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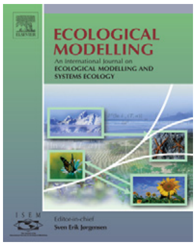

# Improving the budburst phenology subroutine in the forest carbon model PnET

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ABSTRACT

The timing of leaf expansion in spring and leaf senescence in fall determines growing season length; hence leaf phenology is important in modelling carbon production. Previous work monitoring net ecosystem exchange using eddy flux technology found phenological timing to be a key factor determining ecosystem carbon balance. Growing degree days (GDD; the sum of daily mean temperature above 0 °C) have long been used to track tree phenological behavior. Ecosystem carbon balance simulations should employ models that reliably track leaf phenological activities. Our goals for this study were to evaluate the GDD-based phenological algorithm for the forest carbon simulation model PnET and to develop a robust budburst model for the implementation of PnET in the forests of Ohio. We obtained 11 years (1990–2000) of leaf budburst phenology data from Harvard Forest, MA and found large inter-annual variations on the date of budburst. Contrary to the previous sensitivity analysis on GDD, we used the observed range in the data to inform our new GDD sensitivity analyses. In fact the broad inter-annual variation of the budburst phenology had substantial impacts on the annual net primary production. Moreover, GDD did not provide reliable prediction on the date of budburst although it was employed by the PnET family of models. The predictions of budburst dates were largely improved by incorporating a chilling factor, with 16 of 17 deciduous tree species showing significant linear relationships between predicted and observed dates of budburst. However, this updated phenology model showed geographic specificity that is not suitable for our simulations in southern Ohio. For successful development of a more comprehensive phenological model, locally developed and long-term leaf phenology records are required.

## 1. Introduction

Process-based models of forest productivity have been developed in various ecosystems with different levels of complexity (Hanson et al., 2004) and are crucial to our understanding of the role forest ecosystems play in carbon budgets and climate change. These models, as reviewed and compared by Hanson et al. (2004), primarily consist of: (1) the amount and type of vegetation; (2) the duration of the "green" period; (3) physiological processes (photosynthesis, respiration, nutrient uptakes, water transports, etc.); (4) stand carbon allocation; (5) physical environmental variables (e.g., microclimatic drivers and edaphic properties). Among these components, the duration of "green" period, i.e., leaf phenology is gaining more attention due to its relevance to global climate change, because shifts in phenological timing have been observed widely (Schwartz, 1998).

Phenology is the study of seasonal timing of recurring biological events, such as flowering, fruiting, budburst, and leaf senescence (Lieth, 1974). Increasingly, ecosystem scientists

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interested in tracking site productivity are focusing on leaf phenology due to its impacts on ecosystem carbon balance (Jackson et al., 2001). Variance in leaf budburst and senescence determines the length of growing season, which strongly impacts net ecosystem productivity (Goulden et al., 1996; Keeling et al., 1996; Chen et al., 1999; White et al., 1999). Eddy flux studies have shown net ecosystem productivity (NEP) to be particularly sensitive to leaf budburst. In the Harvard Forest, a 6–10-day shift in budburst resulted in an increase of 20–40% in net ecosystem carbon exchange (Goulden et al., 1996). In an old aspen forest at Prince Albert National Park, Saskatchewan, Canada, in 1994, spring time temperature was 4.8 °C higher than 1996 (March to May) with a corresponding 18–24 days earlier leaf emergence. In comparison of these 2 years, the warmer spring and earlier budburst resulted in 54% higher NEP (Chen et al., 1999). Changes in leaf phenology also impacted global atmospheric $CO_2$ balance, which were manifested by the increasing amplitude of fluctuations in seasonal atmospheric $CO_2$ concentration with increasing length of growing season (Keeling et al., 1996).

One of the challenges in implementing carbon balance modelling is to reliably predict leaf phenological activities which can vary up to several weeks from year to year. With the absence of a process-based phenological model (Arora and Boer, 2005), the prediction of leaf budburst solely relies on empirical models, and data are often limited (e.g., Cannell and Smith, 1983; Raulier and Bernier, 2000; Rötzer et al., 2004). For a biologically and physically simplified system like an agricultural field, simple temperature summation functions such as growing degree days (GDD) have been widely used to predict the phenological changes of crops as well as their pathogens. Other phenological models have incorporated both summed degree days and summed chilling days, and researchers have found these to be interactive parameters (Cannell and Smith, 1983). More complex systems such as forests encompass complex vertical structures, house a far greater species richness and occupy more dynamic physical environments, making it difficult to use a simple model such as GDD to predict phenological activities. Moreover, empirical models are usually location-dependent and their development requires multiyear *in situ* observations in combination with climate data. Since long-term and ground-based phenological data are rare (Schwartz, 1998), the availability of site-specific phenological models are very limited.

PnET-Day is a daily time-step, canopy photosynthesis model that was developed and validated in the Harvard Forest, MA (Aber et al., 1996). Despite many limitations of GDD-based phenological models (reviewed by Arora and Boer, 2005), PnET-Day, as well as other members of PnET family (PnET-II, Aber et al., 1995; PnET-CN, Aber et al., 1997; PnET-BGC, Gbondo-Tugbawa et al., 2001), use GDD that accumulate from the first day of every year as the predictor of leaf budburst (Aber et al., 1995; Aber et al., 1996). For the deciduous forest type, by default, the onset of leaf budburst occurs once GDD (with threshold temperature = 0 °C) reaches 100. However, probably due to the low sensitivity of GDD required for leaf budburst (<1% decrease in gross carbon exchange with 10% increase in GDD requirement for bud break; Aber et al., 1996), the reliability of PnET's phenology algorithm, to our knowledge, has not been rigorously validated. However, one study demonstrated that leaf development predicted by PnET is several weeks before the actual leaf budburst in the Harvard Forest (Wythers et al., 2003). An important reason for the low sensitivity of the GDD predictor is the low default value. A 10% increase of GDD requirement for budburst (GDD = 100) would only delay the date of budburst for 2–5 days in the early spring; however, the typical inter-annual variations in the date of budburst can reach 1–2 weeks (O'Keefe, 2004). In addition, the estimate of GDD required for the onset of leaf budburst in deciduous forests of eastern North America based on the mean of 19 studies was 379 with standard deviation of 79 degree days (Radtke et al., 2001). The validity of using default GDD for the onset of leaf budburst should be more rigorously tested.

This study is part of a larger effort to parameterize the PnET models to evaluate the impact of oak silvicultural options (thinning and/or burning) on NPP in southern Ohio forests. The specific objectives of this study are to (1) evaluate how variance in budburst phenology impacts the outputs of carbon balance in PnET-Day simulations; (2) evaluate the phenology subroutine that is currently employed by PnET models; (3) improve the reliability of the phenology subroutine that can potentially be incorporated in PnET models. Due to the geographical specificity of GDD required for budburst (Berninger, 1997; Jenkins et al., 2002), we also compare the phenological data between sites at southern Ohio and the Harvard Forest, MA in order to see whether an established phenology model can be applied in different geographical areas.

## 2. Methods

### 2.1. Site description

The PnET-Day simulations were parameterized based on the field data collected at the Raccoon ecological management area (REMA; 39°12′N, 82°28′W). REMA is one of the three replicates of the Ohio Hills Fire and Fires Surrogate (FFS) study site (Sutherland and Hutchinson, 2003). The study site is part of the unglaciated, maturely dissected Allegheny Plateau with high hills and sharp ridges in southern Ohio. The vegetation is dominated by oak (e.g., *Quercus prinus*, *Q. alba*, *Q. velutina*, and *Q. coccinea*) and hickory (*Carya* spp.) species in the overstory and a mixture of American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), and black gum (*Nyssa sylvatica*) in the subcanopy and understory (Sutherland and Hutchinson, 2003; Albrecht and McCarthy, 2006).

