

Comparing carbon flux and high-resolution spring phenological measurements in a northern mixed forest

Mark D. Schwartz^{a,*}, Jonathan M. Hanes^b, Liang Liang^c

^a Department of Geography, UW-Milwaukee, Milwaukee, WI 53201-0413, USA

^b Department of Earth, Environment, and Geographical Sciences, Northern Michigan University, Marquette, MI 49855, USA

^c Department of Geography, University of Kentucky, Lexington, KY 40506, USA

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ABSTRACT

Vegetative canopies play a crucial role in the energy balance and composition of the atmospheric boundary layer via biotic control over evapotranspiration and carbon sources/sinks. Accurately predicting the onset/increase of carbon uptake/transpiration during the spring leaf development period using coarse resolution tower-based and satellite-derived data alone is difficult. Thus, understanding stand-level spatial patterns of spring plant phenological development and the processes that drive them may be crucial for improving landscape level estimates of evapotranspiration and carbon accumulation.

In this study, high-resolution spatial and temporal tree phenology data were recorded in field campaigns over approximately 5 weeks during spring 2006 and 2007 (within a 625 m × 275 m area), and over similar periods during spring 2008, 2009, and 2010 (within two 625 m × 625 m areas) near the WLEF eddy covariance flux tower site near Park Falls in northern Wisconsin. Our findings demonstrate that phenological variations between individual trees in a specific microclimate can be adequately represented with a sample of 30 or more individuals. Further, visual phenological observations can be generally related to under-canopy light levels, and for spring phenology measurements in similar microclimates, a sampling interval of every 4 days minimizes data uncertainty and field work expenses. An analysis of the relationships among phenology, climate, and gross primary productivity (GPP) during the spring indicate that the phenology of the dominant tree species is responsible for an overall positive trend in carbon assimilation, but climate is the cause of day-to-day variation.

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1. Introduction

Greater understanding of atmosphere-biosphere interactions is needed to improve models of Earth's physical systems. Detection of continental-scale biotic responses to climate change is limited both temporally and spatially, and rarely co-located with the detailed measurements available for the climate itself (Root et al., 2003; NEON Science Workshop 2004; Hijmans et al., 2005). This difference is primarily due to the existence of a dense and effective meteorological data network (many locations include over a century of information), and lack of a comparable biospheric network (Schwartz, 1999; van Vliet et al., 2003; Betancourt et al., 2005; Friend et al., 2007; Keller et al., 2008). Until recently, biospheric data existed only as simple land cover/land use types or sporadic observations for most areas, with detailed information (such as phenology) available for just a few sites (Willis et al., 2008; Morissette et al., 2009). The advent of satellite measures created

the opportunity to use empirical data for improved understanding of bioclimatic processes (Goward, 1989; Zhang et al., 2007). Satellite measures of vegetation activity are one of the key components of both downscaling climatic information and upscaling ground-based plant function measures (Jarvis, 1995; Sellers et al., 1997; Turner et al., 2003). However, the overall utility of coarse-resolution satellite data (e.g., Advanced Very High Resolution, AVHRR or Moderate Resolution Imaging Spectroradiometer, MODIS) for repeated continental-scale monitoring can be considerably enhanced when combined with higher temporal and spatial resolution ground-based (e.g., leaf development and microclimate) data and high spatial resolution satellite data (e.g., Quickbird or IKONOS) to facilitate scaling (Liang and Schwartz, 2009; Liang et al., 2011). Similarly, tower-based measurements of ecosystem carbon flux may also benefit from a detailed comparison with high-resolution phenology in order to better reveal the underlying biophysical driver of the seasonality of ecosystem exchange.

Vegetative canopies play a crucial role in the energy balance and composition of the atmospheric boundary layer via biotic control over evapotranspiration and carbon sources/sinks. Through the leaf stomata, plants regulate the rate of exchange of these

* Corresponding author. Tel.: +1 414 229 3740; fax: +1 414 229 3981.
E-mail address: mds@uwm.edu (M.D. Schwartz).

gases between the land surface and the atmosphere. Consequently, canopy average stomatal conductance (G_s) is one of the most important variables needed to predict atmospheric, hydrologic, and biospheric dynamics in response to the integrated effects of multiple stressors (White et al., 2000; Ewers et al., 2001; Thornton et al., 2002; Bond-Lamberty et al., 2005) and has been used successfully to scale between stands and the landscape level during the height of the growing season (Mackay et al., 2002). However, being able to understand and model these interactions at the start of the growing season is of equal or even greater importance, given the large impact of spring onset variations on total seasonal evapotranspiration and carbon accumulation (Ricciuto et al., 2008). The leaf development phenomenon is of particular interest as a dynamic feature resulting from close atmosphere-biosphere interaction (Schwartz, 1998). In spring, increasing solar radiation allows vegetation to resume growth, but the appearance of foliage causes rapid increases in near-infrared reflectance and transpiration (Rosenberg, 1983; Kaufmann, 1984). These biospheric effects in turn feedback upon the lower atmosphere, through modification of the surface energy and moisture balances, resulting in detectable changes in surface daily maximum temperatures (Schwartz and Karl, 1990; Schwartz, 1992). Evidence suggests that due to these interactions, the onset of spring in the lower atmosphere is a modally abrupt, rather than gradual seasonal transition (Schwartz, 1996; Fitzjarrald et al., 2001).

