

Phenological responses in maple to experimental atmospheric warming and CO₂ enrichment

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Due to a printer's error, the key to the data distributions in Fig. 3 and 4 is missing.

solid squares: control
open squares: elevated CO₂
solid diamonds: elevated temperature
open diamonds: elevated CO₂ and temperature

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Abstract

Evidence that global warming has altered the phenology of the biosphere, possibly contributing to increased plant production in the northern hemisphere, has come from a diversity of observations at scales ranging from the view of the back yard to satellite images of the earth. These observations, coupled with an understanding of the effects of temperature on plant phenology, suggest that future changes in the atmosphere and climate could alter plant phenology with unknown or unpredictable consequences. We assessed the effects of simulated climatic warming and atmospheric CO₂ enrichment on the spring and autumn phenology of maple trees (*Acer rubrum* and *A. saccharum*) growing for four years in open-top field chambers. CO₂ enrichment (+ 300 ppm) had no consistent effects on the timing of budbreak and leaf unfolding in the spring or leaf abscission in the autumn. Warming (+ 4 °C) usually had predictable effects: in two of the three years of assessment, budbreak occurred earlier in warm chambers than in ambient temperature chambers, and leaf abscission always occurred later. The lengthening of the growing season could contribute to increased productivity, although effects of temperature on other physiological processes can concurrently have negative effects on productivity. In 1995, budbreak was unexpectedly delayed in the warmer chambers, apparently the result of advanced budbreak leading to injury from a late-spring frost. Likewise, there was increased risk associated with longer leaf retention in the autumn: in 1994, leaves in the warm chambers were killed by freezing temperatures before they had senesced. These observations support the premise that global warming could increase the length of the growing season. Phenological responses should, therefore, be part of any assessment of the possible consequences of global change, but our results also suggest that those responses may not always have positive effects on production.

Key words: *Acer rubrum*, *Acer saccharum*, budbreak, global change, growing season length, leaf abscission, phenology

Received 13 August 2002; revised version received 14 March 2003 and accepted 26 August 2003

Introduction

The seasonal oscillation of CO₂ in the atmosphere is a powerful integrator of the biological activity of the planet; it represents the breathing of the biosphere. Keeling *et al.* (1996) observed that the amplitude of the seasonal CO₂ cycle in the northern hemisphere has been increasing since the early 1960s, and that the springtime decline in CO₂ had advanced by about 7 days, suggesting a lengthening of the growing season. They

proposed that the increasing amplitude reflects increasing CO₂ assimilation by plants over a longer growing season in response to climatic warming. Satellite observations of the normalized difference vegetation index (NDVI) supported the premise that increases in global temperature have been associated with a lengthening of the growing season and regionally significant increases in biological activity (Myneni *et al.*, 1997). This association between climatic warming and a seasonal advance in biology (phenology) has been observed at local scales as well: the arrival of birds at the Leopold farm in Wisconsin (Bradley *et al.*, 1999), the first flowering dates of 385 plants in England (Fitter & Fitter, 2002), leaf unfolding of trees in Europe

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(Chmielewski & Rötzer, 2001; Peñuelas *et al.*, 2002). A meta-analysis of such studies concluded that a significant impact of global warming is discernible in plant and animal populations (Root *et al.*, 2003).

The length of the growing season can be an important determinant of annual net primary productivity (NPP) and accounts for much of the inter-annual variation in NPP for a given site, as well as for NPP differences between sites at different latitudes (Goulden *et al.*, 1996). The growing season has been defined in climatological terms (e.g., frost-free period) or by the phenological responses of plants to climate. For a deciduous forest, the phenologically defined growing season can be expressed in physical terms, such as canopy duration (e.g., the period between bud burst and complete leaf fall), or in ecophysiological terms, such as the carbon uptake period, which better correlates with net ecosystem carbon exchange (White & Nemani, 2003). Phenological events, such as the release of vegetative buds from winter dormancy, are controlled by a complex suite of environmental signals, of which temperature and photoperiod are most important (Kaszkurewicz & Fogg, 1967; Campbell & Sugano, 1979; Wielgolaski, 2001). The inference from the global observations, that climatic warming (caused by increasing concentrations of CO₂ and other radiatively active gases in the atmosphere) has lengthened the growing season, provides a mechanism, supported by ecosystem models, for increased net ecosystem production and a negative feedback on atmospheric CO₂ concentration (White *et al.*, 1999).