The climate in this region is cool, temperate, and mesic with mean annual temperature of 11.3 °C and mean annual precipitation of 1024 mm. The geology is predominantly sandstone and shale of Pennsylvanian period. Soils are mostly loams and silt loams that are acidic and well drained (Sutherland and Hutchinson, 2003).

### 2.2. Field and laboratory measurements

Maximum specific leaf weight (SLWMax; $g\,m^{-2}$) and foliar nitrogen content (FolNCon; % mass) were obtained from 60 leaf samples for each of the three species, including *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus alba*. Samples were collected from the top of tree canopies using a 20-gauge shotgun. Leaves collected in the field were kept below 0 °C in a cooler. Within 24 h after field work, leaf area was first measured using Li-3000 portable area meter (Li-Cor Inc., Lincoln, NE, USA). Leaves were then rinsed with distilled water and oven dried for 72 h at 70 °C. SLWMax was calculated as the ratio between foliar dry weight and one-sided area. Five leaf samples for each of the three species were finely ground using SPEX CertiPrep 8000 M Ball mill (SPEX CertiPrep Inc., Metuchen, NJ, USA). The ground leaf samples were analyzed for nitrogen content using Elementar CN analyzer (Elememtar Analysensysteme GmbH, Germany).

Leaf budburst phenology of 20 mature trees for each of the three species (*Quercus alba*, *Liriodendron tulipifera*, and *Acer rubrum*) was observed every 4–7 days from late March to mid-May in 2004 and 2005. The date of budburst was determined for each tree when 50% of the buds had leaves recognizable through binocular observation. The SLWmax, FolNCon, and budburst phenology of those three species were used to run the PnET-Day model in REMA.

### 2.3. *PnET-Day model description and parameterization*

PnET-Day (Aber et al., 1996) is daily time step canopy photosynthesis model that uses FolNCon (% mass) to predict the maximum photosynthesis rate ($A_{\max}$). Deviation from the optimal air temperature, vapor pressure deficit (VPD), and photosynthetically active radiation (PAR) are used to reduce the maximum photosynthesis to realized rates. Basal respiration is a constant fraction (default = 0.1) of $A_{\max}$. Day and night time temperature is applied in $Q_{10}$ (default $Q_{10} = 2$) function for the calculation of realized respiration rates. The gradient in specific leaf weight (SLW, $\mathrm{g\,m^{-2}}$) along the vertical profile of the forest stand is used to account for changes in photosynthesis rate at different canopy layers. The dates of leaf budburst and maximum leaf area are set by GDD (GDDFolStart and GDDFolEnd, respectively; Aber et al., 1996).

To conduct the sensitivity analysis of the budburst phenology in REMA, we selected three common tree species with contrasting leaf traits (Table 1). Of these, *Acer rubrum* has both lower FolNCon and SLWMax; *Liriodendron tulipifera* has high FolNCon and low SLWMax; *Quercus alba* has low FolNCon but high SLWMax (Table 1). We used the default photosynthesis and canopy parameters (Aber et al., 1996) except FolNCon and SLWMax, which were both obtained from REMA. Daily weather data required for PnET-Day simulations were obtained from Ohio Agricultural Research and Development Center at Jackson branch (39.02°N, 82.60°W; http://www2.oardc.ohio-state.edu/centernet/stations/jchome.asp). Daily mean photosynthetically active radiation (PAR; $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) was converted from energy units (Joule) assuming 1 mol photons containing $2.17 \times 10^5$ J of energy (McCree, 1981).

Sensitivity analyses were performed by comparing the gross primary productivity (GPP), NPP and autotrophic respiration ($H_a$) and daily net photosynthesis rate in PnET-Day model runs between default phenology estimators (GDDFolStart = 100) and realized budburst date. Similar sensitivity analyses were performed evaluating the effects of leaf-off dates, which were found to have negligible influence on carbon balance (data not shown). PnET-Day was run separately for three species, including *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus alba* and combined based on the relative basal area (RBA; D.A. Yaussy, personal communication). *Q. alba* was selected to represent all *Quercus* species (RBA of *Quercus* = 75%), *A. rubrum* covered 9% of RBA and *L. tulipifera* covered 6% of RBA.

### 2.4. *Development of phenological models*

Eleven years of leaf phenology data (1990–2000) were obtained from the Harvard Forest, where the observations were made by J. O'Keefe on 2–5 individuals of 33 woody species along a 2 km trail near the Harvard Forest headquarters. The visits were at an interval of 3–7 days from April to June (O'Keefe, 2004). The date of budburst was determined when 50% of the buds had recognizable leaves. In this study, we selected a subset of 17 deciduous tree species (see Fig. 1), and randomly selected one tree from 4 to 5 individuals of each species for the validation of phenology models. The other 3–4 trees of each species were used for the development of phenology models.

The 11 years of budburst data and the corresponding weather data in the Harvard Forest were used to build phenology models. The spring warming model employed by PnET models assumed constant thermal sum with temperature threshold of 0 °C ($\mathrm{GDD_0}$; $s = 1$; Eq. (1)) in every spring. The mean $\mathrm{GDD_0}$ for each of the 17 species over 11 years was used as the predictor of budburst.

The spring warming and pre-spring chilling model (Cannell and Smith, 1983) assumed the relationship between spring warming requirement and pre-spring chilling days following an exponential decay function (Eq. (2)); thus, the spring warming requirements for budburst can vary every year depending on the number of chilling days before spring. $\mathrm{GDD_{tg}}$ calculated by Eqs. (1) and (3) was used to fit the exponential decay function (Eq. (2)). The starting date of GDD accumulation ($s$) for both Eqs. (1) and (3) are 60 (1 March):

$$\mathrm{GDD_{tg}} = \sum_{\mathrm{doy}=s}^{\mathrm{bb}} (t_{\mathrm{doy}} - \mathrm{tg}), \quad (t_{\mathrm{doy}} - \mathrm{tg}) \geq 0 \tag{1}$$

$$\mathrm{GDD_{tg}} = a + b\,\mathrm{e}^{-cD_{\mathrm{tc}}} \tag{2}$$

$$\mathrm{GDD_{tg}} = \sum_{\mathrm{doy}=s}^{\mathrm{bb}} t_{\mathrm{doy}}, \quad (t_{\mathrm{doy}} - \mathrm{tg}) \geq 0 \tag{3}$$

where $\mathrm{GDD_{tg}}$ is the growing degree days with threshold temperature for heat sum (tg), doy the day of year, $s$ the starting day for the calculation of $\mathrm{GDD_{tg}}$, bb the day of year for leaf budburst, $t_{\mathrm{doy}}$ the daily mean temperature, and $D_{\mathrm{tc}}$ is the number of chilling days since 1 November the previous year. Threshold temperature for chilling days (tc) is used to differentiate chilling days from non-chilling days. $a$, $b$, and $c$ are the parameter estimates determined by non-linear fitting procedure.

