum summer LAI, as a function of the day of year when canopy reached 30% LAI.

(*Quercus prinus* and *Q. alba)* and *Acer rubrum* (an early flushing maple), along with other *Quercus* species, *Nyssa sylvatica* (blackgum), and *Liriodendron tulipifera* (tulip poplar; Tschaplinski & Hanson, 2003; Hanson *et al.*, 2003b). To accommodate such diversity, one approach is to account for the mixture of species according to their patterns of sensitivity, particularly if the objective is to explore the competitive implications of climate change (Kramer *et al.*, 2000; Badeck *et al.*, 2004). Model approaches at the global or continental scale, however, often seek universal, rather than species-specific, relationships, e.g., with GDD, chill hours, photoperiod, or a composite index (White *et al.*, 1997; Botta *et al.*, 2000; Arora & Boer, 2005; Jolly *et al.*, 2005; Schwartz *et al.*, 2006; Delpierre *et al.*, 2009). For those purposes, data from a small number of species or locations, or from shorter-time series, may not scale appropriately (Botta *et al.*, 2000; Badeck *et al.*, 2004).

For forecasting future forest composition, however, species differences can be important, as observed on WBW and across regions of the eastern United States damaged by the 2007 freeze. In that widespread freeze, species with buds still closed, or with leaves well-expanded, were less vulnerable and showed less damage than those with small, newly emerged leaves (Gu *et al.*, 2008; Augspurger, 2009). As a result, a few species, e.g., *A. rubrum* (Gu *et al.*, 2008) were largely undamaged, suggesting possible competitive advantages of both early and late BB if climate variability increases.

The WBW record is short, when compared to the 30 to 100 years records from dedicated phenology networks, and recent enough to examine for interactions.
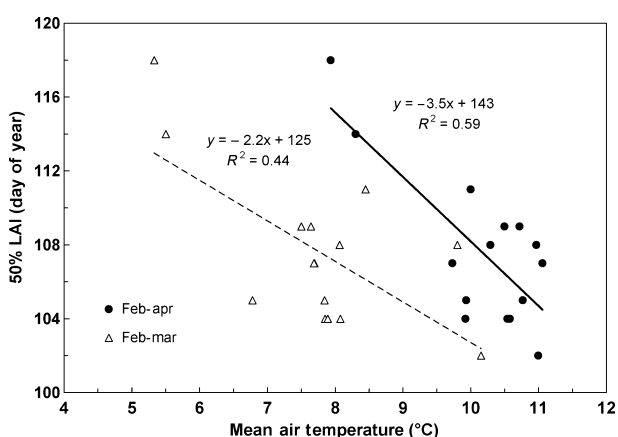

Fig. 11 Spring phenology of an upland deciduous forest on Walker Branch Watershed. Day of year when the canopy reached 50% of maximum leaf area index (LAI), as a function of mean spring temperatures, either February–April, or February–March.

At 16 years, however, it is one of the longer "short-term" studies focused on forest phenology and climatic change (cf. 2–18 years for ground-based or satellite monitoring, as cited, 2–7 years for common gardens, and 1–4 years for temperature manipulations, with the current study the longest). Longer records reduce the influence of an individual year with anomalous weather, but embrace more overall noise from inter-annual variability (cf. Gordo & Sanz, 2005; Menzel *et al.*, 2006; Richardson *et al.*, 2006; Morin *et al.*, 2009; Ibáñez *et al.*, 2010).

Scaling autumn responses presents additional problems. Although the green period in many species is extended by warmer autumns, the relationship is not always significant, or even detectable in long-term records. The WBW record was similarly obscure. Leaf offset date (50% LAI) varied by 17 days from year to year (Fig. 9c), which argues against an overwhelming photoperiod control. There was no significant correlation however, between dates of canopy offset (30%, 50%, or 70% LAI), and any combination of mean monthly temperatures, August through November. Figure 9c, however, shows that offset dates tended to follow mean August–September T, as in the OTC experiment, with several exceptions. In 1998 for example, leaf fall was early, despite a warm autumn, because the unusually high August and September temperatures were accompanied by the lowest July–September rainfall total since data collection began (1951), and generally low rainfall June through November. The combination of high temperatures and low rainfall produced a regional drought, with sustained low water potentials at the WBW site (http://tde.ornl.gov/) and reduced physiological function at other local forest sites (Gunderson *et al.*, 2002). A similar, smaller, discrepancy occurred in 2005 (Fig. 9c), when total May–December rainfall was also very low, but July rainfall was near normal, providing a degree of relief.