Our ability to accurately predict the onset and increase of carbon uptake and transpiration during the spring leaf development period (the time from bud burst to maximum photosynthetic and transpiration rates) using satellite-derived data alone is limited (Turner et al., 2003; White et al., 2009). Accurate representation of these dynamics at regional to global scales requires an ability to obtain spatially extensive G_s and leaf level photosynthetic estimates over relatively short timescales (sub-daily to weekly). Measures of the timing of specific levels of plant leaf development (phenological events) have proven to be effective general proxies for transpiration and other plant growth-driven processes during spring (Fitzjarrald et al., 2001; Schwartz and Crawford, 2001). Annual variation in surface phenology models (Spring Indices, Schwartz and Reiter, 2000, determined from micrometeorological temperature data recorded near the Chequamegon Ecosystem-Atmosphere Study [ChEAS] tall tower site near Park Falls, WI from 1998 to 2005) show a 19–21 days range in the onset of spring, implying 34–52 days variability on the century time scale (when compared to nearby long-term temperature stations). Such quantification of temporal variability still leaves a knowledge gap in the simultaneous spatial variability which precludes rigorous upscaling in this heterogeneous landscape. Thus, understanding stand-level spatial patterns of spring plant phenological development and the processes that drive them may be the key knowledge needed to improve landscape level estimates of evapotranspiration and carbon accumulation derived from flux towers and coarse resolution remote sensing data.

In this study, high-resolution spatial and temporal tree phenology data were recorded in field campaigns over approximately 5 weeks during spring 2006 and 2007 (within an initial 625 m × 275 m area), and over similar periods during spring 2008, 2009, and 2010 (within two expanded 625 m × 625 m areas) near the Chequamegon Ecosystem-Atmosphere Study (ChEAS) WLEF tall tower site in northern Wisconsin (an EOS Land Validation Core Site). We assess/model the characteristics of these data, link them to environmental measurements and flux tower estimates of gross primary production (GPP) during the spring, and lay the foundations for explicit connections of all these measures to leaf function and G_s during the crucial spring leaf development period. The results of these analyses demonstrate whether micrometeorological measurements and visual phenology observations with high spatial and temporal resolutions can be scaled up to

accurately model GPP during the spring. Further, we test the effects of decreases in the temporal sampling frequency and number of sampled individuals on overall measurement error. Thus, this work is intended to provide valuable methodological and logistical guidance for future studies in similar environments.

2. Materials and methods

2.1. Overall development of study areas

Spatial phenological variability was quantified in two sampling blocks representing two different types of vegetation boundary conditions in the mixed forest of northern Wisconsin, within the Chequamegon-Nicolet National Forest, a composite of northern temperate, sub-boreal, and boreal species (Fig. 1). Because this forest type is representative of large areas that change from carbon sources to sinks based on age and species type (Davis et al., 2003; Denning et al., 2003; Desai et al., 2005) and sources of seasonal evapotranspiration (Ewers et al., 2002, 2008; Mackay et al., 2002) such areas are important for global change research. This forest consists of monoculture and mixed stands of deciduous broadleaf and conifer needle-leaf species in upland and wetland conditions. The region around the WLEF AmeriFlux tall tower now has a 17-year tower flux record (since 1995), and many supporting measures for shorter time periods (Mackay et al., 2002; Burrows et al., 2002, 2003; Cook et al., 2004; Ewers et al., 2007; Loranty et al., 2008).

The study site lies within a broadly forested 200 km × 200 km region, near Park Falls in northern Wisconsin. The focal point is the WLEF-TV AmeriFlux tower, located at 45.946°N, 90.272°W. Within the footprint of this unusually tall (447 m) eddy covariance tower lie the field blocks. The two phenology sampling blocks in this project are distributed across major species and landform gradients necessary for scaling to the WLEF tower (Mackay et al., 2002). The study area is covered approximately 30% by coniferous species and 70% by deciduous species in four major cover types (Ewers et al., 2002; Mackay et al., 2002): (1) aspen uplands consisting mostly of *Populus tremuloides*-trembling aspen and *Abies balsamea*-balsam fir; (2) northern hardwoods, primarily *Acer saccharum*-sugar maple; (3) conifer groves dominated by *Pinus resinosa*-red pine; and (4) forested wetlands with mixtures of *Alnus rugosa*-speckled alder, *Thuja occidentalis*-white cedar, *Acer rubrum*, and *A. balsamea*.

2.2. Initial area

During summer 2005, the three largest dominant species trees were identified, tagged, and measured for diameter at breast height (DBH) at each of 72 plots (arranged following a 25 m grid 3/7 cyclic sampling design, Burrows et al., 2002) in an initial 625 m × 275 m area near the WLEF tower (northern half of the southern 625 m × 625 m sampling block, which contains a transition from aspen upland to forested wetland, Fig. 1). Our cyclic sampling took 3 of 7 evenly spaced potential plots (spaced at 25 m intervals) so that the selected plots from multiple cycles were separated by a full range of spatial intervals (e.g., 25, 50, 75, and 100 m). These 216 trees were observed in phenological monitoring campaigns in spring 2006 and spring 2007 to test the sampling methodology.