We performed a non-linear fitting of Eq. (2) (PROC NLIN in SAS; Gauss-Newton method; SAS Institute, 2000) for each of the 17 species over 11 years with varying temperature thresholds for both GDD (tg) and chilling days (tc). Temperature thresholds varied between 0 and 12.5 °C with intervals of 2.5 °C. A combination of tg and tc that rendered the highest

**Table 1 – Parameter inputs and model outputs of PnET-Day simulations at REMA site in southern Ohio in 2004**

| Variables | *Acer rubrum* | *Liriodendron tulipifera* | *Quercus alba* | Forest stand |
|---|---|---|---|---|
| Model inputs | | | | |
| Latitude | 39.28 | 39.28 | 39.28 | – |
| FolNCon[a] (% mass) | 1.64 | 2.32 | 1.67 | – |
| SLWMax[b] ($g\,m^{-2}$) | 60.33 | 64.25 | 108.16 | – |
| GDDFolStart[c] (degree days) | 484 | 450 | 590 | – |
| Maximum foliar mass ($g\,C\,m^{-2}\,y^{-1}$) | 270 | 270 | 270 | – |
| Model outputs | | | | |
| Gross primary productivity ($g\,C\,m^{-2}\,y^{-1}$) | | | | |
| Default budburst | 453.07 (+9.51%) | 805.22 (+8.42%) | 741.18 (+10.42%) | 716.64 (+10.21%) |
| Observed budburst | 413.73 | 742.67 | 671.25 | 650.26 |
| Net primary productivity ($g\,C\,m^{-2}\,y^{-1}$) | | | | |
| Default budburst | 165.05 (+16.41%) | 322.58 (+13.32%) | 441.96 (+12.52%) | 406.31 (+12.71%) |
| Observed budburst | 141.78 | 284.67 | 392.80 | 360.49 |
| Auto trophic respiration ($g\,C\,m^{-2}\,y^{-1}$) | | | | |
| Default budburst | 288.02 (+5.91%) | 482.64 (+5.38%) | 299.22 (+7.46%) | 310.33 (+7.09%) |
| Observed budburst | 271.95 | 458.00 | 278.45 | 289.77 |

PnET-Day simulations were made using default leaf budburst (GDD required for budburst = 100) and GDD corresponding to the observed dates of budburst. Model outputs of the forest stand were calculated by the weighted mean of the three modeled species (weight = relative basal area; 9%, 6%, and 75% for *A. rubrum*, *L. tulipifera*, and *Q. alba*, respectively). Values in parentheses are percent differences of model outputs between two phenological settings.

[a] Foliar nitrogen concentration; mass basis.

[b] Maximum specific leaf weight.

[c] Growing degree days (GDD) required for leaf budburst.

$R^2$ of each non-linear fit was selected for Eq. (2) (Raulier and Bernier, 2000), which was then used to predict the $GDD_{tg}$ requirement for budburst on the subset of trees used for model evaluation. We evaluated the performance of phenology models based on the phenology record of one tree for each of the 17 species, which was randomly selected in advance for the purpose of model validation, and therefore not included in the modelling fitting procedure. The validation is performed

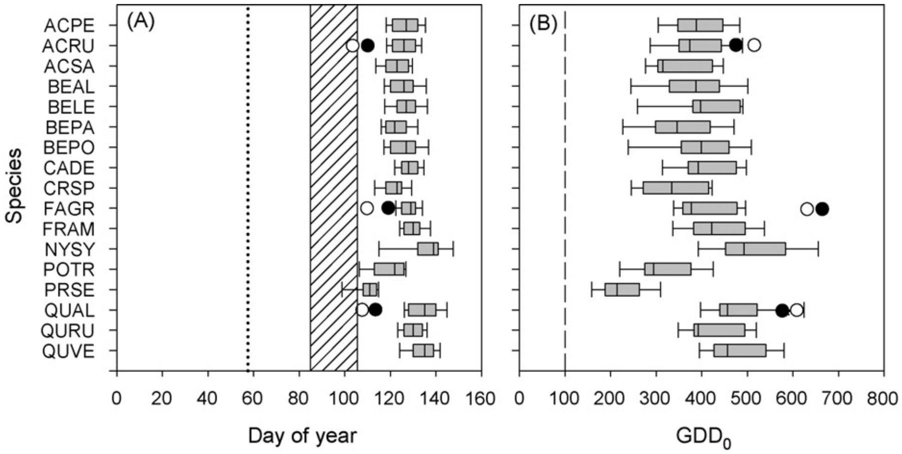

**Fig. 1 – Budburst phenology of major hardwood species in the Harvard Forest, MA, from 1990 to 2000. Growing degree days are calculated from the first day of each year with the threshold temperature of 0 °C ($GDD_0$). A line within each box marks the median day of year or growing degree day of budburst for each species. The boundaries of each box represent the 25th and 75th percentile. Whiskers (error bars) to the left and right of each box represent the 10th and 90th percentile. The hatched area represents the day of year, from 1991 to 1994, where $GDD_0 = 100$ (Aber et al., 1996). The dotted line represents the prediction of leaf budburst by PnET-Day in Ohio site with GDDFolStart equaling 100. The dash line represents the default GDD required for leaf budburst of deciduous forest (GDDFolStart = 100) in PnET models. Closed and open circles represent mean budburst day of year and $GDD_0$ observed in 2004 and 2005, respectively, for three species from the Raccoon ecological management area (REMA) in southern Ohio for 2004. *Note:* ACPE, *Acer pensylvanicum*; ACRU, *Acer rubrum*; ACSA, *Acer saccharum*; BEAL, *Betula alleghaniensis*; BELE, *Betula lenta*; BEPA, *Betula papyrifera*; BEPO, *Betula popilofolia*; CADE, *Castanea dentata*; CRSP, *Cretageus* sp.; FAGR, *Fagus grandifolia*; FRAM, *Fraxinus Americana*; NYSY, *Nyssa sylvatica*; POTR, *Populus tremuloides*; PRSE, *Prunus serotina*; QUAL, *Quercus alba*; QURU, *Quercus rubra*; QUVE, *Quercus velutina*.**

by relating the predicted date to the observed date of budburst (PROC REG in SAS).

## 3. Results

### 3.1. Budburst phenology of major deciduous tree species

Based on the long-term (1990–2000) phenology record in the Harvard Forest, MA, the date of budburst ranged from late April to early May (Fig. 1A). Species did not exhibit substantial differences in the date of budburst, except for *Populus tremuloides* and *Prunus serotina*, which had earlier budburst than other species. *Nyssa sylvatica* had the largest year to year variation in the date of budburst.

The corresponding growing degree days with a threshold temperature of 0 °C ($GDD_0$; accumulate from 1 January each year) for the budburst of each year exhibited wide variation with the median $GDD_0$ between 214 (*Prunus serotina*) and 493 (*Nyssa sylvatica*; Fig. 1B). The onset of leaf emergence predicted by PnET-Day between 1991 and 1994 ranged from late March (day of year (DOY) = 86) to mid-April (DOY = 106) as marked by hatched area in Fig. 1A (Aber et al., 1996). The date of leaf emergence predicted by PnET-Day was 15–36 days earlier than the actual date of budburst observed in the Harvard Forest.

The coefficient of variation for each species ranged from 14% to 22% for $GDD_0$ and 3–7% for DOY. Despite the lack of year to year consistency in $GDD_0$ requirement for budburst, $GDD_0$ is employed by PnET models for the prediction of budburst (GDDFolStart = 100; Aber et al., 1996). The default requirement of $GDD_0$ for leaf budburst as marked with a vertical dash line (Fig. 1B) is outside the range of 11 years phenological data for all species.

Three of the 17 species (*Acer rubrum*, *Fagus grandifolia*, and *Quercus alba*) shown in Fig. 1 were the subjects of our phenological survey in REMA. Compared to the data from the Harvard Forest, all three species exhibited earlier dates of budburst, however, with larger requirements for $GDD_0$ (Fig. 1). The date of budburst predicted by PnET-Day (GDDFolStart = 100; marked as dotted line in Fig. 1A) were 40–60 days earlier than the observed dates.