The accumulating evidence that phenology has responded to recent changes in the global climate increases the importance of understanding the potentially important consequences for the global carbon budget. However, it remains difficult to predict how plant phenology will change with future increases in atmospheric CO₂ concentrations and global temperature. The ecological consequences of phenological changes are highly uncertain. Relationships between critical phenological events and temperature are apparent in the obvious differences in phenology across latitudinal transects. However, latitudinal differences in temperature regime are confounded with differences in photoperiod regime, which will remain unchanged amidst a globally changing environment. Relationships between phenology and year-to-year differences in weather can be described, but these relationships may or may not predict the phenological response to a gradual change in climate caused by an altered radiation balance. It is also unclear what the implications of temperature effects on phenology might be in combination with other global change variables (e.g., increased [CO₂]) and effects of warming on other plant

processes during the growing season. General vegetation models can incorporate routines that determine phenology or growing season length from climatological input, but these routines do not necessarily allow for changes in phenological relationships in response to climatic change (Norby *et al.*, 2001). Hence, the phenological routines are likely to lose accuracy when predicting responses to the new conditions associated with future global change (Hänninen, 1995). Experimental observations of phenological responses to realistic simulations of future atmospheric conditions are badly needed.

As part of a multi-faceted, 4-year study of the responses of maple trees to elevated [CO₂] and temperature, we observed the two phenological events that are determinants of the length of the growing season for winter-deciduous trees – vegetative bud break in the spring and leaf abscission in the fall. We relate these observations to the integrated response of the experimental system and consider the potential consequences for future forests.

Methods

We assessed phenological responses of young sugar maple (*Acer saccharum* Marsh.) and red maple (*A. rubrum* L.) trees grown in small stands for four growing seasons in open-top field chambers on the Oak Ridge National Environmental Research Park in Roane County, Tennessee (35°54'N; 84°20'W). Twelve 3 m diameter chambers were modified to control air temperature to be the same as ambient air or to maintain a constant 4 °C elevation in air temperature (Norby *et al.*, 1997). Fans continuously pushed air through double-walled polyvinyl chloride chamber panels and out the open chamber tops at 0.6 m³ s⁻¹. The airstream was conditioned by evaporative coolers (to maintain ambient temperature) and voltage-regulated electrical resistance duct heaters. A proportional-integral-differential (PID) feedback control system regulated the cooling and heating systems to maintain air temperature inside the chambers at +0 °C or +4 °C relative to ambient air outside the chamber. Soil temperature at 10 cm depth was increased by 1.2 °C by the warmer air in the elevated temperature chambers (Edwards & Norby, 1998). The temperature treatments were combined with ambient or elevated (+300 ppm) CO₂ concentrations. A constant flow of pure CO₂ was introduced into the airstream entering the chambers; the flow rate was manually adjusted to maintain a constant differential with ambient air. The temperature treatments were maintained throughout the year, but the CO₂ treatments were suspended during the winter (November–March). The four treat-

ments, comprising a 2×2 factorial arrangement of the two levels of temperature and $[\text{CO}_2]$, were replicated three times in a randomized complete block design. One-year-old maple seedlings were obtained from a commercial nursery in central Tennessee at similar latitude as the research site; the seed source was local, but there was no control of genotypes. The seedlings were planted into the soil within the chambers in spring 1994, and additional seedlings were planted in spring 1995 for a total of 10 plants per species per chamber. The trees were harvested in September 1997, ending the experiment. More details about the research site, chamber operation, and environmental conditions are provided by Norby *et al.* (1997, 2000).

Spring phenology was assessed in the second through fourth growing seasons (1995–1997) through visual observation of the terminal buds of each tree. A score was assigned representing the stage of development (Kriebel & Wang, 1962): 1, no activity; 2, buds swelling; 3, buds just opening; 4, leaves unfolding; 5, leaves curled; 6, leaves flat (Fig. 1). The assessments were made at approximately weekly intervals from the

first sign of activity (mid- to late March) until most trees (approximately 80%) had fully expanded leaves (mid-April). The progression through these developmental stages was approximately linear with time. In 1995, the assessments did not begin until after the onset of bud activity; it was the casual observation of an apparently important difference in phenology that prompted this study.

The timing of leaf abscission in the autumn of the first through third growing seasons (1994–1996) was characterized by the loss of leaf area, which corresponds roughly to the trees' photosynthetic capacity. Leaves were collected from each plant as they fell, primarily during the month of November. (The experimental trees were harvested in September, 1997, prior to leaf abscission, in order to meet other experimental objectives, so abscission data are not available for 1997.) Dry mass of the abscised leaves was converted to leaf area based on the specific leaf area of a subset of 12 leaves per chamber. The data were expressed as the percentage of total plant leaf area that had abscised by each collection date.