2.3. Expanded areas

Subsequently, during summer 2007, using the same sampling design described above, the plots were expanded to two 625 m × 625 m areas (Fig. 1). One was a southward extension of the initial “south” study area, and the other a new “north” area containing a transition from northern hardwoods to conifer groves. Each area contained 3 trees at each of the 144 plots, for a total of

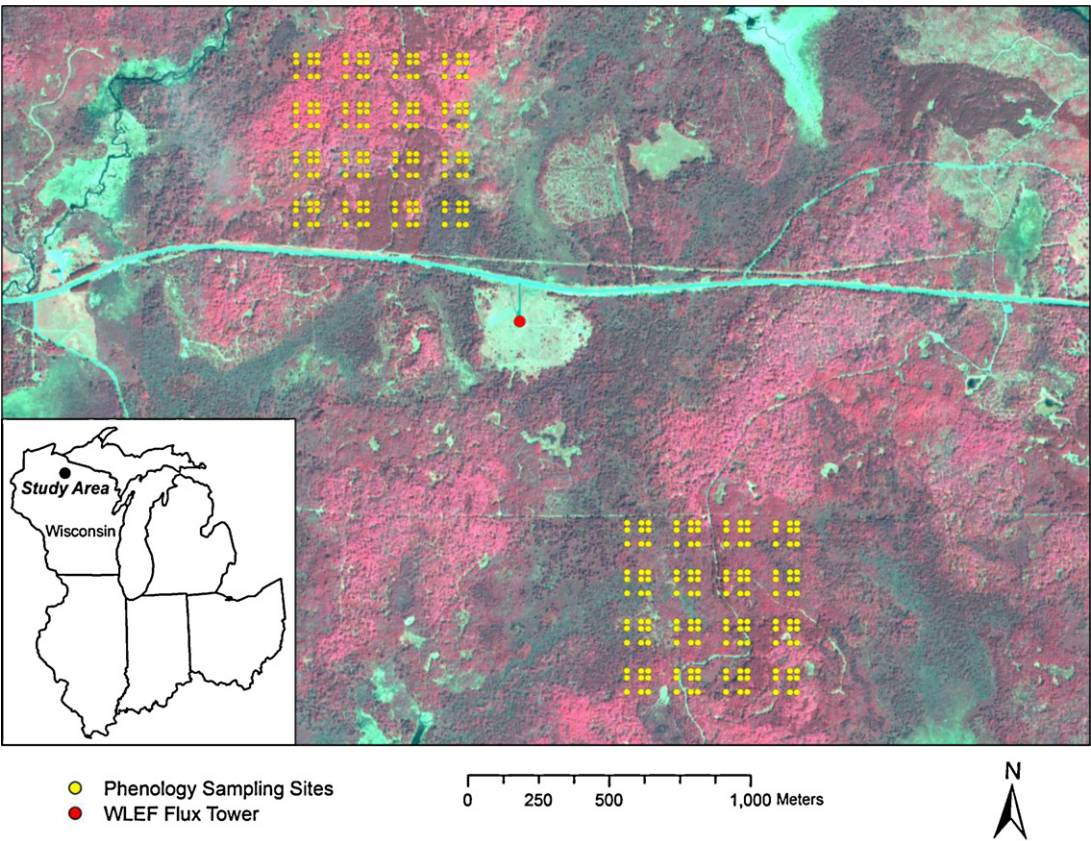


Fig. 1. “North” and “South” 625 m × 625 m study areas with a total of 888 tagged trees (the WLEF/Park Falls, WI tall tower site [45.946°N, 90.272°W] is in the cyan-colored area near the center of the image). The initial study area was the northern half of the south study area. Background produced from Quickbird imagery acquired 18 May 2007, courtesy of NASA.

288 plots and 864 trees. Phenological observation campaigns were conducted in these expanded areas in the springs of 2008, 2009, and 2010. In the northern area an additional 24 *Tilia americana* (basswood) trees were also included for comparison to on-going observations of the same species in a small woodlot on the University of Wisconsin-Milwaukee campus (43.081°N, 87.881°W). The distribution of species in the study areas is shown in Table 1.

2.4. Phenological observation protocols and procedures

Clear criteria were used to identify the characteristics of each species' phenological events, and were modified from those used in a weekly tree phenological survey conducted at the Morgan-Monroe, Indiana AmeriFlux site (J.C. Randolph, personal correspondence), with additions from other protocols and experience gained from the 2006 initial campaign (Table 2; Meier, 2001). When the earliest species growth onset appeared imminent, the

monitoring team was transported to the Kemp Natural Resource Station “base camp” (45.833°N, 89.667°W, Woodruff, WI—located about a 60-min drive east from the study area) and began to monitor the phenology at 2-day intervals over an approximately 5-week period (from initial bud-burst until most trees have reached full leaf expansion). All observers acquainted themselves with phenological stages of all trees to be observed, with sequential observations on the same trees typically rotating between observers, to minimize any individual biases on the overall sequence. The spring 2006 and 2007 field campaigns were conducted by 1–2 individuals on 216 trees in the initial study area, with the 2008 and 2009 field campaigns conducted by four individuals on 888 trees in the expanded study areas. Based on collection information from previous years, two individuals monitored all trees in the expanded study areas during spring 2010 at a reduced temporal frequency for individuals (4-day intervals), but with half still monitored every 2 days (by alternating between the north and south areas).

Table 1
Distribution of tree species samples in the study areas.