The dates of budburst for those three species observed in REMA were 3–10 days earlier in 2005 than in 2004 (Fig. 1A); however, the corresponding $GDD_0$ required for budburst was slightly higher for *Acer rubrum* and *Quercus alba* (but not for *Fagus grandifolia*). The earlier leaf emergence of 2005 in REMA cannot be explained by changes in $GDD_0$.

### 3.2. Sensitivity analysis of budburst phenology on carbon exchange simulation

The default budburst predictor (GDDFolStart = 100) had brought forward the accumulation of leaf mass and net photosynthesis in 2004 to 27 February, which is 49, 46, and 55 days earlier than the observed budburst date of *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus alba* stands, respectively (Figs. 1A and 2). Due to the late summer drought, both *A. rubrum* and *L. tulipifera* exhibited negative net photosynthesis while *Q. alba* maintained positive net photosynthesis during the same period. The combined stand exhibited similar pattern of changes in net photosynthesis and foliar mass to that of *Q. alba* because REMA was dominated by *Quercus* species (Fig. 2). With the advance of the budburst date, the use of the default budburst predictor (GDDFolStart = 100) resulted in up to 8–10%, 12–16%, and 5–7% increase in annual GPP, NPP, and $R_a$, respectively (Table 1).

### 3.3. Incorporation of chilling factor for the prediction of leaf budburst

With the substantial influence of leaf phenology on carbon exchange and the inconsistency of $GDD_0$ requirements for budburst, we sought to improve the prediction of budburst by adopting a leaf phenology model that incorporated both spring warming and pre-spring chilling factor (Cannell and Smith, 1983). Although the $GDD_{tg}$ was usually calculated as the accumulation of difference between daily mean temperature and threshold temperature (Eq. (1); Cannell and Smith, 1983; Raulier and Bernier, 2000), we found that cumulating daily mean temperature (Eq. (3)) resulted in better model performance (see Appendix A). Here we only present the parameter inputs for a slightly modified Cannell and Smith (1983) model where $GDD_{tg}$ is calculated using Eq. (3).

A combination of temperature thresholds for both chilling and GDD that resulted in the highest coefficient of determination ($R^2$) for the non-linear curve fitting of Eq. (2) was selected for each of the 17 deciduous tree species (Table 2). For example, both the chilling and GDD temperature thresholds of 5 °C resulted in the optimum non-linear fitting for *Acer saccharum* (Fig. 3). Interestingly, there were multiple peaks of $R^2$ for *Quercus rubra* (Fig. 3). The temperature thresholds of 2.5 °C for both chilling and GDD resulted in the optimum fit for *Q. rubra* (Fig. 3). All species met the criteria for the convergence in a non-linear fitting procedure (PROC NLIN; SAS Institute, 2000) and 12 of the 17 species had significant model fit (Table 2; $P < 0.05$). Among the significant model fits, 28–71% of variations in $GDD_{tg}$ were accounted for by the non-linear functions (Table 2).

Prediction of leaf budburst using $GDD_0$ alone resulted in poor performance with only *Acer pensylvanicum* showing significant and *P. tremuloides* showing marginally significant linear relationships between predicted and observed date of budburst (Fig. 4; see Appendix A for test results). With the addition of a chilling factor, the prediction of the date of budburst was largely improved (Fig. 4). The modified Cannell and Smith model which employed Eq. (3) for the calculation of $GDD_{tg}$ had 16 of the 17 species showing significant ($P < 0.05$), and *Betula papyrifera* showing marginally significant ($P < 0.10$), relationships between predicted and observed date of budburst (Appendix A). Compared to the original Cannell and Smith model, the modified Cannell and Smith model generally had better performance (higher $R^2$) and only four species, including *Cretageus* sp., *P. tremuloides*, *Prunus serotina*, and *Quercus alba* (six species for the original Cannell and Smith model) deviated from the 1:1 line (Appendix A).

### 3.4. Application of the modified Cannell and Smith model in southern Ohio

We used the modified Cannell and Smith model (see Table 2 for parameter inputs) to predict the $GDD_{7.5}$ and $GDD_{5.0}$ required

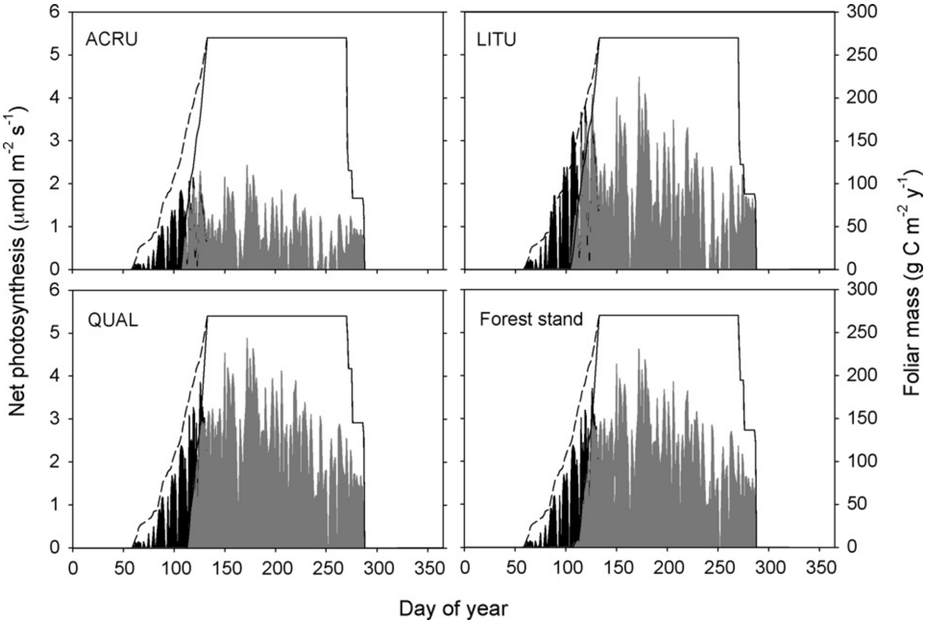

**Fig. 2 – PnET-Day simulations of net photosynthesis in three hypothetical stands: Acer *rubrum* (ACRU), *Liriodendron tulipifera* (LITU), and *Quercus alba* (QUAL). Simulations were based on the parameter inputs of REMA site in southern Ohio (see Table 1). Model outputs of the forest stand were calculated by the weighted mean of the three modeled species (weight = relative basal area; 9%, 6%, and 75% for ACRU, LITU, and QUAL, respectively). The black areas represent the excessive net photosynthesis due to the use of PnET default GDD requirement for budburst (GDDFolStart = 100). The gray areas represent the net photosynthesis corresponding to the observed leaf budburst dates. Dash and solid lines represent the dynamics of foliar mass for PnET default (GDDFolStart = 100) and observed budburst phenology, respectively.**

for the budburst for *Acer rubrum* (Fig. 5A) and *Fagus grandifolia* (Fig. 5B). The number of chilling days for both species (daily mean temperature <2.5 °C; Table 2) on REMA site was outside the range of data used to derive this non-linear function, resulting in extremely high GDD requirements for both species (Fig. 5A and B; as shown in open triangles). Based on the modified Cannell and Smith model, *A. rubrum* and *F. grandifolia* would require 775 of $GDD_{7.5}$ and 1552 of $GDD_{5.0}$, respectively,