Fig. 1 Stages of budbreak and leaf unfolding in *Acer saccharum*, as described by Kriebel & Wang (1962). 1, no activity; 2, buds swelling; 3, buds just opening; 4, leaves unfolding; 5, leaves curled; 6, leaves flat.

The phenological scores were considered an ordinal data set and accordingly were analyzed statistically using the Wilcoxon rank-sum non-parametric test. The significance of the main effects of CO₂ and temperature on the rank sums of the scores was evaluated using a two-tailed p-value for a normal approximation (Statistix Ver. 7, Analytical Software, Tallahassee, FL, USA). Effects of CO₂, temperature, and their interaction on leaf abscission on the date when approximately 50% of all leaves had abscised were analyzed using analysis of variance, with experimental error (block × treatment) as the error term.

Results

Temperature records

The monthly mean ambient temperatures in the period from fall 1994 to spring 1997 were generally similar to 30-year (1961–1990) average temperatures (source: Atmospheric Turbulence and Diffusion Division, National Oceanic and Atmospheric Administration, Oak Ridge, Tennessee). The notable exceptions were the

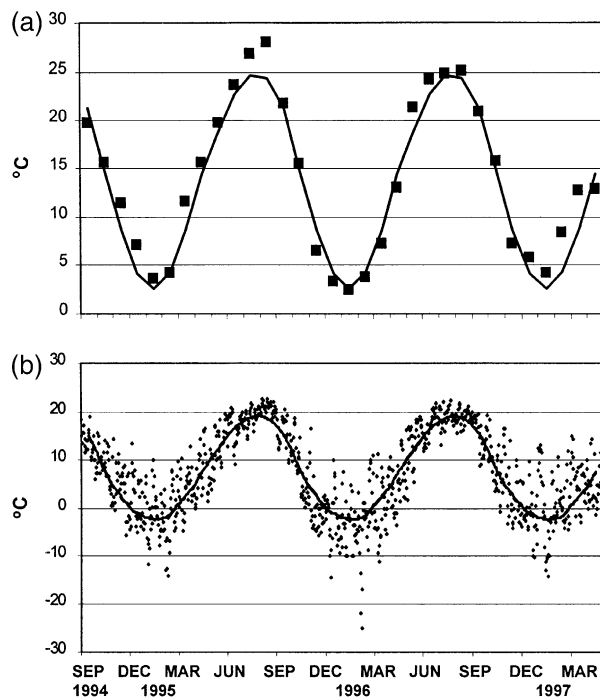


Fig. 2 Ambient air temperature at the experimental site. (a) Monthly mean ambient temperatures in the period from fall 1994 to spring 1997 (symbols) and 30-year (1961–1990) monthly average temperatures (line) from the Atmospheric Turbulence and Diffusion Division, National Oceanic and Atmospheric Administration, Oak Ridge, Tennessee. (b) Daily minimum temperatures over the same period.

warmer than average winters of 1994–1995 and 1996–1997 and the much higher temperatures in summer 1995 (Fig. 2a). The last episodes of sub-zero minimum temperatures in the spring occurred on 2 April 1995, 12 April 1996, and 14 April 1997 (Fig. 2b).

Spring phenology

Bud expansion began in mid- to late March (Fig. 3), which is typical for native trees of these species in the region (McGee, 1986). In 1996 and 1997, buds began swelling and opening earlier in chambers maintained at elevated temperature, and leaf expansion was significantly more advanced in the elevated temperature chambers at the developmental midpoint (Table 1). The pattern in 1995, however, was strikingly different – development occurred earlier in ambient temperature than in elevated temperature in both species. Effects of [CO₂] in either species were small, inconsistent, and usually not statistically significant.

A simple, predictive model of the timing of leaf initiation was based on soil temperature, measured at 10 cm depth. The average daily soil temperature (calculated from hourly averages) was accumulated starting on 1 March each year. The temperature sum in ambient temperature chambers was 410–430 degree-days on the day of bud opening (stage 3) in each of the three years, despite an 8-day difference in bud opening between years. The same soil temperature sum (420 degree-days) adequately predicted (within 1 or 2 days) the earlier bud opening in elevated temperature chambers in 1996 and 1997, but in 1995 the 420 degree-day threshold occurred in the elevated temperature chambers 12 days prior to bud opening.