Latin name	Common name	North	N ½ South	S ½ South	All
<i>Acer saccharum</i>	Sugar Maple	173	6	6	185
<i>Acer rubrum</i>	Red Maple	83	33	49	165
<i>Populus tremuloides</i>	Trembling Aspen	17	71	47	135
<i>Abies balsamea</i>	Balsam Fir	21	58	41	120
<i>Pinus resinosa</i>	Red Pine	79	0	26	105
<i>Alnus rugosa</i>	Speckled Alder	4	23	11	38
–	Ten others ^a	79	25	36	140
Total		456	216	216	888

^a *Betula alleghaniensis* (Yellow Birch), *Betula papyrifera* (White Birch), *Fraxinus nigra* (Black Ash), *Larix laricina* (Tamarack), *Picea glauca* (White Spruce), *Picea pungens* (Blue Spruce), *Pinus strobus* (White Pine), *Populus grandidentata* (Big Tooth Aspen), *Thuja occidentalis* (White Cedar), and *Tilia americana* (Basswood).

Table 2

Visual phenology protocol (modified from weekly phenological survey used at Morgan Monroe Forest [Indiana] Ameriflux site J. C. Randolph, personal correspondence).

Code	Deciduous phenophase	Percentage	Balsam fir phenophase	Code
0	No buds visible	0	No buds visible	0
100	Buds visible	<10%	Buds visible	100
110	Buds visible	10–50%	Buds visible	110
150	Buds visible	50–90%	Buds visible	150
190	Buds visible	>90%	Buds visible	190
200	Buds swollen	<10%	Buds swollen	200
210	Buds swollen	10–50%	Buds swollen	210
250	Buds swollen	50–90%	Buds swollen	250
290	Buds swollen	>90%	Buds swollen	290
300	Bud open (leaf visible)	<10%	Bud open (candle visible)	300
310	Bud open (leaf visible)	10–50%	Bud open (candle visible)	310
350	Bud open (leaf visible)	50–90%	Bud open (candle visible)	350
390	Bud open (leaf visible)	>90%	Bud open (candle visible)	390
400	Leaf out (not fully unfolded)	<10%	Candle out (not unfolded)	400
410	Leaf out (not fully unfolded)	10–50%	Candle out (not unfolded)	410
450	Leaf out (not fully unfolded)	50–90%	Candle out (not unfolded)	450
490	Leaf out (not fully unfolded)	>90%	Candle out (not unfolded)	490
500	Full leaf unfolded	<10%	Needles unfolding from candle	500
510	Full leaf unfolded	10–50%	Needles unfolding from candle	510
550	Full leaf unfolded	50–90%	Needles unfolding from candle	550
590	Full leaf unfolded	>90%	Needles unfolding from candle	590
600	Leaf expansion	Size <25% of full		
625	Leaf expansion	Size = 25–50%		
650	Leaf expansion	Size = 50–75%		
675	Leaf expansion	Size >75% of full		

2.5. Environmental measurements

Micrometeorological spatial measurements of air temperature and humidity were collected using HOBO (Pro Series, model H08-032-08, Onset Corporation) sensors deployed across the initial 625 m × 275 m study area at locations with likely microclimatic differences, based on topographic position and cover type, starting 1 week prior, and continuing during the spring 2006 phenological campaign (Fig. 2). Raw data were collected at 10-min intervals. The HOBOs were tied to the north side of trees at approximate National Weather Service standard “shelter height” of 1.5 m. A similar deployment was used for the spring 2007 phenology campaign (Fig. 2). In 2008 and 2009, HOBOs with air and soil temperature measurement capability (soil probes placed at a depth of 20 cm) were added (model H08-031-08) and all were deployed across the expanded study areas using the same general strategy as in previous years (Fig. 2).

To facilitate a comparison of the phenology, carbon flux, and micrometeorological measurements, average daily daytime values of temperature and relative humidity were calculated by averaging the 10-min values over the daily periods when photosynthetically active radiation (PAR) measured at the WLEF flux tower was greater than zero. WLEF PAR data were provided courtesy of Dr. Ankur Desai (University of Wisconsin-Madison). PAR is the photosynthetically active component of radiation that has wavelengths between 400 and 700 nm and is considered to be the primary driver of CO₂ uptake by vegetation (Waring and Running, 2007). Average daily daytime values were calculated for each meteorological variable and used in this study because forest trees only assimilate CO₂ during daytime hours. Averaging these microclimatic variables across the two study areas is justified given that the time series of air temperature and relative humidity do not vary substantially. During the time periods studied, the standard deviation of average daily daytime air temperature across the sites measured in the two study areas never exceeded 0.83 °C and the standard deviation of average daily daytime relative humidity never exceeded 9.05%. Given its potential influence on CO₂ exchange, vapor pressure deficit (VPD) was derived from the average daily daytime values of temperature and relative humidity using the procedures described in Prenger and Ling (n.d.).

In addition to the microclimatological measurements, HOBO pendant light sensors (model UA-002-64, Onset Corporation) were used to assess the reduction of light levels under the canopy in selected locations in 2008 and 2009 (Fig. 2). Data collected between 10:00 am and 2:00 pm (LST) in both forested and non-forested areas were used to calculate the fraction of light intercepted by the forest canopy at each forested site. Initially, the average daytime light level below the canopy was subtracted from the average daytime light level in the open areas (which served as a proxy for the amount of light received at the top of the forest canopy). The difference was then divided by the average daytime light in the open areas to derive the fraction of light intercepted by the canopy. These measurements were compared to the visual phenology observations in maple canopies (red and/or sugar maple) throughout the north study area in 2008 and 2009. We focused our analysis on maple canopies in the north study area because multiple light sensors were located under this canopy type. Furthermore, the leaf area and canopy closure associated with maple canopies result in time series of light interception that clearly represent leaf development during the spring. We averaged the measurements of canopy light interception across sites with canopies composed predominantly of red and/or sugar maple. For each year, piece-wise linear regression was used to determine the approximate day when the fraction of light intercepted by the canopy began to increase in the spring. The timing of this increase was compared to study area-wide averages of visual phenology for red and sugar maple to examine whether the light measurements can be related to visual phenology observations.