**Table 2 – Non-linear fitting between the growing degree days ($GDD_{tg}$) required for budburst and the number of chilling days ($D_{tc}$) for 17 deciduous tree species in the Harvard Forest, MA**

| Species | tg | tc | SSE | d.f. | SST | d.f. | *P* | $R^2$ | *a* | *b* | *c* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ACPE | 7.5 | 2.5 | 44,192 | 24 | 64,816 | 26 | 0.0101 | 0.32 | 162.90 | 417,160 | 0.0783 |
| ACRU | 7.5 | 2.5 | 63,164 | 33 | 98,650 | 35 | 0.0006 | 0.36 | 118.20 | 12,097 | 0.0416 |
| ACSA | 5.0 | 5.0 | 5,366 | 15 | 18,449 | 17 | <0.0001 | 0.71 | 151.60 | 67,070 | 0.0491 |
| BEAL | 7.5 | 0.0 | 29,931 | 15 | 39,805 | 17 | 0.1179 | 0.25 | 11.09 | 574 | 0.0128 |
| BELE | 7.5 | 2.5 | 26,422 | 15 | 52,631 | 17 | 0.0057 | 0.50 | 170.00 | 292,047 | 0.0717 |
| BEPA | 10.0 | 10.0 | 17,602 | 23 | 56,658 | 35 | <0.0001 | 0.69 | 21.05 | 1,114,689 | 0.0548 |
| BEPO | 7.5 | 0.0 | 43,300 | 24 | 60,083 | 26 | 0.0196 | 0.28 | 189.10 | 323,469 | 0.1099 |
| CADE | 2.5 | 2.5 | 18,163 | 15 | 40,734 | 17 | 0.0023 | 0.55 | 295.80 | 185,741 | 0.0680 |
| CRSP | 7.5 | 0.0 | 19,484 | 14 | 35,918 | 16 | 0.138 | 0.46 | 127.00 | 404,619 | 0.1103 |
| FAGR | 5.0 | 2.5 | 35,873 | 24 | 68,947 | 26 | 0.0004 | 0.48 | 243.40 | 102,580 | 0.0623 |
| FRAM | 7.5 | 0.0 | 61,797 | 28 | 102,720 | 30 | 0.0008 | 0.40 | 216.90 | $8.40 \times 10^8$ | 0.2111 |
| NYSY | 7.5 | 7.5 | 33,218 | 15 | 46,271 | 17 | 0.0833 | 0.28 | 187.90 | 9805 | 0.0273 |
| POTR | 10.0 | 2.5 | 11,387 | 7 | 19,888 | 9 | 0.142 | 0.43 | −89.24 | 1166 | 0.0156 |
| PRSE | 7.5 | 2.5 | 20,325 | 15 | 23,642 | 17 | 0.3218 | 0.14 | −223.00 | 461 | 0.0032 |
| QUAL | 10.0 | 0.0 | 59,454 | 15 | 69,148 | 17 | 0.3221 | 0.14 | 172.40 | 259,000,000 | 0.2043 |
| QURU | 2.5 | 2.5 | 29,753 | 24 | 60,856 | 26 | 0.0002 | 0.51 | 315.40 | 1,116,775 | 0.0859 |
| QUVE | 5.0 | 0.0 | 63,685 | 24 | 107,810 | 26 | 0.0018 | 0.41 | 338.10 | $1.75 \times 10^{10}$ | 0.2494 |

Threshold temperatures of GDD (tg) and chilling days (tc) that resulted in highest $R^2$ were selected. Parameter *a*, *b*, and *c* were derived from the non-linear fitting procedures (see Eq. (2) in text). The phenology model was modified based on Cannell and Smith (1983). See Fig. 1 for species acronyms.

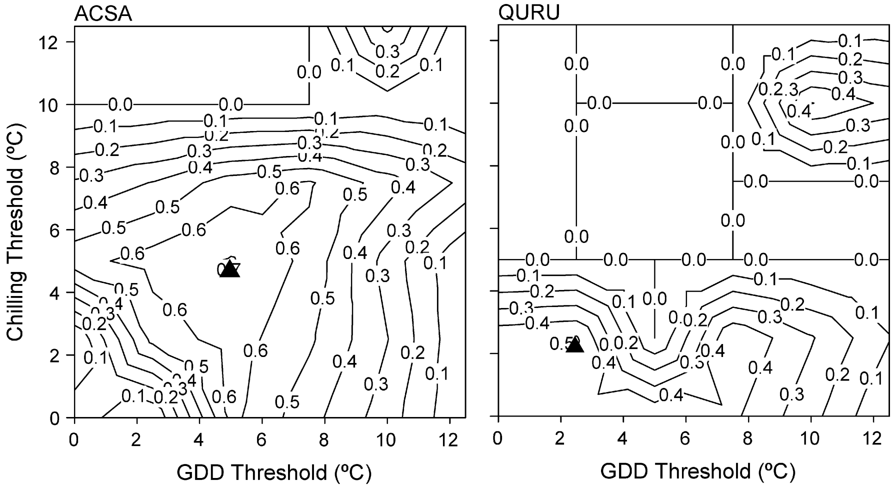

**Fig. 3 – Response surfaces of the coefficient of determination ($R^2$) in the non-linear fitting of the Cannell and Smith (1983) phenological model (see Eq. (2)) for *Acer saccharum* (ACSA) and *Quercus rubra* (QURA). $R^2$ varies with changing chilling and GDD temperature thresholds. The solid triangle represents the chilling and GDD threshold temperatures that provide the optimum fit.**

before the onset of budburst in REMA, which would correspond to 18 May and 19 June 2004 (Fig. 5C and D; as shown in open triangles). Compared to the observed date of budburst in 2004, the model predicted a 31 and 51 days delay of budburst (Fig. 5C and D). For *Quercus alba*, of which the budburst phenology was also monitored in REMA site, the predicted $GDD_{10}$ requirement for budburst ($GDD_{10} = 21{,}645$, given 46 days of chilling) was never met in 2004.

## 4. Discussion

Leaf phenology not only determines the duration of carbon assimilation of a forest but also reflects the dynamics of carbon allocation in a forested ecosystem. Leaf budburst during spring time particularly has large impacts on carbon balance of a deciduous forest (Goulden et al., 1996). With large year to year variation in leaf budburst, ecosystem carbon balance models should utilize a more reliable phenology model to track the onset of budburst.

### 4.1. *Utility of GDD in predicting leaf phenology*

Based on the 11 years of phenological observation at the Harvard Forest, we found that $GDD_0$ alone, which is employed by PnET models, is a poor predictor for the leaf budburst of each individual species. A fixed $GDD_0$ of most species cannot account for the yearly variations in budburst phenology. This is also manifested by large yearly variations in $GDD_0$ corresponding to the date of budburst. Moreover, the use of $GDD_0$ equaling 100 (GDDFolStart = 100) consistently predicted the date of budburst 15–34 days earlier than the mean budburst date of the 17 hardwood species between 1990 and 1996 (Aber et al., 1996). PnET-Day attempted to account for the earliest photosynthetic activity (Aber et al., 1996) and showed a close match on the timing of positive gross carbon exchange (gross primary production) in early spring between the modeled and eddy flux data (Aber et al., 1996). The early occurrence of carbon assimilation in the system (late March to mid-April) was probably due to the photosynthetic activity of evergreen species because no deciduous species (including understory shrubs) appear to break buds during that period of time (O'Keefe, 2004). Thus, although the default setting of leaf phenology predictor (GDDFolStart = 100) reflected the timing of photosynthetic activity (Aber et al., 1996), it did not reflect the phenology of budburst in the Harvard Forest.

