

Phenology of a northern hardwood forest canopy

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Abstract

While commonplace in other parts of the world, long-term and ongoing observations of the phenology of native tree species are rare in North America. We use 14 years of field survey data from the Hubbard Brook Experimental Forest to fit simple models of canopy phenology for three northern hardwood species, sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). These models are then run with historical meteorological data to investigate potential climate change effects on phenology. Development and senescence are quantified using an index that ranges from 0 (dormant, no leaves) to 4 (full, green canopy). Sugar maple is the first species to leaf out in the spring, whereas American beech is the last species to drop its leaves in the fall. Across an elevational range from 250 to 825 m ASL, the onset of spring is delayed by 2.7 ± 0.4 days for every 100 m increase in elevation, which is in reasonable agreement with Hopkin's law. More than 90% of the variation in spring canopy development, and just slightly less than 90% of the variation in autumn canopy senescence, is accounted for by a logistic model based on accumulated degree-days. However, degree-day based models fit to Hubbard Brook data appear to overestimate the rate at which spring development occurs at the more southerly Harvard Forest. Autumn senescence at the Harvard Forest can be predicted with reasonable accuracy in sugar maple but not American beech. Retrospective modeling using five decades (1957–2004) of Hubbard Brook daily mean temperature data suggests significant trends ($P \leq 0.05$) towards an earlier spring (e.g. sugar maple, rate of change = 0.18 days earlier/yr), consistent with other studies documenting measurable climate change effects on the onset of spring in both North America and Europe. Our results also suggest that green canopy duration has increased by about 10 days (e.g. sugar maple, rate of change = 0.21 days longer/yr) over the period of study.

Key words: bud break, climate change, growing season length, Harvard Forest, Hubbard Brook Experimental Forest, leaf fall, leaf out, northern hardwood forest, phenology, senescence

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Introduction

Phenology is the study of the seasonal occurrence of developmental or life cycle events, such as budbreak, flowering, or autumn leaf drop (Rathcke & Lacey, 1985). The timing of these events is known to be sensitive to short- and long-term variability in climate, and is thus a robust indicator of the effects of climate change,

especially observed rising temperatures (White *et al.*, 1997; Fitter & Fitter, 2002; Peñuelas *et al.*, 2002; Schwartz *et al.*, 2002; White & Nemani, 2003; Badeck *et al.*, 2004; Chuine *et al.*, 2004). In Britain, mean flowering dates of 385 plant species advanced by 4.5 days during the 1990s compared with the 1954–1990 mean, and this is almost certainly linked to recent warming trends (Fitter & Fitter, 2002). In the northeastern United States, changes in lilac, apple, and grape phenology suggest that spring has advanced by ≈ 2 –8 days over the last three or four decades, consistent with patterns across North America as a whole (Schwartz & Reiter, 2000; Wolfe *et al.*, 2005).

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Furthermore, there is also strong indirect evidence that the onset of spring has been occurring progressively earlier in recent decades (Keeling *et al.*, 1996; Fitzjarrald *et al.*, 2001; Badeck *et al.*, 2004). A warming experiment with two *Acer* species indicates that warmer temperatures will likely lengthen the growing season, but earlier budbreak and later senescence may expose plants to damaging frosts in the spring, and incomplete resorption of foliar N in the autumn (Norby *et al.*, 2003).

Here, we focus on the phenology of canopy development (budbreak and leaf expansion) and senescence (coloration and leaf drop). The timing of such events is important because leaves are the organs by which plants convert solar energy to chemical energy through the fixation of atmospheric carbon dioxide into carbohydrates (Lechowicz, 1984). Thus, it is to be expected that growing season length should be an important control on primary productivity (Lieth *et al.*, 1975; Running & Nemani, 1991; Aber *et al.*, 1995; Goulden *et al.*, 1996; Keeling *et al.*, 1996; Churkina *et al.*, 2005; but see White & Nemani, 2003, for a counter-example).

Many studies of woody plant phenology utilize a 'thermal time' approach, the idea being that particular events, such as budbreak, occur when a specified thermal sum (in accumulated degree-days) has been reached. In other words, 'growth units' are accumulated in thermal time, rather than calendar time (Cannell & Smith, 1983). The degree-day thermal sum, DD_{k,DOY_1,DOY_2} is calculated above a base (or threshold) temperature k , from day of year DOY_1 to day of year DOY_2 , as in Eqn (1) (\bar{T}_i is daily mean temperature on day of year i):

$$DD_{k,DOY_1,DOY_2} = \sum_{i=DOY_1}^{DOY_2} \begin{pmatrix} (\bar{T}_i - k) & \text{for } \bar{T}_i > k \\ 0 & \text{for } \bar{T}_i \leq k \end{pmatrix} \quad (1)$$

The origins of this developmental paradigm are nearly 300 years old, and date at least to Réaumur in 1730 (see Hunter & Lechowicz, 1992). Thermal time is generally a far more robust predictor of budbreak than calendar time, and 'spring warming' models have been shown to work well for many species (e.g. Hunter & Lechowicz, 1992). However, increased late-winter chilling can reduce the thermal sum required for the induction of spring development (Cannell & Smith, 1983), which argues for a more complex model than one based simply on heating degree-days. Raulier & Bernier (2000) thus used a model that combined accumulated heating degree-days with winter chilling requirements to predict leaf emergence in sugar maple. This model worked well across the entire native range of the species. However, the nature of chilling requirements is debated (e.g. parallel, sequential, or alternating chilling models, see Chuine *et al.*, 1998), and Hunter &

Lechowicz (1992) found that models incorporating chilling requirements performed no better for sugar maple than model based on accumulated degree-days. In fact, this was the case for half of the tree species (13 of 26) in their historical data set. Other models attempt to provide physiologically based representations that improve the realism and generality of the simple models that have been used in the past (e.g. Hänninen, 1995; Chuine, 2000; Schaber & Badeck, 2003). These models can involve numerous parameters (nine in the case the 'unified model' proposed by Chuine, 2000), and optimization of model parameters requires sophisticated fitting algorithms (e.g. simulated annealing, Press *et al.*, 1993). Despite their increased complexity, these models often perform no better (especially when validated against an independent data set) than models based solely on accumulated degree-days (Chuine *et al.*, 1999). One factor may be that chilling temperatures often do not vary enough from year to year to adequately constrain the chilling submodel (Chuine *et al.*, 1998). Alternatively, in cold temperate natural systems, any chilling requirements may be routinely met long before enough degree-days have been accumulated for budburst. Hänninen (1995) argued that experimental data are needed to develop (and adequately test) realistic, physiologically based models: only with an experimental approach can otherwise correlated factors (photoperiod, accumulated chilling, and heating) be independently (and sufficiently) manipulated.

At present, there is no agreement among researchers on an appropriate model structure for autumn senescence (Schaber & Badeck, 2003), although the date of leaf drop has been observed to be quite consistent from year to year (Lee *et al.*, 2003), which suggests that senescence may be controlled by photoperiod rather than temperature.

There have been recent attempts to link satellite-derived signals (e.g. the normalized difference vegetation index (NDVI)) to phenology (White *et al.*, 1997; Jenkins *et al.*, 2002; Schwartz *et al.*, 2002; Fisher *et al.*, 2006). Satellite imagery has the advantage of spatial integration (cf. field measurements on a limited number of individuals), but its main problem is that the physiological significance of various remote sensing indices is not entirely clear. Field measurements are therefore necessary in order to determine the level of canopy development that corresponds to a particular NDVI threshold (Fitzjarrald *et al.*, 2001).