2.6. Eddy covariance flux measurements

Hourly measurements of net ecosystem exchange (NEE), gross primary productivity (GPP), and ecosystem respiration (ER) for 2006–2009 from the WLEF tower were provided courtesy of Dr. Ankur Desai (University of Wisconsin-Madison). Measurements of NEE are derived at three different levels on the WLEF tower (30 m, 122 m, and 396 m). Davis et al. (2003) developed a method of deriving “optimal” measurements of NEE based on all three of the levels. The component fluxes of NEE (GPP and ER) were derived using a detailed methodology described by Desai et al. (2005). Average

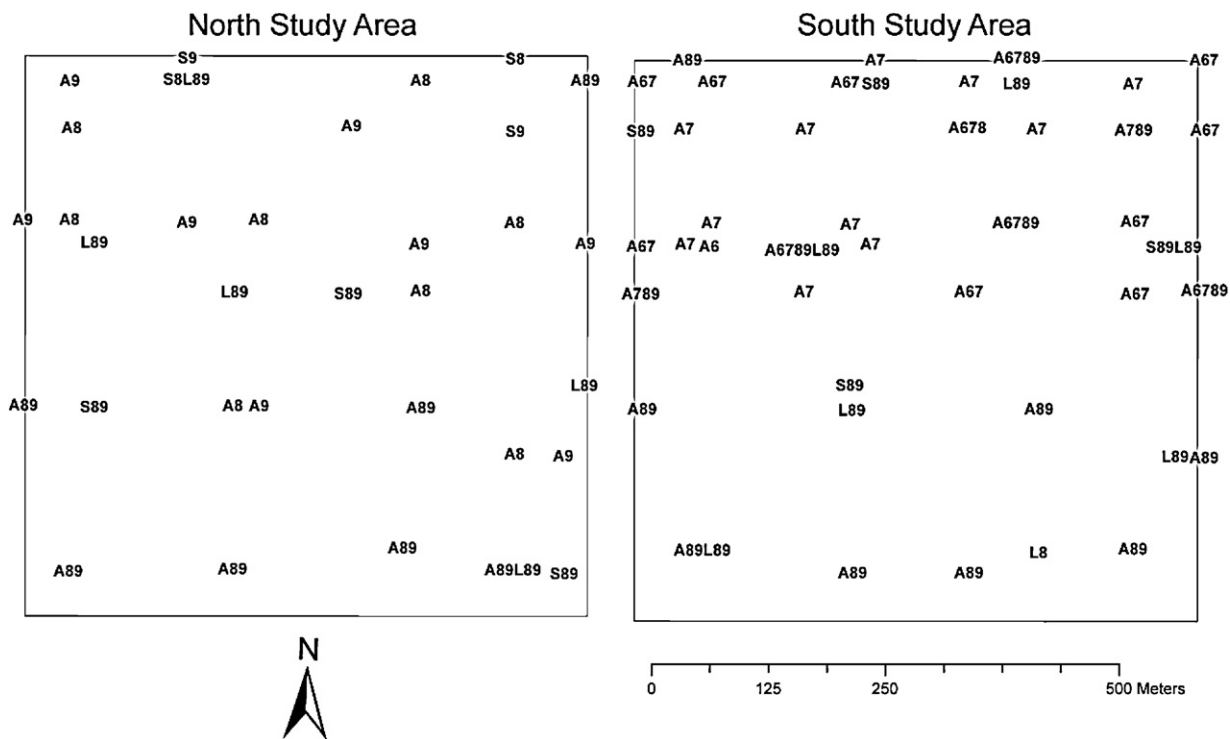


Fig. 2. HOBO temperature and light sensor locations within the north and south study areas, 2006–2009. Letters represent sensor type: A = Air temperature and relative humidity, S = Soil temperature, L = Light sensor; numbers represent years: 6 = 2006, 7 = 2007, 8 = 2008, 9 = 2009; labels are centered on sites; some sites have multiple sensors (e.g., A6789L89 = air temperature and relative humidity data for 2006–2009 and light sensor data for 2008–2009).

daily daytime values of these three variables were calculated using hourly measurements when PAR was greater than zero.

2.7. Testing for temporal resolution-impacts of reductions in sampling frequency on accuracy

Given the desirability of reducing numerical and temporal sampling frequency as much as possible due to logistical and cost considerations, their effects on overall measurement uncertainty were explored. Standard error rates for the base (every other day) observations including every pair of consecutive phenological observations levels (segments such as 300–310, 310–350, 350–390, etc., see Table 2) were first calculated and then averaged for each of five major species. Next, the increase in uncertainty (difference between the recorded value's timing and one determined using a linear interpolation between increasing sampling periods, in days) was calculated for each segment as the sampling interval was increased to 4, 6, and 8 days. The base species standard error values were used to normalize the change in phenological measurement uncertainty as the normalized sampling interval was doubled, tripled, and quadrupled (increased to 4, 6, and 8 days relative to the base [every other day] observations). These species-level results and an average of all five species were graphed for comparison.