The application of this default budburst predictor in the Ohio forest resulted in a predicted 40–60 days earlier budburst than the observed budburst dates in spring 2004. Thus, The default phenology setting (GDDFolStart = 100) would produce wildly inaccurate results if applied in Ohio. Further, the use of a single, locally derived, GDDFolStart value for the prediction of budburst may be questionable. Despite the lack of reliability, GDDFolStart has been commonly used for the prediction of leaf budburst (e.g., ASPECTS, Rasse et al., 2001; LANDIS, Scheller and Mladenoff, 2004; CASTANEA, Davi et al., 2005; sim-CYCLE, Ito, 2005; IBIS, Kucharik et al., 2000). Our observations of leaf budburst for 2004 and 2005 also showed that the pattern between GDD and DOY was not consistent among species. As compared to 2004, the earlier budburst of most species in 2005 was not accompanied by less $GDD_0$ corresponding to the budburst date (e.g., *Acer rubrum* and *Quercus alba* in Fig. 1).

### 4.2. *Sensitivity of leaf phenology on model outputs*

The impacts of leaf phenology on NPP largely depend on the environmental conditions of that growing season. Under favorable growth conditions (e.g., without drought), early budburst can result in a substantial gain of net carbon assimilation within a forested ecosystem (Goulden et al., 1996). Another eddy covariance study also indicated the importance of leaf phenology on the carbon balance of a forested ecosystem (Chen et al., 1999). However, given the strong influence of

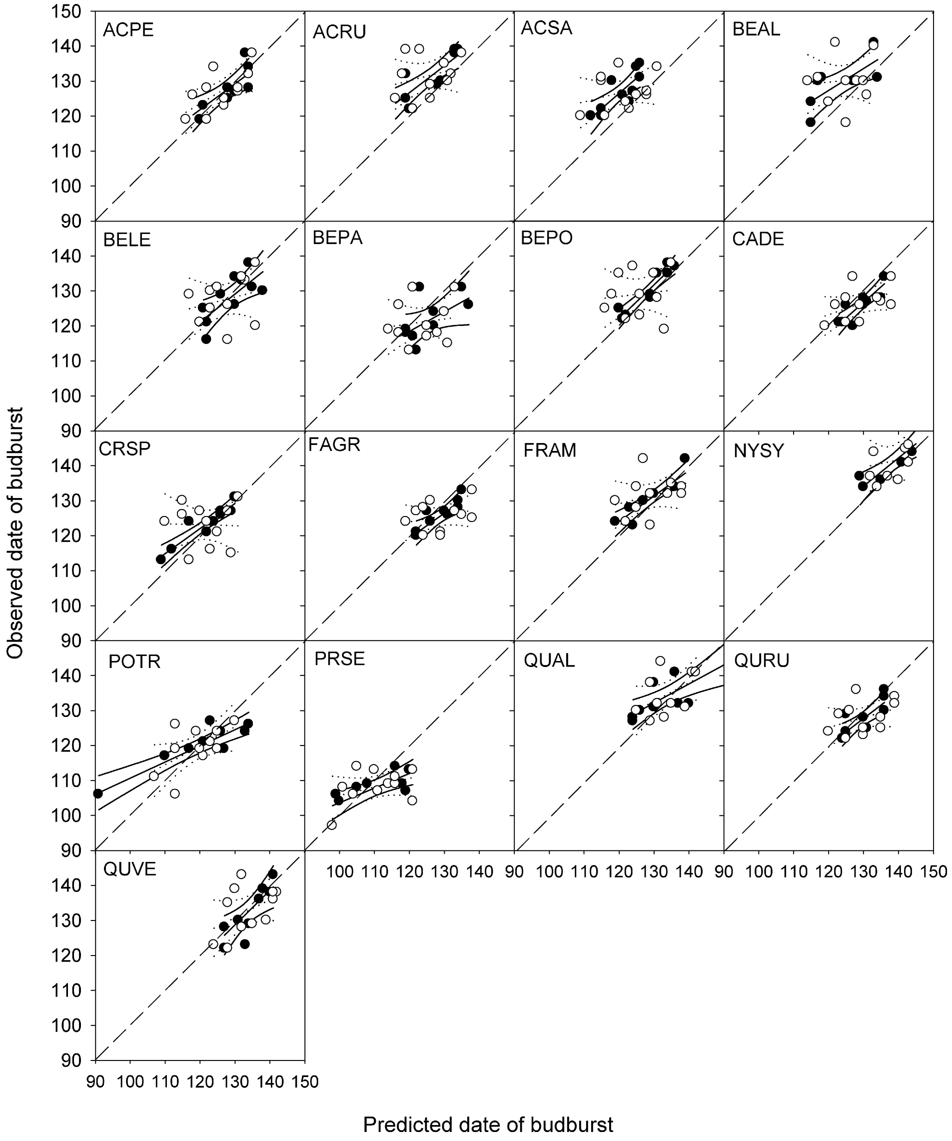

**Fig. 4 – Observed and predicted date of budburst in the Harvard Forest, MA from 1990 to 2000. Open circles and dotted lines represent the GDD model employed by PnET models. Solid circles and lines represent the phenological model modified from Cannell and Smith (1983). Dash lines represent the 1:1 lines which indicate the perfect predictions. A regression line and 95% confidence intervals for each model are shown for each species. See Fig. 1 for species acronyms.**

budburst phenology on ecosystem carbon exchange, the leaf phenology predictor (GDDFolStart) employed by PnET-Day (as well as other PnET models) was not considered as a sensitive variable (<1% change in NPP with 10% change in GDDFolStart; Aber et al., 1996) and therefore could have been overlooked in future applications of PnET. The sensitivity analysis performed in Aber et al. (1996) adjusted the parameter input by ±10% of the default value (i.e., GDDFolStart = 90 and 110; Aber et al., 1996), corresponding to only 2–5 days differences based on the mean temperature of the early spring. The natural variation of budburst dates in 11 years can be up to 3 weeks for many tree species and therefore should have substantial impacts in the PnET model outputs. Hence, sensitivity analysis should take into consideration the range of variance in the biological data rather than an arbitrary value (e.g., ±10%).

### 4.3. *Chilling factor greatly improved the prediction of budburst*

Our evaluation of a phenology predictor ($GDD_0$) employed by PnET models showed a poor predictive capability; however, with an addition of a chilling factor, the prediction on the date of budburst was greatly improved. Chilling is an important factor to break dormancy. More chilling days in winter reduces the requirement of temperature sum ($GDD_{tg}$) for budburst. This is a manifestation of the parallel model (Hänninen, 1987) and considered as a mechanism to reduce the risk of premature budburst in mid-winter (Jackson et al., 2001).

A modified Cannell and Smith model where threshold temperature was used only to exclude low temperatures (less than threshold temperature) for the summation of $GDD_{tg}$ (Eq. (3))