Abscission

The onset of leaf abscission in both species was delayed in the warmer chambers each year (Fig. 4), and trees in the warmer chambers retained significantly more leaf area during most of the autumn (Table 2). The effects of CO₂ enrichment were inconsistent and significant only for red maple in 1994, when abscission was delayed by elevated [CO₂] in the ambient temperature chambers only.

Length of growing season

The length of the growing season in each treatment in 1995 and 1996 was calculated as the number of days between approximate midpoints of leaf expansion (bud stage 4) and leaf abscission (50% abscised), by reading values from the graphs of treatment means in Figs 3 and 4. These end points were chosen to approximate the period of physiological activity of the canopy. In

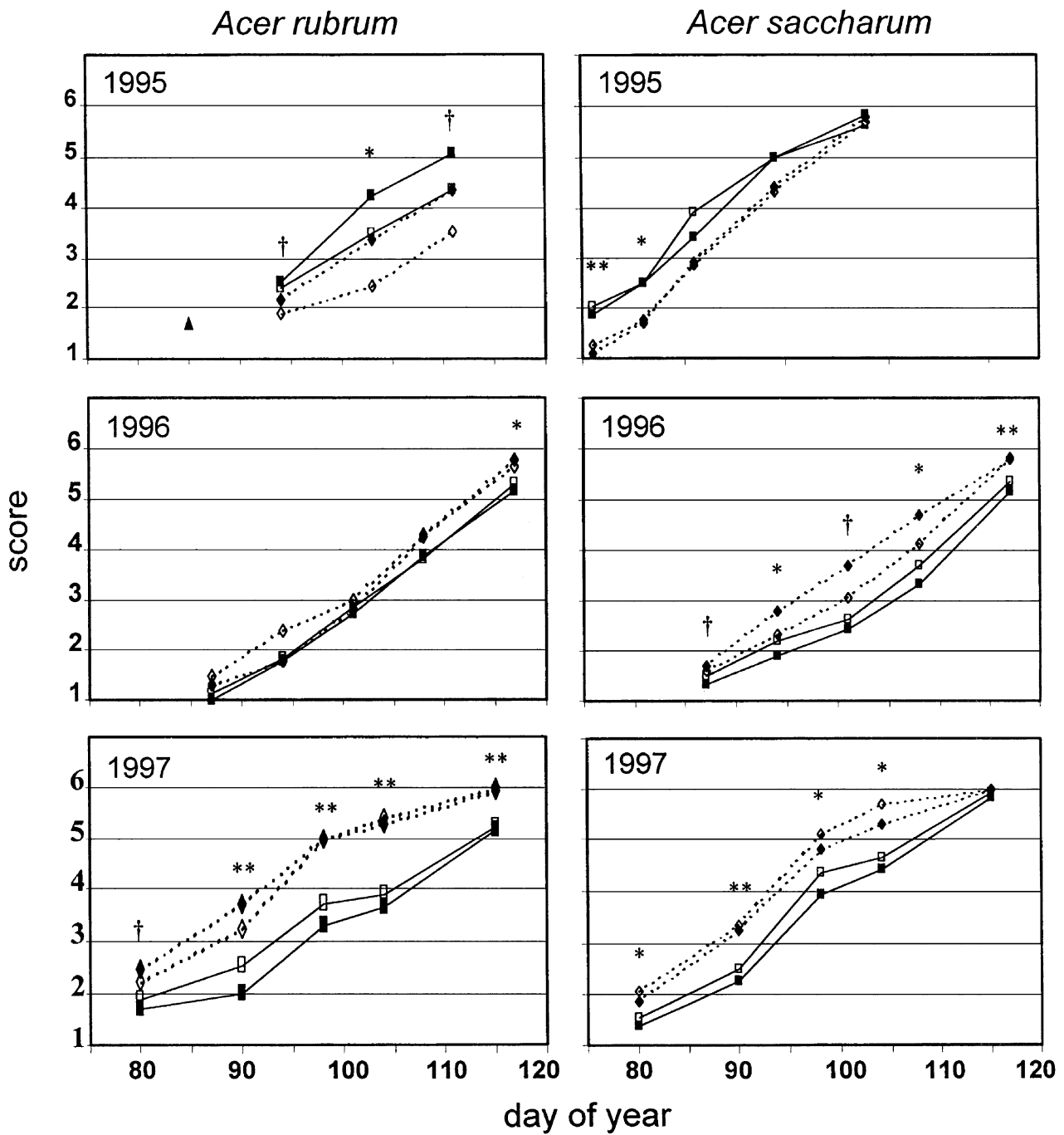


Fig. 3 Timing of bud break and leaf unfolding in *Acer rubrum* and *A. saccharum* during the spring in 1995–1997. Data are the average score (see Fig. 1) of the plants in the three replicate chambers of each treatment. The first data point for *A. rubrum* in 1995 is an estimate based on experiment-wide observations. Statistical significance of the main effect of temperature (Wilcoxon rank-sum test) is indicated: † $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