In this study, we use 14 years of data from weekly field surveys at the Hubbard Brook Experimental Forest to establish parameter values for simple models to predict the timing of spring and autumn phenological changes. The data we use are somewhat unique among long-term phenological data sets, in that a 'phenology

index', on a scale from 0 to 4, is used to describe the entire course of canopy development and senescence. By comparison, previous studies have generally been based on analysis of the timing of single events, such as budburst or flowering, and models developed to predict events (e.g. Hänninen, 1995; Chuine, 2000; Schaber & Badeck, 2003) are not directly applicable to ordinal scale data. Instead, we use a logistic growth model with a prediction range that is consistent with our 0–4 scale. The model is validated against a number of independent data sets from other sites in New England, including a 13-year record from the Harvard Forest. We then run the models using long-term daily meteorological data from Hubbard Brook to investigate potential climate change effects on northern hardwood forest phenology.

There is a long history of phenological studies in Europe and Japan; one family in the United Kingdom kept their own phenological records from 1736 to 1958 (Sparks & Menzel, 2002), and efforts to establish standardized International Phenological Gardens across Europe have been underway since 1959 (Menzel & Fabian, 1999). In North America, however, the situation is somewhat different (but see Betancourt *et al.*, 2005). There are far fewer phenology data sets available, and long-term, ongoing studies of the phenology of native forest trees are rare indeed. Thus, the Hubbard Brook and Harvard Forest data sets used here give unique insight into the forest phenology of New England over the last decade and a half.

Data and method

Field measurements

Our analysis is based on a 14-year data set (1989–2002) from the Hubbard Brook data archives (<http://www.hubbardbrook.org/>). The Hubbard Brook Experimental Forest is located within the White Mountain National Forest in central New Hampshire (43°56'N 71°45'W, el. 222–1015 m ASL). Likens & Bormann (1995) give a detailed description of climate, hydrology, topography and vegetation at Hubbard Brook. The climate is humid continental with short, cool summers (mean July temperature, 19 °C) and long, cold winters (mean January temperature, –9 °C). At low- and mid-elevations, the northern hardwood forest at Hubbard Brook is dominated by the study species, sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.).

Sample plots are located at nine different locations within the Hubbard Brook valley, across an elevational range from \approx 250 to 825 m ASL (Table 1). For each of the three study species, and at each plot, three co-dominant trees whose crowns were clearly visible from an existing trail network were selected for monitoring and permanently marked at the beginning of the study.

Each spring and autumn, plots have been visited approximately weekly, and the developmental stage of each marked tree is rated on a 0–4 canopy 'phenology

Table 1 Characteristics of permanent phenology plots at the Hubbard Brook Experimental Forest

Plot	Elev.	Aspect	Stand age	Phenology index threshold			
				Spring DOY	Autumn DOY	Spring HDD ₄	Autumn CDD ₂₀
1B	488	South	Mature	137	289	157	–421
4B	503	South	Immature	135	288	153	–422
4T	744	South	Immature	144	280	156	–377
5B	482	South	Immature	138	288	167	–414
5T	756	South	Immature	148	284	177	–451
6T	786	South	Mature	144	277	150	–345
7B	616	North	Mature	142	281	170	–381
7T	823	North	Mature	149	278	170	–386
HQ	259	South	Mature	134	291	179	–392

The plot ID indicates the plot location: watershed number and bottom (B) or top (T). HQ plot is located near the station headquarters. The reported phenology index threshold values represent the mean point (in terms of both day of year and thermal heat sums) at which sugar maple trees reached critical developmental stages ($\bar{P}_{\text{spring}} = 3$, leaves 50% of final length; $\bar{P}_{\text{autumn}} = 1$, 50% of leaves have fallen), based on 0–4 'phenology index' scale (see text for details). Means are based on inversion of plot-specific models fit separately to each year (1989–2002) of data. DOY, day of year. HDD₄ and CDD₂₀ are heating and chilling degree-days, based on 4 °C and 20 °C base temperatures, respectively. 'DOY' columns based on inversion of Model 1; 'HDD₄' and 'CDD₂₀' columns based on inversion of Model 2 (see text for model details). Elevation correlates strongly with DOY-based thresholds, but not degree-day based thresholds.

index' (P) scale in accordance with the criteria in Table 2. In this scheme, $P_{\text{spring}} = 0$ and $P_{\text{autumn}} = 0$ both correspond to a dormant canopy in winter condition, and $P_{\text{spring}} = 4$ and $P_{\text{autumn}} = 4$ both correspond to a full, green canopy in summer condition. However, canopy physiology differs between spring and autumn for the other index values. We define the 'canopy duration' to be the number of days between $P_{\text{spring}} = 3$ and $P_{\text{autumn}} = 1$; these phenology index values correspond to a canopy that is 50% full (Table 2). Similar, but not identical, indices have been used by other researchers (e.g. Norby *et al.*, 2003).

For each survey date, the mean phenology index, \bar{P} , is calculated for each species as the arithmetic mean of the individual index value of each of the three trees at each plot. There are a total of more than 800 spring-time \bar{P} ratings, and 1000 autumn ratings, per species, in the data set. It should be noted that, because of serial correlation (as well as other sources of nonindependence) in these time series data (due, in part, to the fact that development proceeds in one direction only), estimates of model error variance and parameter uncertainties are biased downward. Thus, although we have hundreds of individual measurements, from a practical perspective, we may have as few as just 14 degrees of freedom (plots are not independent of each other for a given sampling period; sampling periods are not independent of each other over time; and it is even arguable whether or not species are independent of each other). For this reason, we use the fitted models only as tools to characterize the patterns of development, rather than for formal hypothesis testing or statistical inference.

We used daily mean temperature data from a weather station at the Hubbard Brook station headquarters (259 m ASL) to calculate degree-day temperature sums.

Heating degree-day sums (HDD_k) are based on degree-days above the base temperature, k , whereas chilling degree-days (CDD_k) are based on degree-days below the base temperature, from January 1 (spring) and August 15 (autumn). Both heating and chilling degree-days sums are calculated for each season; the same base temperature, k , is used for HDD_k and CDD_k within a season, but different base temperatures are used for spring and autumn. We compared model fits using base temperatures from 0 to 12 °C in 2 °C increments (spring) and 0 to 30 °C in 5 °C increments (autumn). We extrapolated temperatures measured at HQ to the other eight plots using a lapse rate of 0.6 °C/100 m, which has been shown to be appropriate for this region (Richardson *et al.*, 2004).

Statistical analysis

By necessity, our approach differs from budburst modeling, where a threshold forcing value, F^* , is specified or fit, and the model prediction is essentially a binary variable (0, budburst has not occurred; 1, budburst has occurred). We used a simple sigmoid-shaped logistic curve (Eqn (2)) to model the phenology index, $P \in [0, 4]$. Our parsimonious modeling approach balances the relatively short-time series available at Hubbard Brook (cf. six centuries of Burgundy grape harvest date data, see Chuine *et al.*, 2004) against the richness of a data set that fully describes canopy development and senescence. The logistic function is commonly used in biometric and growth modeling applications (Sit & Poulin-Costello, 1994), and is the basis of accumulating temperature sums in some phenological models (Sarvas, 1972; Chuine *et al.*, 2000). It is an appropriate choice for modeling P because, unlike a linear model, the logistic function has horizontal

Table 2 Criteria for the determination of spring and autumn "phenology index" ratings