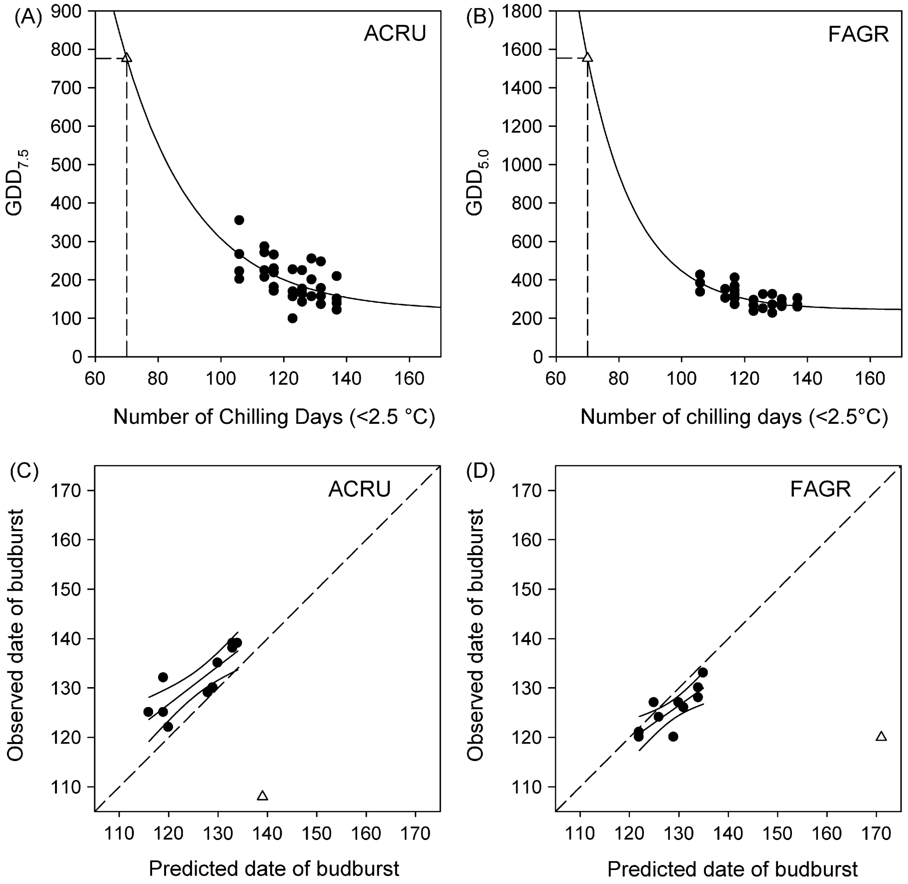

**Fig. 5 – Application of modified Cannell and Smith phenology model in southern Ohio. Panel A and B exhibit the non-linear curve fittings of Eq. (2) for *Acer rubrum* (ACRU) and *Fagus grandifolia* (FAGR) based on the phenology data from the Harvard Forest. Panel C and D exhibit the validation results of the modified Cannell and Smith model of both species (solid lines represent the regression lines and their 95% confidence intervals; dash lines represent the 1:1 line). Within each panel, solid circles represent the data from the Harvard Forest and an open triangle represents the data corresponding to REMA site in southern Ohio in the spring 2004. The number of chilling days in Ohio (70 days for both species) was outside the range of data in the Harvard Forest (A and B), resulting in a highly deviated prediction of budburst dates (C and D).**

provided more reliable prediction of the date of budburst than the original Cannell and Smith model, where $GDD_{tg}$ is calculated by the summation of temperature difference between daily mean temperature and threshold temperature (Eq. (1)). The calculation of temperature sum by accumulating actual temperatures instead of temperature differences may provide a better index or “time scale” for the phenological developments.

The incorporation of the modified Cannell and Smith phenology model in the PnET family of models can better track the yearly variation of budburst and therefore provide more realistic simulations the “green-up” period for the deciduous stands in the northeastern United States. The modified Cannell and Smith model is robust and useful for incorporation into other forest carbon balance models in the northeastern United States.

Although the modified Cannell and Smith model exhibited reliable prediction on the date of budburst in the Harvard Forest, it is not suitable for the prediction in Ohio site. Before the development of a process based phenological model, ecosystem carbon balance models should employ phenological models that are locally developed. For a larger scale modelling of forest carbon balance that encompasses different geographic regions, it is necessary to develop a more comprehensive and mechanistic model that is better coupled to the environmental cues. This would require a long-term phenology observation network across study sites. With a rapid pace of climate change, this model would enable us to produce more realistic carbon balance models that track the phenological activities under climate change.

### 4.4. *The relevance of phenological predictors in forest production modelling*

Ecosystem ecologists are increasingly attentive to patterns of leaf phenology due to its relevance to global climatic change. Leaf phenology is a biological response that both influences stand carbon balance and yet is influenced by changing climate. For example, relying solely on empirical inputs of leaf phenological cycles will yield no predictive inference and therefore, in such models, leaf phenology becomes decoupled from climatic changes. Forest carbon modelling efforts