2.8. Testing for spatial resolution-impacts of increased number of samples on accuracy

The impact of increased numbers of individual trees in the sample was explored by determining the difference in departure of different sample means from the average of all trees observed for the species (as a population mean proxy) for three key phenological observation levels (390, 490, 590) of one of the more numerous species (*Populus tremuloides*) as the number of individuals in the sample increased. Phenological observations of aspen in both study

areas in 2008 were used for this analysis. Phenology data for other years had not yet been collected when this analysis was conducted.

2.9. Composite measures of phenology-recording area-wide inter-annual change

Given that the initial observations (during 2006 and 2007) were made in a smaller area than subsequent phenological measurements (in 2008 and 2009), we used *t*-tests to determine any significant differences among the average dates when the 390, 490, and 590 stages were reached for each dominant species in the various sections of the study area. Specifically, comparisons were made between the northern half and southern half of the south study area, as well as between the entire north and south study areas. This was necessary to determine the best approach to computing the average phenological development for the dominant species and overall composite annual measures of phenology. These comparisons also facilitated an assessment of the micro-environmental impacts on phenological observations.

The phenological observations of individual trees of the same species were averaged across the south study area or both study areas if the dates of at least two of three growth stages were not significantly different between these areas ($\alpha = 0.05$).

2.10. Comparing phenology and DBH

To investigate a potential relationship between phenology and DBH, we compared the DBH of individual trees representing the major species (those listed in Table 3) to their 390, 490, and 590 dates using linear regression analysis.

2.11. Relationships among phenology, climate, and carbon flux

To evaluate the relationships among phenology, climate, and carbon flux, a series of regression analyses were conducted using

Table 3

Minimum, average (in bold), and maximum “390” and “490” (phenological level) day-of-year dates (2006 and 2007 are based on the northern half of the south study area and 2008 and 2009 are based on the north and south study areas) for major tree species.

Year-level	<i>Acer rubrum</i>	<i>Alnus rugosa</i>	<i>Acer saccharum</i>	<i>Populus tremuloides</i>	<i>Abies balsamea</i>
2006–390	119 ^a , 122 , 130	119 ^a , 123 , 130	119 ^a , 122 , 124	119 ^a , 123 , 139	124, 131 , 143
2006–490	119 ^a , 127 , 133	121, 128 , 139	121, 126 , 130	119 ^a , 126 , 141	128, 138 , 147
2007–390	119, 125 , 129	119, 122 , 133	119, 124 , 127	119, 127 , 131	129, 133 , 145 ^b
2007–490	123, 129 , 133	123, 127 , 135	123, 127 , 133	121, 131 , 135	131, 137 , 145 ^b
2008–390	130, 137 , 148	122, 134 , 148 ^b	130, 137 , 148	128, 137 , 150 ^a	140, 146 , 150 ^b
2008–490	134, 141 , 150 ^b	134, 140 , 146 ^b	132, 143 , 150 ^b	128, 140 , 148 ^b	146, 149 , 150 ^b
2009–390	127, 135 , 145	125, 131 , 141	125, 136 , 141	123, 130 , 143	135, 141 , 148 ^b
2009–490	129, 138 , 145	129, 137 , 141	131, 138 , 145	127, 133 , 143	141, 144 , 148 ^b

^a The phenophase occurred prior to the observation period for some trees. In these cases the dates for the affected trees were set to the first day of observation.

^b The phenophase occurred after the observation period for some trees.

the average phenological development of the dominant species (referred to collectively as “phenology”), the average daily daytime values of air temperature, PAR, and VPD (referred to collectively as “climate”), and the average daily daytime values of GPP. These analyses concentrated specifically on GPP because vegetation influences carbon exchange primarily through photosynthesis. Furthermore, GPP is a direct measure of vegetation activity, whereas ER reflects heterotrophic and autotrophic sources of carbon. The measurements of NEE, GPP, and ER during each spring season show that GPP was greater than ER during the vast majority of all the spring seasons and, as such, was the primary determinant of NEE in spring. For these reasons, studying GPP facilitated a more specific analysis of the phenological and climatic controls on NEE. The results of these analyses demonstrate whether microclimatic measurements and visual phenology observations with high spatial and temporal resolutions can be scaled up to accurately model GPP derived from the tower instrument-based estimates of NEE during the spring.

Prior to conducting regression analyses using these data, factor analysis was used with the average phenology time series for each dominant species to derive a single independent variable that captured most of the variation that exists among the dominant species. This was necessary because of high correlations among the phenologies of the major species. For each year studied, there was only one factor/latent variable that had an Eigen value above 1 and was highly correlated with all of the dominant species ($r > 0.96$ in each year studied). The use of this latent variable ensured that the positive relationship between phenology and average daily daytime GPP would be preserved when conducting the regression analyses and comparing the predicted GPP values to the observed GPP values.

3. Results

Major deciduous species phenologies (*A. rugosa*, *P. tremuloides*, *A. rubrum*, and *A. saccharum*) were combined by determining the median phenological stage of development of all trees on each day of each spring's field campaign (Fig. 3). Fig. 3 shows interannual comparisons only for trees in the northern half on the south study area, where measurements are available for all 5 years (2006–2010; we created a similar graph using projected data [detailed later] from all major deciduous species in both study areas, and it showed a similar pattern of interrelationships between the 5 year's phenological sequences).