Rating	Description
<i>(A) Spring</i>	
0	No change from winter conditions, unexpanded buds only
1	Bud swelling noticeable
2	Small leaves or flowers visible, initial stages of leaf expansion, leaves about 1 cm long
3	Leaves 50% of final length, leaves obscure 50% of sky as seen through crowns
3.5	Leaves 75% expanded, sky mostly obscured through crown, crowns not yet in summer condition
4	Canopy appears in summer condition, leaves fully expanded, little sky visible through crowns
<i>(B) Autumn</i>	
4	Canopy appears in summer condition, only scattered leaves or branches have any color change
3	Many leaves have noticeable reddening or yellowing, much green still present
2	Most leaves yellow, red or colored, few leaves have fallen, leaves still obscure 50% of the sky as seen through crown
1	No more green in canopy, half of leaves have fallen, leaves still obscure half of sky as seen through crown
0.5	Most leaves fallen
0	All leaves fallen except remnants on beech, winter condition

asymptotes of $P = 0$ (at $x = -\infty$) and $P = 4$ (at $x = +\infty$). Model predictions are therefore constrained to fall within the range of possible phenology index values (the model will not, for example, predict out-of-range values of $P = -2$ or $P = 6$). We specified the curve as a function of n independent variables, x_1, \dots, x_n ; the model has $n + 1$ fitted parameters, b and c_1, \dots, c_n :

$$P(x_1, \dots, x_n) = \frac{4}{1 + \exp(b - c_1x_1 - \dots - c_nx_n)} \quad (2)$$

Interpretation of the model parameters is easiest for the $n = 1$ (two parameter, b and c_1) case. The instantaneous rate of development is given by the partial derivative of P with respect to x_1 (Eqn (3)). At a given stage of development (i.e. for a particular P), $\partial P / \partial x_1$ scales directly with c_1 , but not b . For a given x_1 , $\partial P / \partial x_1$ is a function of the c_1 parameter and the value of $P(x_1)$, which is itself a function of both b and c_1 parameters (Eqn (2)). Changes in the b parameter cause parallel shifts in the response function when c_1 is fixed, whereas with b fixed, changes in c_1 affect the overall steepness of the response to variable x_1 :

$$\frac{\partial P}{\partial x_1} = c_1 P - \frac{c_1 P^2}{4} \quad (3)$$

Inversion of the two-parameter model gives a straightforward solution for the value of x_1 at which a given P occur. This reduces to $x_1 = b/c_1$ for $P = 2$:

$$x_1 = \frac{1}{c_1} \left(b - \log \left(\frac{4 - P}{P} \right) \right) \quad (4)$$

We fit four versions of this model to the data for each species. Model 1 is based strictly on day of year (*DOY*); similar to Hunter & Lechowicz (1992) and Chuine (2000), we consider this to be a null model used as a benchmark for evaluating other models. Model 2 is based on accumulated degree-days: either *HDD* (for spring phenology) or *CDD* (for autumn phenology). Model 3 includes both *DOY* and either *HDD* (spring) or *CDD* (autumn). For both spring and autumn, Model 4 includes *HDD* and *CDD*, although the base temperatures used for accumulating degree-days differ between the two seasons (for springtime, Model 4 is thus similar to the alternating model of chilling; see Chuine *et al.*, 1998).

Analysis of residuals was conducted to determine whether omitted variables could account for any of the residual variance.

Validation data

To validate the statistical models fit to the Hubbard Brook data, we used two independent data sources. At the Harvard Forest in central Massachusetts (42°32'N 72°11'W, el. 340 m ASL), spring and autumn phenology of a range of woody species have been monitored since 1990 (<http://harvardforest.fas.harvard.edu/>; data ser-

ies HF-003). We used the 1990–2002 data for sugar maple, yellow birch and American beech. The data are recorded using a different set of criteria than is applied at Hubbard Brook, but are sufficiently detailed to permit conversion to the Hubbard Brook index scale. Unlike Hubbard Brook, however, these data reflect individual tree assessments rather than plot averages. Springtime data were converted to the Hubbard Brook index using B_{CON} (bud condition, from no swelling through to bud break), L_{FIN} (size of leaves relative to fully expanded leaf size), L_{75} (percentage of leaves that are at least 75% of final size) and L_{95} (percentage of leaves that are at least 95% of final size). Autumn observations were converted using L_{COLOR} (percentage of leaves that have changed color) and L_{FALL} (percentage of leaves that have fallen from the tree). Daily mean temperature data from a weather station at the Harvard Forest were used to determine cumulative degree-days. Phenological development of suburban sugar maple trees in Guilford, CT (41°16'N 72°41'W, 3 m ASL) and Kittery Point, ME (43°05'N 70°41'W, 10 m ASL) was assessed in 2003 (spring only) and 2004 (spring and autumn), respectively, following the Hubbard Brook phenology index criteria. To determine cumulative degree-days at these sites, daily mean temperature data from the nearby Bridgeport, CT (41°10'N 73°08'W, 2 m ASL, COOP ID 060806) and Kennebunkport, ME (43°21'N 70°28'W, 6 m ASL, COOP ID 174193) NOAA weather stations were obtained online from the National Climatic Data Center (<http://cdo.ncdc.noaa.gov/CDO/cdo>).

Retrospective modeling

To assess the potential effects of climate change at Hubbard Brook, we conducted a retrospective modeling exercise. Once model parameters were determined using the 1989–2002 field data, we ran Models 2 to 4 back to 1957 using the daily temperature record from the Hubbard Brook headquarters meteorological station. The dates at which $P_{\text{spring}} = 3$ and $P_{\text{autumn}} = 1$ were determined by model inversion and then used to estimate the canopy duration for each year. Time trends were determined using the Sen slope estimate (Gilbert, 1987), and the statistical significance of the trend was determined using the nonparametric Mann–Kendall test (Helsel & Hirsch, 2002). Analyses were conducted using a customized SAS program (Winkler, 2004).

Results

Overall patterns

For sugar maple, $\bar{P}_{\text{spring}} = 3$ is reached, on average, at day 134 (May 14) at the Hubbard Brook station

headquarters plot ('HQ plot', 259 m ASL, Table 1). For every 100 m increase in elevation, this stage is reached 2.7 ± 0.4 days later (slope estimate ± 1 SE; $n = 9$, $r^2 = 0.86$, $P \leq 0.001$) (Fig. 1). $\bar{P}_{\text{autumn}} = 1$ is reached at day 291 (October 18) at the headquarters plot. For every 100 m increase in elevation, this stage occurs 2.5 ± 0.4 days earlier ($n = 9$, $r^2 = 0.82$, $P \leq 0.001$). As a result, the canopy duration (crowns at 50% or more of full summer condition, from $P_{\text{spring}} = 3$ to $P_{\text{autumn}} = 1$) averages 157 days at the headquarters plot and decreases by 5.2 ± 0.6 days/100 m increase in elevation ($n = 9$, $r^2 = 0.92$, $P \leq 0.001$).