1995, the delayed leaf abscission in the warmer chambers offsets the delayed leaf initiation, and the growing season was similar in all treatments (Table 3). In 1996, the growing season was 17 to 24 days longer in the warm chambers, and the later abscission date had a larger influence than the earlier leaf expansion date.

Exposure to elevated [CO₂] had no consistent effect on growing season length. Although growing season length cannot be assessed for 1994 or 1997, the responses observed in the fall of 1994 and spring of 1997 suggest that temperature elevation would have lengthened the growing season as in 1996.

Table 1 Statistical comparison of the scores describing the stage of budbreak and leaf unfolding

Species	Date	Mean rank of bud score			Ambient temperature	Elevated temperature	P
		Ambient CO ₂	Elevated CO ₂	P			
<i>Acer rubrum</i>	21 Apr 1995	35.7	24.2	0.009	34.7	26.0	0.046
<i>Acer rubrum</i>	17 Apr 1996	30.9	29.3	ns	25.9	34.0	0.036
<i>Acer rubrum</i>	8 Apr 1997	27.8	31.7	ns	19.2	40.5	<0.001
<i>Acer saccharum</i>	4 Apr 1995	33.1	32.9	ns	37.8	28.3	0.031
<i>Acer saccharum</i>	17 Apr 1996	32.6	33.5	ns	23.9	41.8	<0.001
<i>Acer saccharum</i>	8 Apr 1997	29.0	37.3	0.061	24.2	41.5	<0.001

The data are the mean ranks of bud scores of trees in three replicate chambers; higher mean ranks indicate higher average bud scores (more advanced development) on the given date. Data are shown for the observation date when the average bud score across all treatments was approximately 4, corresponding to leaves that were unfolding. Statistical comparisons of the main effects of CO₂ concentration and temperature were made using the Wilcoxon rank sum test statistic and a normal approximation. The significance of the effect of temperature for other observation dates is shown in Fig. 3. ns, not significant.

Discussion

An acceleration of spring phenology was the expected response to elevated temperature. Although a fundamental mechanistic understanding is lacking, empirical observations suggest that once a critical photoperiod has been attained and winter chilling requirements are met, bud development progresses more rapidly with warmer temperatures (Kaszakiewicz & Fogg, 1967; Hänninen, 1995). This is what happened in 1996 and 1997: bud expansion was advanced by 4–12 days in chambers with air temperature maintained 4 °C warmer than in chambers with ambient temperature air. Our empirical, predictive model of leaf initiation based on soil temperature, which was used an integrator of air temperature, was consistent with the assumption that initiation would be earlier in years with warmer springs or in response to temperature elevation, with the important exception of 1995. In other field chamber experiments with trees, budbreak was advanced 6 to 15 days by elevated (+ 4 °C) temperature in *Pseudotsuga menziesii* (Guak *et al.*, 1998) and by 23–27 days in *Pinus sylvestris* in + 5 °C (Repo *et al.*, 1996).

The opposite response to temperature occurred in 1995, and it was the initial recognition of that surprising pattern that prompted this study. Our initial hypothesis to explain the retardation of bud expansion in elevated temperature in 1995, occurring 12 days later than predicted based on soil temperature sum, was that bud development was delayed due to insufficient winter chilling. The winter of 1994–1995 was considerably warmer than normal (Fig. 2a), and it was even warmer, of course, in the elevated temperature chambers. Buds require prolonged exposure to chilling temperatures to break the rest phase of winter