**Table A.1 – Validation results from the phenological models**

| Species | GDD model | | | | | Connell and Smith model | | | | | Modified Connell and Smith model | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Estimate | L95 | U95 | $R^2$ | $P$ | Estimate | L95 | U95 | $R^2$ | $P$ | Estimate | L95 | U95 | $R^2$ | $P$ |
| ACPE | | | | | | | | | | | | | | | |
| *a* | 51.00 | −16.70 | 118.69 | 0.42 | 0.0313 | 98.57 | 49.80 | −147.33 | 0.18 | 0.2185 | 33.16 | −27.73 | 94.05 | 0.61 | 0.0076 |
| *b* | 0.60 | 0.07 | 1.14 | | | 0.22 | −0.16 | 0.60 | | | 0.74 | 0.26 | 1.22 | | |
| ACRU | | | | | | | | | | | | | | | |
| *a* | 99.63 | 14.19 | 185.07 | 0.07 | 0.4208 | 96.62 | 73.70 | 119.53 | 0.61 | 0.0077 | 34.47 | −15.31 | 84.25 | 0.72 | 0.0020 |
| *b* | 0.25 | −0.43 | 0.94 | | | 0.28 | 0.10 | 0.46 | | | 0.77 | 0.37 | 1.16 | | |
| ACSA | | | | | | | | | | | | | | | |
| *a* | 96.56 | 30.18 | 162.93 | 0.11 | 0.3286 | 28.41 | −29.08 | 85.91 | 0.66 | 0.0042 | 22.06 | −38.46 | 82.59 | 0.67 | 0.0040 |
| *b* | 0.25 | −0.30 | 0.80 | | | 0.82 | 0.34 | 1.29 | | | 0.87 | 0.37 | 1.37 | | |
| BEAL | | | | | | | | | | | | | | | |
| *a* | 118.32 | 23.27 | 213.37 | 0.01 | 0.7855 | 96.55 | 68.11 | 124.99 | 0.49 | 0.0241 | 52.38 | −5.79 | 110.54 | 0.55 | 0.0146 |
| *b* | 0.10 | −0.67 | 0.86 | | | 0.27 | 0.05 | 0.050 | | | 0.63 | 0.16 | 1.09 | | |
| BELE | | | | | | | | | | | | | | | |
| *a* | 95.49 | −1.63 | 192.61 | 0.06 | 0.4739 | 24.54 | −50.88 | 99.96 | 0.56 | 0.0131 | 25.18 | −51.76 | 102.12 | 0.54 | 0.0148 |
| *b* | 0.25 | −0.51 | 1.01 | | | 0.81 | 0.22 | 1.39 | | | 0.80 | 0.20 | 1.40 | | |
| BEPA | | | | | | | | | | | | | | | |
| *a* | 103.65 | 15.12 | 192.17 | 0.02 | 0.6659 | 17.96 | −49.40 | 85.32 | 0.61 | 0.0075 | 51.16 | −29.66 | 131.97 | 0.34 | 0.0787 |
| *b* | 0.14 | −0.57 | 0.86 | | | 0.82 | 0.29 | 1.36 | | | 0.56 | −0.08 | 1.20 | | |
| BEPO | | | | | | | | | | | | | | | |
| *a* | 114.09 | 16.36 | 211.82 | 0.01 | 0.7361 | 29.06 | −18.43 | 76.55 | 0.75 | 0.0012 | 6.63 | −31.93 | 45.19 | 0.89 | 0.0001 |
| *b* | 0.12 | −0.66 | 0.90 | | | 0.79 | 0.42 | 1.17 | | | 0.96 | 0.66 | 1.26 | | |
| CADE | | | | | | | | | | | | | | | |
| *a* | 81.11 | 18.04 | 144.18 | 0.23 | 0.1379 | 42.85 | −26.51 | 112.20 | 0.49 | 0.0238 | 11.56 | −39.74 | 62.87 | 0.77 | 0.0009 |
| *b* | 0.35 | −0.14 | 0.84 | | | 0.65 | 0.11 | 1.19 | | | 0.89 | 0.49 | 1.28 | | |
| CRSP | | | | | | | | | | | | | | | |
| *a* | 126.48 | 42.40 | 210.56 | 0.00 | 0.9292 | 57.80 | 7.52 | 108.07 | 0.54 | 0.0161 | 35.78 | 6.82 | 64.74 | 0.88 | 0.0002 |
| *b* | −0.03 | −0.72 | 0.66 | | | 0.55 | 0.13 | 0.96 | | | 0.72 | 0.48 | 0.96 | | |
| FAGR | | | | | | | | | | | | | | | |
| *a* | 101.69 | 42.48 | 160.89 | 0.08 | 0.3852 | 63.03 | 6.96 | 119.10 | 0.45 | 0.0328 | 34.43 | −22.81 | 91.66 | 0.63 | 0.0063 |
| *b* | 0.19 | −0.27 | 0.64 | | | 0.48 | 0.05 | 0.92 | | | 0.71 | 0.26 | 1.15 | | |
| FRAM | | | | | | | | | | | | | | | |
| *a* | 99.42 | 22.49 | 176.34 | 0.09 | 0.3702 | 25.27 | −13.60 | 64.14 | 0.83 | 0.0002 | 36.21 | −1.09 | 73.51 | 0.81 | 0.0004 |
| *b* | 0.25 | −0.35 | 0.84 | | | 0.82 | 0.52 | 1.12 | | | 0.73 | 0.45 | 1.02 | | |
| NYSY | | | | | | | | | | | | | | | |
| *a* | 113.33 | −44.17 | 270.83 | 0.03 | 0.6780 | 235.46 | −109.05 | 579.97 | 0.07 | 0.5058 | 28.91 | −34.46 | 92.27 | 0.76 | 0.0050 |
| *b* | 0.20 | −0.94 | 1.35 | | | −0.74 | −3.22 | 1.75 | | | 0.81 | 0.35 | 1.27 | | |
| POTR | | | | | | | | | | | | | | | |
| *a* | 54.50 | −13.15 | 122.15 | 0.34 | 0.0579 | 91.91 | 52.58 | 131.24 | 0.25 | 0.1433 | 64.43 | 44.20 | 84.66 | 0.83 | 0.0002 |
| *b* | 0.55 | −0.02 | 1.11 | | | 0.22 | −0.09 | 0.54 | | | 0.46 | 0.29 | 0.63 | | |
| PRSE | | | | | | | | | | | | | | | |
| *a* | 81.16 | 33.22 | 129.11 | 0.15 | 0.2319 | 33.02 | 0.96 | 65.07 | 0.78 | 0.0006 | 61.86 | 31.26 | 92.47 | 0.60 | 0.0082 |
| *b* | 0.25 | −0.19 | 0.68 | | | 0.68 | 0.39 | 0.96 | | | 0.42 | 0.14 | 0.69 | | |
| QUAL | | | | | | | | | | | | | | | |
| *a* | 64.05 | −26.02 | 154.11 | 0.26 | 0.1081 | 102.71 | 54.84 | 150.57 | 0.023 | 0.1639 | 80.90 | 29.40 | 132.39 | 0.42 | 0.0431 |
| *b* | 0.53 | −0.14 | 1.20 | | | 0.24 | −0.12 | 0.60 | | | 0.40 | 0.02 | 0.78 | | |
| QURU | | | | | | | | | | | | | | | |
| *a* | 91.50 | 25.44 | 157.56 | 0.15 | 0.2424 | 92.08 | 43.31 | 140.85 | 0.26 | 0.1309 | 28.18 | −31.42 | 87.78 | 0.65 | 0.0049 |
| *b* | 0.28 | −0.23 | 0.79 | | | 0.27 | −0.10 | 0.63 | | | 0.77 | 0.31 | 1.22 | | |
| QUVE | | | | | | | | | | | | | | | |
| *a* | 64.23 | −34.81 | 163.27 | 0.21 | 0.1513 | −33.73 | −163.44 | 95.97 | 0.52 | 0.0183 | 0.39 | −95.18 | 95.97 | 0.56 | 0.0129 |
| *b* | 0.51 | −0.23 | 1.25 | | | 1.24 | 0.27 | 2.20 | | | 0.99 | 0.27 | 1.70 | | |

Simple linear regression models (observed date of budburst = $a + b \times$ predicted date of budburst) were created to evaluate the model performance of each species. Lower and Upper 95% confidence limits (L95 and U95, respectively) were used to examine whether the regression lines deviated from 1:1 line. Connell and Smith model used Eq. (1) (see text), while modified Connell and Smith model used Eq. (3) (see text), for the calculation of growing degree days. See Fig. 1 for species acronyms.

should therefore pay particular attention to how phenology is addressed. However to date this has not been the case.

Since 2000, in fact, at least 45 papers have been published with regard to forest growth/carbon balance simulations just in the journal *Ecological Modelling*. Interestingly, of our sample of 45 papers, 31 contained no information on how leaf phenology was addressed in their modelling efforts. A possible explanation is that 16 of the 31 papers were modelling evergreen forests. For the papers containing information about phenology (14 of the 45 papers), most of them used either simplistic models (such as GDD with varied temperature threshold or starting date of accumulation) or empirical inputs with no predictive phenology subroutine (e.g., greenness determined by NDVI).

One of the important findings of our work was that GDD alone was found to be a poor predictor for leaf budburst in MA and OH. We demonstrated using PnET that not accounting for budburst correctly when modelling forest production resulted in up to 10% bias in the estimates of annual NPP. In light of the number of groups doing this kind of research, who have yet to explicitly address predictive phenology, we feel this result will be informative (two-thirds of the 45 papers included no descriptions of how they handled phenological forest dynamics).

It is worth mentioning a recent exception: Kucharik et al. (2006) examined the effect of a simplistic (GDD = 100) and more sophisticated phenology subroutine in their IBIS model. Their IBIS model simulation evaluated a large scale phenology model (White et al., 1997) which was developed by relating the environmental parameters (air temperature, soil temperature, precipitation, and daylength) with NDVI data and this substantially improved the prediction of leaf phenological cycles (Kucharik et al., 2006). The scale of the IBIS model is regional to continental, in contrast with the stand-level, species-specific results presented in our current study.

## 5. Conclusions

Because of the increasing interest in modelling forest carbon dynamics, leaf budburst phenology is becoming a major focus for ecosystem study. In this paper, we found that a simple algorithm like a fixed GDD for the prediction of leaf phenology yielded poor performance although it has been employed by PnET family of models, which have been widely used to simulate ecosystem carbon, water, and nitrogen balances. With the inclusion of a chilling factor (e.g., the number of chilling days) and the model optimization procedure (selecting the combination of chilling and heating threshold temperature), we largely improved the precision and accuracy for the prediction of the budburst days of major hardwood species in the Harvard Forest. This improved phenological subroutine can be readily used and incorporated in the PnET simulations at the Harvard Forest. However, by comparing the phenological observations at southern Ohio and the Harvard Forest, we found geographical specificity for this new phenological subroutine. Because leaf budburst phenology controls the period of potential forest carbon assimilation, locally derived phenological datasets are required before one can optimize budburst prediction models for using PnET in a new forest type.

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## Appendix A. Validation results of phenology models

See Table A.1.

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