There is no correlation between plot elevation and the degree-day requirements for sugar maple to reach different phenology index thresholds. For example, neither the correlation between plot elevation and HDD_4 at which $\bar{P}_{\text{spring}} = 3$, nor the correlation between plot elevation and CDD_{20} at which $\bar{P}_{\text{autumn}} = 1$, is significant ($n = 9$, $P = 0.52$ and $P = 0.49$, respectively)

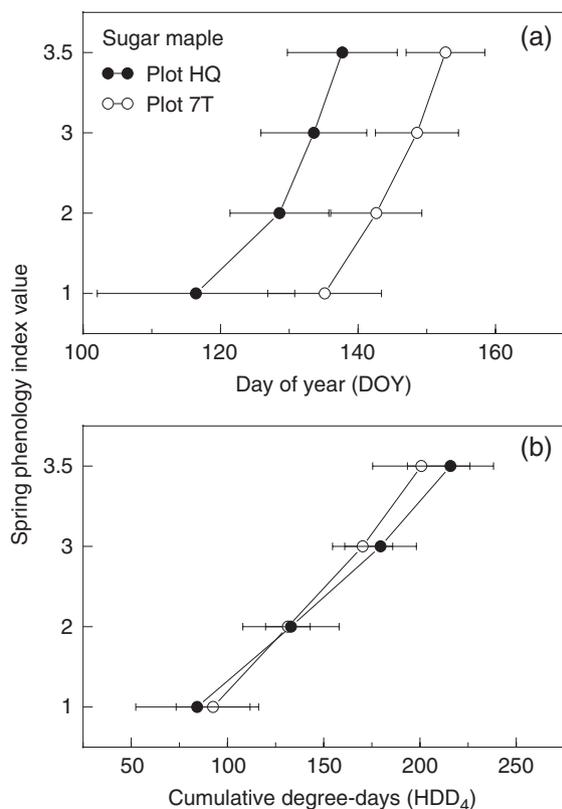


Fig. 1 Trends in spring canopy development (in terms of 0–4 'phenology index' scale described in Table 2) at low elevation plot (HQ plot, 259 m ASL) and high elevation plot (plot 7T, 823 m ASL), in relation to (a) day of year and (b) temperature heat sums (spring heating degree-days above 4 °C reference temperature, HDD_4). Means and standard deviations (error bars) based on inversion of plot-specific models fit separately to each year of field data.

(Table 1). Across all plots, $\bar{P}_{\text{spring}} = 3$ is reached at $HDD_4 = 164 \pm 11$ degree-days (mean ± 1 SD), and $\bar{P}_{\text{autumn}} = 1$ is reached at $CDD_{20} = -399 \pm 31$ degree-days.

Spring phenology model

The null model based on day of year, Model 1, accounts for more than 70% of the variation in \bar{P}_{spring} (Table 3) for all plots. Sugar maple is predicted to reach each of the spring developmental stages about 3 calendar days earlier than yellow birch and 2 days earlier than American beech. For all three species, the progression from $P_{\text{spring}} = 1$ (bud swelling noticeable) to $P_{\text{spring}} = 3.5$ (leaves 75% expanded) is expected to take about 24 calendar days (Fig. 2a).

Model 1 fails to account for either elevation-related differences in temperature, or for inter-annual temperature variability. However, from results in Table 1, we

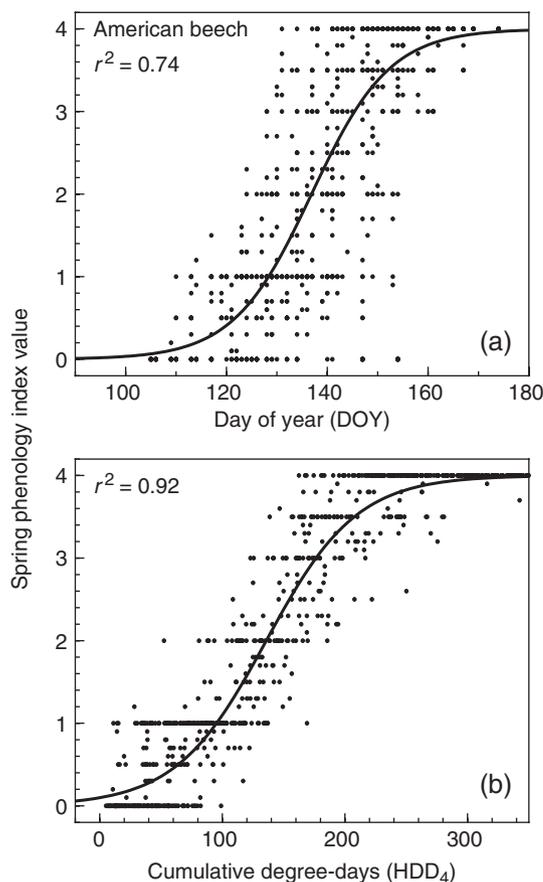


Fig. 2 Comparison of a logistic models of spring phenology (in terms of 0–4 'phenology index' scale described in Table 2) based on (a) day of year and (b) accumulated heating degree-days above 4 °C. Data are shown for American beech, *Fagus grandifolia*.

Table 3 Model statistics for a logistic growth model of spring phenology (see text for details) fit separately for three northern hardwood species, based on 14 years of data from the Hubbard Brook Experimental Forest

		Sugar maple	Yellow birch	American beech
<i>Model 1</i>				
r^2		0.72	0.73	0.74
MSE		0.644	0.625	0.605
b		16.83 ± 0.72	17.24 ± 0.71	17.64 ± 0.72
c_1	DOY	0.125 ± 0.005	0.125 ± 0.005	0.129 ± 0.005
<i>Model 2</i>				
r^2		0.92	0.92	0.92
MSE		0.178	0.181	0.181
b		3.42 ± 0.09	3.60 ± 0.09	3.68 ± 0.09
c_2	HDD ₄	0.028 ± 0.001	0.026 ± 0.001	0.027 ± 0.001
<i>Model 3</i>				
r^2		0.92	0.92	0.93
MSE		0.175	0.175	0.170
b		5.03 ± 0.40	5.69 ± 0.40	6.43 ± 0.41
c_1	DOY	0.014 ± 0.003	0.018 ± 0.003	0.023 ± 0.003
c_2	HDD ₄	0.026 ± 0.001	0.024 ± 0.001	0.023 ± 0.001
<i>Model 4</i>				
r^2		0.92	0.93	0.92
MSE		0.178	0.169	0.177
b		3.75 ± 0.18	4.79 ± 0.19	4.41 ± 0.19
c_2	HDD ₄	0.028 ± 0.001	0.027 ± 0.001	0.027 ± 0.001
c_3	CDD ₄	-0.0003 ± 0.0001	-0.0011 ± 0.0002	-0.0007 ± 0.0002

Model coefficients are ± 1 standard error. All reported coefficients are significant at $P < 0.05$. DOY, day of year; HDD₄, degree-day heating sum with 4 °C base temperature; CDD₄, degree-day chilling sum with 4 °C base temperature.

know that at least the elevation factor affects the timing of spring development. Model 2, which is based on accumulated heating degree-days, provides a considerably better fit than Model 1: r^2 values are much higher (0.92 for all three species), and the mean squared error (MSE) is only about one-third as large as with Model 1 (Table 3; Fig. 2b). The fit of Model 2 depends somewhat on the base temperature used for calculating the degree-day index. We compared model fits using base temperatures between 0 and 12 °C, and found that HDD₄ provides the best fit, although any base temperature in the range of 0–6 °C will give a fit that is more or less comparable (in terms of MSE) to that obtained with HDD₄. However, above 6 °C, model fit degrades rapidly with increasing base temperature.

Based on Model 2, sugar maple is expected to reach each P_{spring} developmental stage about 15–20 degree-days earlier than either American beech or yellow birch. However, regardless of species, about 112 degree-days above 4 °C are required for development to progress from $P_{\text{spring}} = 1$ to $P_{\text{spring}} = 3.5$.