dormancy and attain the growth competence that leads to bud expansion upon prolonged exposure to forcing temperatures (Fuchigami *et al.*, 1982). This has been demonstrated experimentally in both red maple and sugar maple (Perry & Wang, 1960; Kriebel & Wang, 1962). When chilling during the winter months is insufficient, bud expansion is retarded and abnormal. Insufficient chilling was a projected response of *Pseudotsuga menziesii* to climatic warming (Leverenz & Lev, 1987; Kimmins & Lavendar, 1992). However, this explanation cannot be supported for our maple experiment. Bud expansion in 1995 was not retarded: in ambient temperature chambers it began about 2 to 3 weeks earlier than in 1996 or 1997 and was consistent with the model based on soil temperature sum. The winter of 1996–1997 was also much warmer than normal, yet there was no evidence of a chilling deficit. Finally, the apparent chilling requirement for sugar maple from nearby Norris, Tennessee, reported to be 2500 h below 7 °C (Kriebel & Wang, 1962), would have been met in January in 1995. Cannell & Smith (1986) concluded that climatic warming might lead to delayed budbreak only when a tree's chilling requirement is very poorly met under current conditions.

A more likely explanation for the delayed bud expansion under elevated temperature in 1995 is that sub-zero temperatures on 9–11 March 1995 (day 68 to 70), damaged young, expanding buds and reset their phenology. Although there are no direct observations to support or refute frost injury in this experiment (other than the temperature records), we have witnessed such effects of late freezes in previous years. If buds in ambient temperature were still dormant, they would have been more protected from the freezing event. When direct observations of sugar maple bud