Although *T* remains the stronger explanatory variable for abscission in eastern North America, future warming and higher evapotranspiration (ET) could shift conditions toward a Mediterranean-like precipitation control (Arora & Boer, 2005; Gordo & Sanz, 2010). Even in the current climate, in some years precipitation controls the end of the physiologically active GS (Gunderson *et al.*, 2002; Warren *et al.*, 2011) and advances abscission. If data from the precipitation-controlled abscission of 1998 are excluded, the dates for 70% LAI remaining are significantly correlated with mean August–September temperature ($P < 0.01$), with a slope of 3 days $°C^{-1}$ ($P < 0.01$).

Unlike the relationship seen in spring (Fig. 10), there was no relationship between the date that leaf abscission began and the duration of leaf fall, perhaps

because continued leaf fall is dependent not only on physiological senescence, as in the OTCS, but also on the random occurrence of wind and rain. As in spring, unusual temperature patterns can also interfere, e.g., warmer autumn weather followed by a suddenly very cold period cause green leaves to freeze on the tree and fall without normal senescence. This may be more likely with warming, as seen in two *Acer* species during one autumn of a 3 years warming experiment (Norby *et al.*, 2003), and in the present experiment, in 2002, when more leaves remained green in the warmed chambers (E4 > E2 > A), well into December, when they experienced a hard freeze. The still-green leaves in E2 and E4 chambers were more vulnerable, and abscised before the senescent leaves in A did. Had leaf loss been assessed at a later stage, e.g., at 75% abscission, an "advance" of leaf loss with warming would have been recorded. Abscission before senescence can also occur with severe damage from insects, disease, or water stress (Taylor & Whitelaw, 2001), and to the extent that higher temperatures accelerate those, warming, especially in mid- to late summer, could hasten leaf fall (Kramer *et al.*, 2000).

Implications for forest productivity

The length of the active GS is an important component of forest productivity. Higher air temperatures in this experiment extended the GS on both ends, as seen elsewhere (Matsumoto *et al.*, 2003; Vitasse *et al.*, 2009; Gordo & Sanz, 2010; Ibáñez *et al.*, 2010), increasing the potential C uptake period. The advancement in BB was consistently longer than the delay in senescence in *Liquidambar* and *Quercus*. In *Betula,* however, the delay in senescence was more pronounced than the advance in BB, in two of the 3 years, as it was in *Populus* in the year that leaves were healthy. Delays in abscission were more pronounced than delays in color change, however, and only in *Liquidambar* was the effect of treatment on BB larger than that on abscission. Greater temperature sensitivity in autumn than in spring is in keeping with long-term records for five Asian species (Ibáñez *et al.*, 2010; Matsumoto *et al.*, 2003), but in other long-term records, autumn relationships with T were difficult to detect, and responses were smaller than those of BB, thus of less potential importance to productivity (Schaber & Badeck, 2003).

Even if the GS were extended equally in spring and autumn, changes in spring might be more important for ecosystem productivity. Additional C gain is partially offset by an added respiratory load (Richardson *et al.*, 2010) which, in autumn, might be exacerbated by late-season declines in photosynthetic capacity, and by lower total solar radiation than in spring months.

Regardless of which portion of the GS dominates, there is evidence from model simulations and field observations that an extended GS can increase productivity in forest ecosystems. For example, 5 years of eddy co-variance measurements in a deciduous forest revealed that even small temperature-driven differences in growing season length (GSL) had a large cumulative effect on annual C exchange (Goulden *et al.*, 1996). Simulations of productivity in deciduous ecosystems also indicate the importance of using a temperature-driven GSL, particularly in spring (Richardson *et al.*, 2010). Longer GSs in warmer years, or in simulations of warming, often result in higher ecosystem productivity, e.g., predicted biomass was 15% higher in *Picea* (Rötzer *et al.*, 2004) and 11% higher on WBW (Hanson *et al.*, 2005), but there was little predicted change in biomass of *Fagus* (Rötzer *et al.*, 2004). Net productivity increased, e.g., by an average 1.6% (White *et al.*, 1999) or 2% (Picard *et al.*, 2005) for each day added to the GS. For a moderate 10 days increase in GSL, then, based on Figs 8 and 11, net ecosystem productivity could potentially increase by 16–20% in an atmosphere 4 °C warmer than present.

Not all simulations or measurements will indicate increased productivity with warming, if other factors interfere. Physiological limitations, with or without earlier leaf fall and senescence, can be induced by a co-occurring drought, or by soil water stress induced by increased ET (Fig. 9c, 1998; Gunderson *et al.*, 2002; Hanson *et al.*, 2003a; Warren *et al.*, 2011), which can decouple the carbon uptake period from canopy duration *per se* (White & Nemani, 2003).

Despite the differing definitions and criteria for GSL, a longer GS appears to be the most likely outcome of warmer future temperatures, as long as interactions, especially with water, are taken into account. There is thus a potential for increased forest productivity with a warmer atmosphere, until other factors (nutrients, water, etc.) become limiting, and until the temperatures themselves interfere with physiological function or with reproductive phenology (Chuine, 2010).

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