In an analysis of variance with 'plot ID' and 'year' as categorical variables, roughly 5% of the Model 2 residual variance for American beech (the other two species were similar) is accounted for by plot ID, whereas year

accounts for 17% of the residual variance. The plot ID effects are not correlated with plot elevation ($P = 0.84$); nor is there any clear pattern related to either stand age or plot aspect. The year effect indicates that there is a small amount of inter-annual variability in phenology that, while likely climate driven, is not captured by the degree-day index. Because the year effects for one species tend to be correlated with the year effects for the other two species ($r > 0.70$ for all three paired correlations), there is evidence that the inter-annual variability that is not described by Model 2 nevertheless tends to affect the three study species similarly. It is not exactly clear what the cause of this variability might be. Cumulative solar radiation does not account for a significant proportion of the residual variance in any species (all $P \geq 0.20$). Cumulative precipitation accounts for a significant ($P \leq 0.001$) but small ($\approx 2\%$) proportion of the residual variance for sugar maple and American beech but not yellow birch ($P = 0.90$). Accumulated spring chilling (CDD₄) accounts for ≈ 2 –4% of the residual variance in yellow birch and American beech ($P \leq 0.001$), but not sugar maple ($P = 0.12$); it is possible that some other measure of chilling, perhaps related to the frequency, intensity, or duration, of late-spring frosts, is physiologically more relevant than CDD₄.

For spring phenology, Model 3, which includes both day of year and accumulated heating degree-days, represents only a modest improvement over Model 2 (Table 3). The MSE is virtually unchanged, but the uncertainty associated with the model coefficient b is increased about four-fold. Similarly, Model 4, which includes HDD_4 and CDD_4 , is not much of an improvement over Model 2. The CDD_4 coefficients, while significant at $P \leq 0.05$, are very small, and, as would be expected from the above residual analysis, addition of this variable results in only a negligible decrease in MSE.

Autumn phenology

The null model, Model 1, accounts for more than 80% of the variation in \bar{P}_{autumn} (Table 4). Senescence occurs somewhat more slowly for sugar maple than either of the other two species: results indicate that progression from $P_{\text{autumn}} = 3$ (noticeable coloration) to $P_{\text{autumn}} = 0.5$ (most leaves fallen) takes about 23 days, compared with ≈ 19 days for American beech and yellow birch. However, the phenological changes in sugar maple and yellow birch both occur about 5 days ahead of American beech.

Model 2, based on chilling degree-days, provides a better fit to the data (higher r^2 , lower MSE) than Model 1 for sugar maple and American beech (Table 4, Fig. 3). By comparison, Model 1 is a better fit than Model 2 for yellow birch. Although Model 3, which combines DOY and accumulated chilling, gives the lowest MSE for each of the three species, yellow birch is the only species for which Model 3 is markedly better than either Model 1 or Model 2 (Table 4). In terms of MSE, none of the autumn phenology models fit nearly, as well as the best of the spring phenology models (Tables 3 and 4).

For autumn phenology, Model 2 works reasonably well with any base temperature $\geq 20^\circ\text{C}$. However, lower base temperatures lead to substantially inferior model fits. For example, for sugar maple, $\text{MSE} = 0.47$ for CDD_{10} , compared with $\text{MSE} \approx 0.31$ for CDD_{20} , CDD_{25} and CDD_{30} .

Analysis of Model 2 residuals indicates that 10–18% of the residual variance is accounted for by year, and 7–13% by plot. The plot effect is not significantly correlated with elevation for any species (all $P \geq 0.05$). For sugar maple and yellow birch, but not American beech, solar radiation accumulated since August 15 accounts for a very small ($\approx 1\%$) but significant ($P \leq 0.05$) proportion of the residual variance. Precipitation

Table 4 Model statistics for a logistic growth model of autumn phenology (see text for details) fit separately for three northern hardwood species, based on 14 years of data from the Hubbard Brook Experimental Forest

		Sugar maple	Yellow birch	American beech
<i>Model 1</i>				
r^2		0.82	0.89	0.82
MSE		0.445	0.301	0.449
b		-36.5 ± 1.2	-44.4 ± 1.3	-43.2 ± 1.5
c_1	<i>DOY</i>	-0.132 ± 0.004	-0.160 ± 0.005	-0.153 ± 0.005
<i>Model 2</i>				
r^2		0.88	0.87	0.87
MSE		0.315	0.345	0.341
b		-3.91 ± 0.10	-4.24 ± 0.12	-5.08 ± 0.16
c_2	CDD_{20}	0.0117 ± 0.0003	0.0126 ± 0.0004	0.0124 ± 0.0004
<i>Model 3</i>				
r^2		0.88	0.90	0.87
MSE		0.310	0.264	0.326
b		-9.6 ± 1.3	-28.7 ± 1.5	-16.0 ± 1.6
c_1	<i>DOY</i>	-0.023 ± 0.005	-0.097 ± 0.006	-0.043 ± 0.006
c_2	CDD_{20}	0.0098 ± 0.0005	0.0054 ± 0.0005	0.0093 ± 0.0005
<i>Model 4</i>				
r^2		0.88	0.88	0.87
MSE		0.315	0.324	0.341
b		-3.89 ± 0.11	-4.56 ± 0.13	-5.07 ± 0.16
c_2	CDD_{20}	0.0117 ± 0.0003	0.0129 ± 0.0004	0.0124 ± 0.0004
c_3	HDD_{20}	$0.004 \pm 0.005^{\text{ns}}$	-0.040 ± 0.005	$0.002 \pm 0.005^{\text{ns}}$

Model coefficients are ± 1 standard error. All reported coefficients are significant at $P < 0.05$ except where noted (ns). *DOY*, day of year; CDD_{20} , degree-day chilling sum with 20°C base temperature; HDD_{20} , degree-day heating sum with 20°C base temperature. MSE, mean squared error.

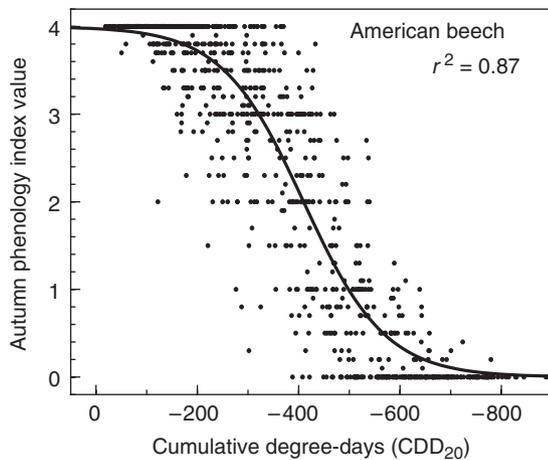


Fig. 3 Logistic model of autumn phenology (in terms of 0–4 ‘phenology index’ scale described in Table 2) based on accumulated chilling degree-days below 20 °C. Data are shown for American beech, *Fagus grandifolia*.

accumulated since August 15 accounts for 3% of the residual variance for sugar maple ($P = 0.03$), but this correlation is not significant for the other two species. The accumulated heat sum HDD_{20} accounts for a very small (≈ 1 –2%) but nevertheless significant ($P \leq 0.05$) proportion of the residual variance for all three species, but in Model 4 (Table 4), the HDD_{20} parameter is not significantly different from zero for sugar maple or American beech (both $P \geq 0.05$) and, therefore, this variable probably should not be included in the model. However, it is possible that in addition to accumulated chilling degree-days, other specific threshold temperatures (e.g. the first autumn frost) may be important for triggering particular stages of autumn senescence.

Validation of Hubbard Brook model with independent data

To provide a baseline against which the validation results could be evaluated, each of the four models was first fit to the Harvard Forest data (Table 5). For springtime phenology at Hubbard Brook, the null model (Model 1) is clearly inferior to the other models, but at the Harvard Forest, Models 2–4 give only a slightly better fit (lower calibration MSE) to the data than does Model 1. In autumn, none of the models gives a very good fit for the senescence patterns in American beech, at least compared with either sugar maple or yellow birch, or model fits at Hubbard Brook. Furthermore, for all species, the calibration MSE of the null model (Model 1) is as low as any of the alternative models. By comparison, at Hubbard Brook Model 1 is clearly inferior to alternative models for autumn phenology in sugar maple and American beech (Table 4).