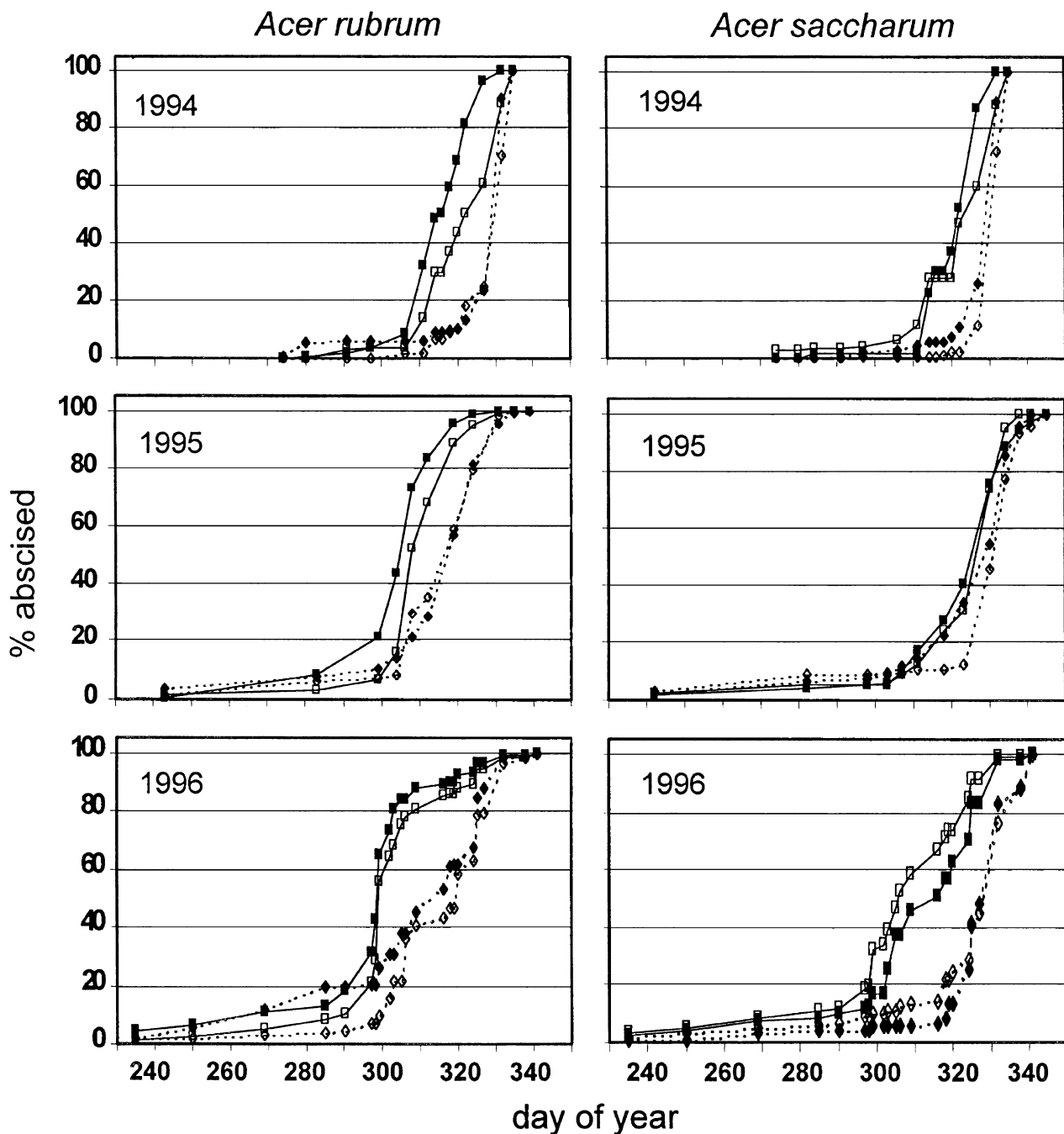


Fig. 4 Timing of leaf abscission in *Acer rubrum* and *A. saccharum* during the autumn in 1994–1996. Data are the means of three replicate chambers of the cumulative percentage of total leaf area that had abscised.

phenology began 6 days later (day 76), the buds in ambient temperature chambers were just swelling or beginning to elongate (stage 2–3) and most likely had been in stage 1 during the sub-freezing temperatures. Several plant and ecosystem models suggest increased risk of frost damage as a possible effect of climatic warming (Cannell & Smith, 1986; Hänninen, 1991; Burton & Cumming, 1995). Accelerated budbreak in a population adapted to a particular range of tempera-

ture and photoperiod may in some cases be detrimental, and the potential benefits may be small: in *Populus trichocarpa*, earlier budbreak was only weakly associated with increased shoot growth (Dunlap & Stettler, 1998). While our results do not directly address the question of frost injury, they do clearly show that warming can in some cases retard leaf development. As suggested by Kramer (1994), models that predict climatic warming to increase risk of frost damage

Table 2 Statistical comparison of the extent of leaf abscission on the observation date when the average abscission across all treatments was approximately 50%

Species	Date	% abscised				Probability level		
		Control	Elevated CO ₂	Elevated temperature	Elevated CO ₂ and temperature	CO ₂	Temperature	CO ₂ × temperature
<i>Acer rubrum</i>	23 Nov 1994	96.7	60.7	23.4	25.0	0.016	<0.001	0.011
<i>Acer rubrum</i>	8 Nov 1995	83.6	68.0	28.2	35.2	ns	0.002	ns
<i>Acer rubrum</i>	30 Oct 1996	80.4	68.4	30.6	21.6	ns	0.001	ns
<i>Acer saccharum</i>	23 Nov 1994	86.9	59.9	26.0	11.7	0.151	0.003	ns
<i>Acer saccharum</i>	26 Nov 1995	76.0	73.8	54.4	45.6	ns	0.009	ns
<i>Acer saccharum</i>	20 Nov 1996	70.3	85.0	25.1	28.6	ns	<0.001	ns

The data are the means of trees in three replicate chambers of the four treatments. ns, not significant ($P > 0.2$).

Table 3 Length of growing season

Year	Species	Treatment	Start day	End day	Duration (days)
1995	<i>Acer rubrum</i>	Control	102	305	203
		High CO ₂	108	307	199
		High temperature	108	317	209
		High CO ₂ /temperature	114*	316	202*
1995	<i>Acer saccharum</i>	Control	89	324	235
		High CO ₂	86	326	240
		High temperature	92	328	236
		High CO ₂ /temperature	92	330	238
1996	<i>Acer rubrum</i>	Control	109	298	189
		High CO ₂	109	298	189
		High temperature	106	312	206
		High CO ₂ /temperature	106	319	213
1996	<i>Acer saccharum</i>	Control	111	316	205
		High CO ₂	109	306	197
		High temperature	103	327	224
		High CO ₂ /temperature	107	328	221

The day of year on which the growing season started was defined as the day when buds reached stage 4. The end of the growing season is the date at which 50% of leaf area had abscised. These values were obtained from Figs 3 and 4.

*Start day estimated by extrapolation.

(because of earlier bud expansion; Hänninen, 1991) and those that predict no increase in frost damage (because minimum temperatures at the time of budbreak are constant or higher; Murray *et al.*, 1989), may both be correct, depending on species, local climatic conditions, and the climatic change scenario. Temperature *per se* is not sufficient to predict the response; rather, the sequence of temperature changes in relation to the plant's growth stage is important (Fuchigami *et al.*, 1982).