We were fortunate to have considerable variation among the spring phenology sequences over the 5 years (Fig. 3). Our first spring (2006) began quite early, but was slowed by a substantial cold snap in mid-May (including accumulating snow). Spring 2007 also started early and stayed warm throughout the observation period, thus also ending quite early. In contrast, spring 2008 was the coolest of the years, starting about 2 weeks later than 2006 and 2007. Spring 2009 was the one “intermediate” year, and was

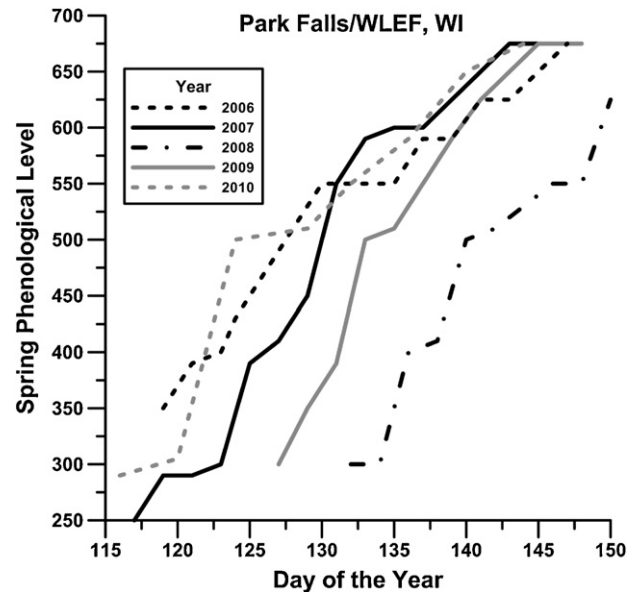


Fig. 3. Median spring phenological levels (Table 2) by year during the observation period for major deciduous species (*Acer rubrum*, *A. saccharum*, *Alnus rugosa*, and *Populus tremuloides*) in the northern half of the south study area.

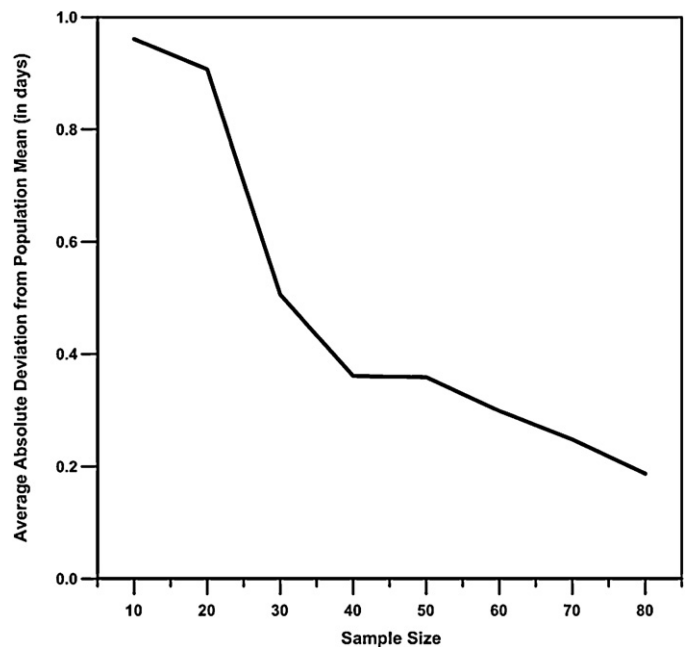


Fig. 4. Comparisons of sample size to error for *Populus tremuloides* across both study areas in 2008.

Table 4
p-Values from t-tests on average 390, 490, 590 (phenological level) dates for major deciduous tree species (values at the 0.05 level of significance or better are shown in bold) showing study area differences.

Year	<i>Acer rubrum</i>	<i>Alnus rugosa</i>	<i>Acer saccharum</i>	<i>Populus tremuloides</i>
2008				
(ns/ss)	0.41, 0.09, 0.21	0.75, 0.64, 0.36	0.08, 0.17, 0.43	0.00 , 0.13, 0.59
(n/s)	0.00 , 0.44, 0.00	0.38, 0.88, 0.77	0.60, 0.77, 0.00	0.13, 0.02 , 0.23
2009				
(ns/ss)	0.35, 0.50, 0.78	0.42, 0.44, 0.03	0.41, 0.86, 0.15	0.24, 0.15, 0.02
(n/s)	0.00 , 0.62, 0.02	0.70, 0.03 , 0.67	0.26, 0.99, 0.01	0.97, 0.26, 0.40

ns/ss = comparing northern and southern halves of the south study area; n/s = comparing entire northern and southern study areas.

perhaps the only one that was close to the longer-term average spring sequence when compared to century-scale climate records (Schwartz et al., 2006). Lastly, spring 2010 turned out to be the earliest of the 5 years in the study, even though (as in 2006) it was slowed by an early-May accumulating snowstorm (however, unlike 2006, the period of colder temperatures was several days shorter, thus having less delaying effect on the tree phenologies).