Table 5 Validation statistics for four phenology models (described in text) calibrated using data from the Hubbard Brook Experimental Forest and tested against data from the Harvard Forest (1990–2002)

	Sugar maple	Yellow birch	American beech
(A) Spring	$n = 790$	$n = 796$	$n = 988$
Model 1	0.62 (0.16)	0.70 (0.17)	0.49 (0.14)
Model 2	0.37 (0.14)	0.48 (0.15)	0.40 (0.16)
Model 3	0.33 (0.11)	0.45 (0.12)	0.26 (0.10)
Model 4	0.35 (0.12)	0.44 (0.12)	0.26 (0.12)
Bias			
Model 1	−0.52	−0.60	−0.46
Model 2	0.26	0.20	0.28
Model 3	0.20	0.14	0.13
Model 4	0.23	0.12	0.06
(B) Autumn	$n = 290$	$n = 320$	$n = 421$
MSE			
Model 1	0.70 (0.29)	0.19 (0.14)	1.08 (0.84)
Model 2	0.39 (0.33)	1.13 (0.20)	1.08 (0.91)
Model 3	0.34 (0.29)	0.38 (0.13)	0.95 (0.83)
Model 4	0.40 (0.33)	0.67 (0.18)	1.09 (0.91)
Bias			
Model 1	−0.41	0.14	−0.28
Model 2	0.12	0.66	0.33
Model 3	0.01	0.32	0.18
Model 4	0.14	0.44	0.34

MSE, mean squared error; Bias = $\Sigma(\text{modeled} - \text{measured})/n$. Calibration MSE statistics (values in parentheses) are calculated for models fit to the Harvard Forest data, and provide a reference for the validation MSE statistics.

Compared with the calibration MSE of models fit to the Harvard Forest data, the validation MSE of the models fit to the Hubbard Brook data and tested against Harvard Forest data is considerably higher (Table 5). For both spring and autumn, Model 3 generally has the lowest validation MSE.

For all three species, spring development at the more southerly Harvard Forest begins somewhat earlier, but proceeds more slowly, than predicted by the Hubbard Brook Model 1; on the whole, the degree of development is under-estimated (i.e. negative bias, Model 1, Table 5). For example, sugar maple at Harvard Forest reach $P_{\text{spring}} = 1$ at day 109 (cf. day 117 at the Hubbard Brook headquarters plot), and $P_{\text{spring}} = 3.5$ at day 145 (cf. day 141).

The onset of canopy development (i.e. $P_{\text{spring}} = 1$, noticeable bud swelling) is reasonably well predicted at Harvard Forest by Hubbard Brook Models 2–4 (e.g. for sugar maple, $HDD_4 = 83$ in the Hubbard Brook model, cf. $HDD_4 = 84$ when the model is fit to Harvard

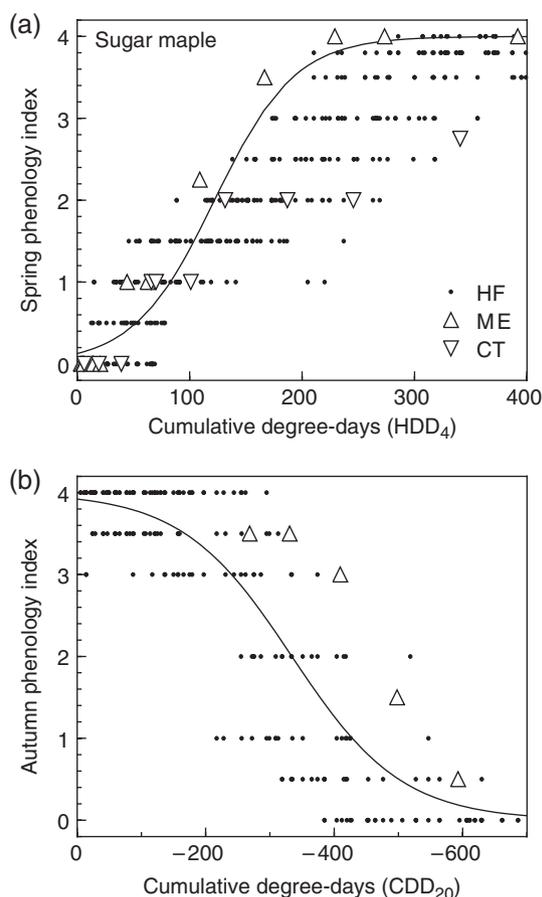


Fig. 4 Validation of logistic models of (a) spring and (b) autumn phenology (in terms of 0–4 ‘phenology index’ scale described in Table 2). Models were initially fit using data from the Hubbard Brook Experimental Forest. Validation is conducted using three independent data sets: Harvard Forest, 1990–2002; Guilford, CT, 2003; and Kittery Point, ME, 2004. All data shown are for sugar maple, *Acer saccharum*.

Forest data), but, as shown for Hubbard Brook Model 2 (Fig. 4a), subsequent phenological stages are not reached as quickly as predicted (also compare actual vs. predicted dates at which $P_{\text{spring}} = 1$ and $P_{\text{spring}} = 3$ in Fig. 5). From Fig. 4a it is clear that at Harvard Forest, more accumulated degree-days are required for full canopy development than at Hubbard Brook. For sugar maple, progression from $P_{\text{spring}} = 1$ to $P_{\text{spring}} = 3.5$ requires 217 degree-days at Harvard Forest, whereas only half as many degree-days are needed at Hubbard Brook. Thus, both in terms of calendar time and thermal time, development occurs more quickly at Hubbard Brook than at Harvard Forest.

Autumn patterns are not as consistent. Autumn senescence at Harvard Forest occurs later than predicted by Hubbard Brook Model 1 for sugar maple and American beech, but the bias for yellow birch is negligible

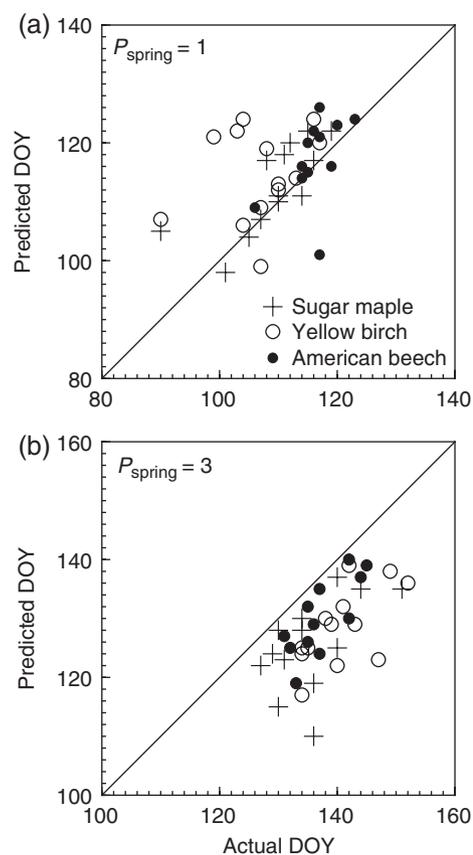


Fig. 5 Comparison of actual dates at which stated spring phenological stages were reached, compared with predicted dates. Data are shown for the Harvard Forest. Predictions are based on models calibrated using data from Hubbard Brook.