Maintaining the photosynthetic capacity of leaves later in the growing season in response to the higher average temperature also entails some risk to normal plant function. In 1994, leaves of trees in elevated temperature were still green at the first occurrence of sustained sub-zero temperature (23–24 November). The

leaves were killed and subsequently broke off before completing the resorption of nitrogenous compounds into perennial tissue. Hence, the leaf litter in elevated temperature had a higher nitrogen concentration and a lower C:N ratio than leaves in ambient temperature (Norby *et al.*, 2000). Although the N returned to the forest floor can later be taken up by trees and used again in physiological processes, some of the N may be lost from the ecosystem through leaching or volatilization, and some immobilized in microbial biomass. Internal cycling is more efficient and supports higher rates of productivity under N-limited conditions. In apple trees, for example, remobilization of foliar-absorbed urea-N supported increased shoot growth the following spring (Cheng & Fuchigami, 2002).

Increased N storage, as might be expected from maximum resorption prior to leaf abscission, was more important to spring growth than increased carbohydrate storage, as might result from longer leaf retention in the autumn. A disruption of internal N cycling related to warming-induced phenological shifts could have adverse, albeit subtle consequences.

Climatic warming, as we have noted, can increase productivity in temperate systems by lengthening the period of net carbon uptake and growth. Dunlap & Stettler (1998) observed a weak correlation between spring phenology and stem growth in *Populus trichocarpa*, but they noted that the correlation between autumn phenology (leaf retention) and stem growth was much stronger. Leaves retained late in the autumn are important for photosynthate production and translocation of carbohydrates to the lower stem and roots, thereby conferring a growth advantage to *Populus* clones with longer leaf retention (Nelson & Isebrands, 1983). Hence, we assume that the extension of the growing season that was observed in this experiment, especially the extension in the autumn that occurred in all three years of observation, could have had a positive influence on productivity. However, all biological processes respond to temperature, and the effects of warming on phenology must be analyzed together with temperature effects on other plant processes. By the end of the second growing season (1995), elevated temperature had significantly *reduced* growth of trees of both species by 21–48% compared with trees grown in ambient-temperature chambers (Norby *et al.*, 2000). This growth response to warming clearly cannot be explained by the effect of warming on phenology; other temperature-sensitive processes must have been more important. Subsequent growth responses of these trees to environmental influences were confounded with their difference in size, and the specific effects of altered phenology on tree growth are difficult to determine. Temperature effects should also be considered in relation to other interacting environmental factors, but in this experiment there was no evidence that elevated [CO₂] had a consistent effect on phenology of the maple trees or altered the phenological responses to temperature. Phenological responses (both spring and autumn) to elevated [CO₂] in other field studies have included accelerated development, delayed development, or (probably most commonly) no response (Murray & Ceulemans, 1998; Norby *et al.*, 1999; Hartz-Rubin, 2001).

Climatic warming could create temperature regimes that local vegetation is not adapted to and that are not synchronized with photoperiod. Plant phenological responses to increased temperature should be part of global change analyses. Evidence that climatic warming could increase productivity by lengthening the growing

season now exists at scales ranging from the individual plant, to ecosystems, to the globe. The growing season extension that we observed in 1996 of 17–24 days in response to a 4 °C warming is consistent with responses that have occurred over the past 30 years of 5 days per 1 °C increase in temperature (Chmielewski & Rötzer, 2001). The responses observed in the fall of three years and spring in two of three years support the conclusion that a lengthening of the growing season is the expected response to temperature elevation. However, the unexpected responses suggested in this study – increased risk of frost damage in spring and incomplete resorption of N prior to leaf abscission – suggest that the effects of warming in ecosystems that are attributable to phenological responses may not always have positive effects on production. Without a strong mechanistic understanding of the environmental signals that control phenology, the representation of growing season length in ecosystem models will necessarily be crude. The integrated response of a system to warming will depend on how changes in phenology interact with other physiological and biogeochemical responses (e.g., Zavaleta *et al.*, 2003) and with the influences of stochastic events such as late frosts or droughts. Our results illustrate that warming may indeed lengthen the growing season as predicted, but the net effect of changes in phenology may be unpredictable, and surprises can be expected.

Acknowledgements

We thank Erika Zavaleta and two anonymous reviewers for their helpful comments and suggestions. Jennifer S. Hartz-Rubin (current address: Department of Ecology, Montana State University-Bozeman) and Maria Verbrugge (current address: School of Veterinary Medicine, University of Wisconsin-Madison) were participants in the Associated Colleges of the Midwest/Great Lakes Colleges Association Science Semester at Oak Ridge National Laboratory. Research was sponsored by US Department of Energy's Office of Science, Biological and Environmental Research Program. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the US Dept of Energy under contract DE-AC05-00OR22725.

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