(Table 5). For sugar maple, Hubbard Brook Models 2–4 all give quite good predictions (low MSE with only modest bias; validation results are more or less comparable to those for the fitted models) for the course of autumn phenology (Model 2 is illustrated in Fig. 4b), whereas none of the models are able to reliably predict these patterns in American beech (Table 5; similarly, the MSE of the fitted models is higher for American beech than the other species). For yellow birch, Model 1 is clearly superior to any alternative models (Table 5); recall that at Hubbard Brook, yellow birch was the only species for which Model 1 performed as well as (or even better than) the alternative models. Although Hubbard Brook Model 3 could predict with reasonable accuracy the average date at which $P_{\text{autumn}} = 3$ or $P_{\text{autumn}} = 1$ at Harvard Forest, the interannual variation in these dates is not especially well-captured, except for sugar maple (Fig. 6).

While sugar maple spring development at the CT site appears similar to that at Harvard Forest (i.e. requiring

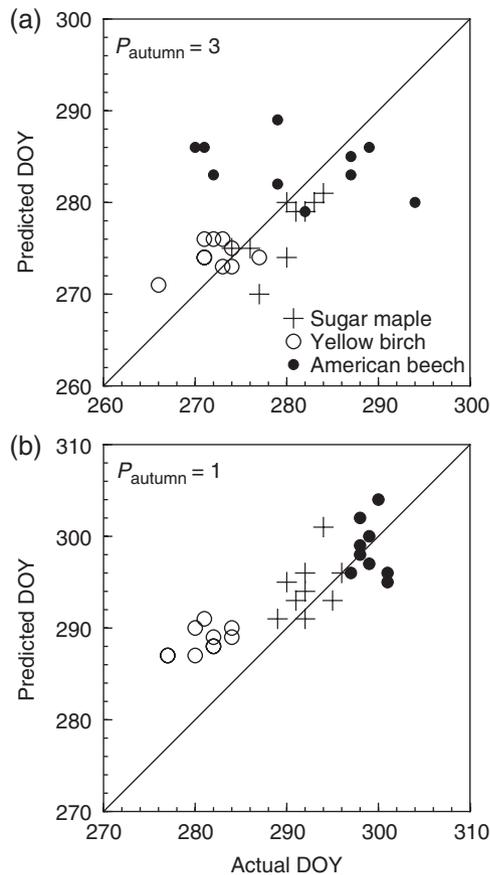


Fig. 6 Comparison of actual dates at which stated autumn phenological stages were reached, compared with predicted dates. Data are shown for the Harvard Forest. Predictions are based on models calibrated using data from Hubbard Brook.

more accumulated degree-days than at Hubbard Brook), spring development at the ME site is in near-perfect agreement with the Hubbard Brook model (Fig. 4a). Given this latter fact, it is interesting that autumn senescence at the ME site occurs somewhat later than would be predicted by the Hubbard Brook model (Fig. 4b).

Retrospective modeling

Models 2–4 were run using the 1957–2004 daily mean temperature data for Hubbard Brook to assess the potential effects of climate change over the last five decades on the timing of spring and autumn phenological development. For any given year, the predicted dates at which $P_{\text{spring}} = 3$ and $P_{\text{autumn}} = 1$ vary among models. For yellow birch, the difference is, in some instances, as large as 15 days in the spring (Model 2 predicts earlier development than Model 4), and 19 days in the autumn (Model 4 predicts later senescence than Model 3). For each model, there is also consider-

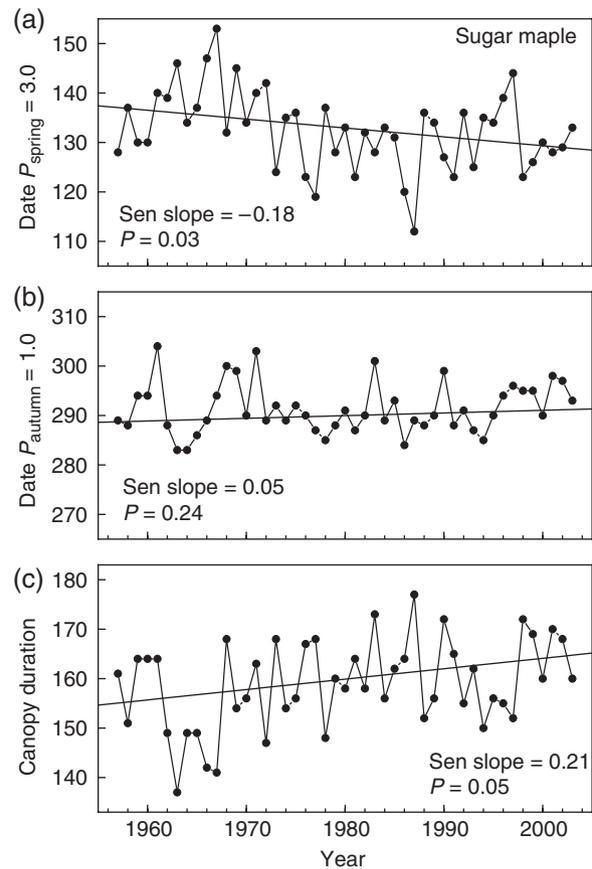


Fig. 7 Modeled reconstruction of spring and autumn phenology at the Hubbard Brook Experimental Forest, 1957–2004. Models (based on heating degree-days above 4°C and chilling degree-days below 20°C , respectively) were calibrated using 1989–2002 field data, and run using daily mean temperature data from an on-site meteorological station. (a) At $P_{\text{spring}} = 3$, leaves are 50% of their final length and leaves obscure 50% of the sky; (b) at $P_{\text{autumn}} = 1$, 50% of leaves have fallen and leaves obscure 50% of the sky; (c) the canopy duration is calculated as the number of days between $P_{\text{spring}} = 3$ and $P_{\text{autumn}} = 1$. Regression lines indicate the nonparametric Sen slope estimate; reported P -values are for the associated Mann-Kendall nonparametric trend test. Data are for sugar maple, *Acer saccharum*.

able interannual variability in the dates at which these particular phenological stages are reached. For example, for Model 2, there is a 40-day range in the date at which sugar maple $P_{\text{spring}} = 3$, and a 20-day range in the date at which sugar maple $P_{\text{autumn}} = 1$ (Fig. 7a, b); for other models and the other species, the range of variation is more or less comparable.

For all three species, the models suggest that, over the last 50 years, the canopy duration has likely increased (Fig. 7c). This is the product of both an earlier spring development and a later autumn senescence, both of which are driven by warmer temperatures. Regardless

of the model or species, the spring trend is significant ($P \leq 0.05$) for all model \times species combinations, except $P = 0.07$ for American beech Models 3 and 4. Estimates of the magnitude of the trend range from -0.12 to -0.20 days/yr (mean -0.16 days/yr). For sugar maple and Model 2 (Fig. 7a), the trend is -0.18 days/yr ($P = 0.03$), with a 90% confidence interval of -0.04 to -0.33 days/yr. The autumn trend ($+0.05$ days/yr), while consistent across species and models, is smaller in magnitude and not significant (all $P \geq 0.10$) for any single model \times species combination (e.g. Fig. 7b). For sugar maple, using Model 2 for both spring and autumn, the canopy duration over the last five decades is predicted to have increased at a rate of $+0.21$ days/year ($P = 0.05$), with a 90% confidence interval of $+0.03$ to $+0.42$ days/year.

Discussion

General observations

Along the elevational gradient at Hubbard Brook, low elevation trees tend to leaf out earlier, and keep their leaves longer, than high elevation trees. Thus, the onset of spring is delayed by 2.7 ± 0.4 days for every 100 m increase in elevation. This is roughly in agreement with Hopkin's Law, which states that for every 30 m increase in elevation, there is a 1 day delay in the onset of spring (Fitzjarrald *et al.*, 2001).

There is variation among species in the timing of phenological events, and previous studies suggest that spring development of sugar maple precedes that of yellow birch, which precedes American beech (Lechowicz, 1984). At Hubbard Brook, sugar maple is the first species to leaf out in the spring, preceding American beech by 2 days and yellow birch by 3 days. Apart from this offset among species, springtime phenology is similar among species, and is adequately described by a model based on accumulated heating degree-days above 4°C . Development in all three species requires about the same number of heating degree-days. By comparison, there are more pronounced cross-species differences in autumn phenology. Senescence occurs more slowly for sugar maple than the other two species, and although American beech senescence occurs relatively quickly, it is nevertheless, the last species to lose its leaves in the fall. Compared with spring development, when the same model structure (e.g. Model 2) worked reasonably well for all three species, yellow birch senescence is best described by a model that takes both autumn chilling and *DOY* into account (Model 3), whereas for sugar maple and American beech, addition of *DOY* gives little improvement over a model based only on autumn chilling.

Our phenology index gives a far more complete picture of the state of the canopy than simply knowing dates of budburst and leaf drop, especially since rates of development may vary among species. In this regard, we anticipate that a more widespread use of the phenology index will prove useful both for the interpretation of remote sensing indices, such as NDVI, and for improved modeling of forest-atmosphere CO_2 exchange.

Model validation

Raulier & Bernier (2000) found that they could account for 84% of the variation in the date of leaf emergence across the native range of sugar maple using a simple model based on heating and chilling degree-days. However, this model was not validated against a fully independent data set. Testing phenological models with an external data set is essential; a number of studies have demonstrated that the models that give the best fit for one data set may perform the worst when validated against an external data set (Chuine *et al.*, 1998, 1999). The models calibrated with the Hubbard Brook data predict the onset of spring (e.g. $P_{\text{spring}} = 1$) at Harvard Forest with reasonable accuracy, but tend to over-estimate (Model 1) or under-estimate (Models 2–4) the rates of subsequent development. Differences among populations in the timing of budbreak have been shown to persist in common garden provenance trials, and this variation therefore appears to be under genetic control (Lechowicz, 1984). Population-specific genetic effects could make it inherently very difficult to parameterize a model that has good predictive power across a wide geographic range, unless the genetic differences are themselves correlated with climate. For example, previous studies have demonstrated that more heating degree-days are needed for budbreak and development at warmer sites than at colder sites (White *et al.*, 1997; Jenkins *et al.*, 2002; White & Nemani, 2003).

A weakness of the models used here is that they are not physiologically based, and may therefore be too simple. A logical next step would be to apply Chuine's (2000) 'unified model' or Schaber & Badeck's (2003) 'promotor-inhibitor model', both of which are physiologically motivated and have been validated for predicting budburst in temperate tree species. However, the problem does not appear to be that the Hubbard Brook models predict the onset of development at Harvard Forest poorly, but rather that they do not predict the later stages of leaf expansion (i.e. $P_{\text{spring}} \geq 2$) very well, because more accumulated degree-days are required at the more southerly Harvard Forest. The number of accumulated degree-days required for canopy development may, therefore, be a physiological

manifestation of genetic differences among different populations (e.g. Hubbard Brook vs. Harvard Forest).

Impacts of climate change

Recent studies have provided relatively consistent estimates of the rate of advancements in the onset of spring over the last several decades. Time trends in the seasonal variation of atmospheric CO₂ concentration suggest that in the northern hemisphere as a whole, spring advanced by roughly 1 week over a 15-year period beginning in the late 1970s (Keeling *et al.*, 1996). Other indirect evidence suggests that spring in the northeastern United States has advanced by ≈ 6 –8 days between the 1956–1975 and 1976–1995 periods (Fitzjarrald *et al.*, 2001). In eastern North America, modeled time series indicated a significant trend towards earlier flowering of elm trees (≈ 2 days/decade over 1956–1997), although no trend was apparent for ash or oak (Chuine *et al.*, 2000). Across North America, a 'spring index' model suggested earlier spring leaf-out (1.8 days/decade) and flowering (1.4 days/decade) trends in lilac phenology over the 1959–1993 period (Schwartz & Reiter, 2000). A related study, using the same modeling approach, reported earlier modeled spring leaf-out (2.1 days/decade) and flowering (1.2 days/decade) for lilac in the northeastern United States over the period 1965–2001 (Wolfe *et al.*, 2005). Additionally, Wolfe *et al.* (2005) found that field observations of spring phenology for a variety of cultivated species (lilac, apple and grape) indicated trends towards earlier spring flowering (≈ 1 –2 days/decade) that were consistent with the model predictions. Analysis of data from a network of common gardens in Europe suggests that spring has advanced, on average, by ≈ 2 days/decade, whereas meta-analyses and review papers have estimated a rate of spring advancement of ≈ 2 –5 days/decade (Peñuelas *et al.*, 2002; Badeck *et al.*, 2004). Our Hubbard Brook models, based on 14 years of field observations of three forest tree species native to New England, predict that spring has advanced by 1–2 days/decade over the last five decades, which is consistent with the above-mentioned studies, and strongly supportive of the idea that human-induced climate change is having marked effects on the terrestrial biosphere.

Although it has been the subject of less research, at least three previous studies have demonstrated that autumn senescence has been occurring later in recent years, by ≈ 1.6 days/decade in Europe (Menzel & Fabian, 1999), ≈ 2.5 days/decade in the Mediterranean (Peñuelas *et al.*, 2002), and ≈ 2 days/decade in Japan (Matsumoto *et al.*, 2003). However, we are not aware of previous studies in which this pattern has been documented for North America. The autumn trend at

Hubbard Brook is nonsignificant, but it is, nevertheless, in the expected direction, and it would appear to strengthen the argument that delayed senescence is a global, and not just regional, phenomenon.

The retrospective modeling results support the idea that timing of spring development is more variable (± 20 days) than that of autumn senescence (± 10 days) (White *et al.*, 1997; White & Nemani, 2003). This variability makes it difficult to detect significant trends in phenology time series of only a decade or two in length. For example, using the modeled Hubbard Brook data, and analyzing only the years 1975–2004, there is a nonsignificant trend (≈ 0.1 days later/yr, $P \geq 0.10$) towards a later, rather than earlier, spring. This trend is even stronger (0.2–0.5 days later/yr; $P \geq 0.10$) when just the years 1985–2004 are used, but for the years 1995–2004, the trend reverts to an earlier spring (0.1–0.5 days earlier/yr, $P \geq 0.10$). This has two implications. First, because it is clearly preferable to directly measure (rather than model) the effects of climate change on forest ecosystems, there is a need for long-term field measurements of canopy phenology. Second, as noted by Schwartz (1998) and Fitzjarrald *et al.* (2001), although remote sensing has tremendous potential as a tool by which phenology can be studied, the data sets are simply not long enough (none are more than ≈ 25 years old) to yet permit definitive statements about recent trends in, for example, the timing of budburst.

Summary and conclusions

Analysis of 14 years of field data from the Hubbard Brook Experimental Forest indicates that spring development and autumn senescence of three northern hardwood species is adequately described by simple models based on day of year and accumulated degree-days. Validation against an independent data set indicates reasonable agreement between observations and model predictions, but highlights two key weaknesses of the models. First, in all three species, models based on accumulated degree-days over-estimate the rate of canopy development at the Harvard Forest, located 150 km to the south of Hubbard Brook. Second, differences among species need to be resolved: patterns in autumn phenology are predicted quite well for sugar maple but not American beech. A physiologically realistic, process-based model may be required.

The large interannual variability observed in the timing of spring and autumn phenological events argues for the continued field monitoring of canopy phenology (see also Betancourt *et al.*, 2005). Such long-term data will be essential for the accurate, direct, assessment of the effects of climate change on the northern hardwood forests of New England.

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