Our experiment to explore the effect of increasing sample size on sample mean error for aspen, relative to the mean for all trees from both study areas of that species in the study (as a proxy for the population mean) showed results similar to other studies, with a flattening of the curve at a sample size of around 30 (Fig. 4; West and Wein, 1971). This threshold was larger than that determined using data from the smaller initial study area ($n=20$), but agreed with typical values often quoted in statistical references (Bluman, 2004).

Overall phenological variation between individuals of the same species was substantial (typically up to 2–3 weeks for deciduous species and somewhat less for balsam fir) and similar among species, and across the two study areas (Table 3). Given the large number of trees sampled, it seems probable that species responses in one portion of the study area would not vary significantly, on average, from that in another portion. This was generally confirmed, though the maples (*A. rubrum* and *A. saccharum*) did show significant differences at some phenological stages (Table 4). We plan to explore these differences, and their potential ability to separate the effects of temperature from other factors in a subsequent study. Thus, we were able to use the average phenological sequences for major deciduous species in the northern half of the south study area (Table 5) to generate estimates for what the

responses for the combined north and south study area's phenological sequences would have been for these same species in 2006 and 2007 (Table 5). With few exceptions, the minimum, mean, and maximum 390 and 490 dates exhibited similar interannual variability during the years studied (Table 3).

Our comparison of the under-canopy light sensor measurements to the visually recorded phenologies for *A. rubrum* and *A. saccharum* indicate that the light sensors do not detect substantial changes until the leaves emerge fully from the buds (Fig. 5). The results of piece-wise linear regression analysis revealed a breakpoint in the time series of light interception near day-of-year 135 in 2008, which marked the beginning of a small increase in the fraction of light intercepted by the canopy that coincided with the 350 and 390 levels. A subsequent, drastic increase in light interception occurred after the 500 level was reached near day-of-year 143. In 2009, the results of piece-wise linear regression indicated a breakpoint in the time series of light interception near day-of-year 136, which marked the beginning of a rapid increase that coincided with the 490 and 500 levels.

Comparison of the effects of increasing sampling interval (by removing observation days from the full sequence to create “degraded” 4, 6, and 8 days sampling series) was quite revealing, both collectively and by species (Fig. 6). Average phenological measurement uncertainty showed a minimal increase (from 0.15 to 0.21

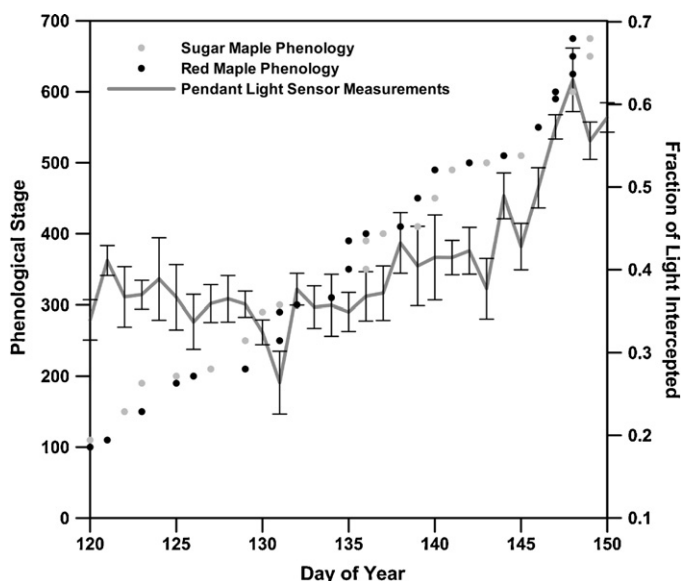


Fig. 5. Comparison of visual observations and light sensor measurements (with ± 1 standard error bars) in the north study area during spring 2008.

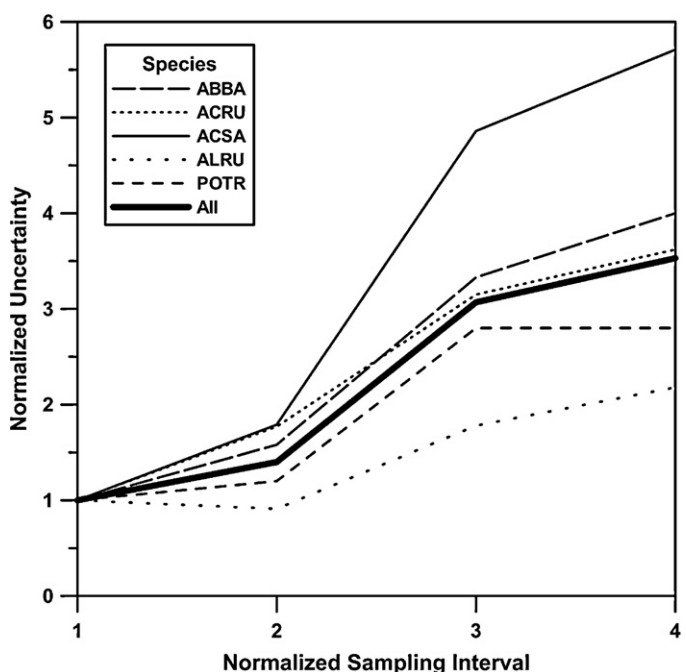


Fig. 6. Comparison of normalized sampling interval and uncertainty for phenological measurements of major tree species in 2008 and 2009. *Alnus rugosa* (ALRU), *Abies balsamea* (ABBA), *Acer rubrum* (ACRU), and *Populus tremuloides* (POTR).

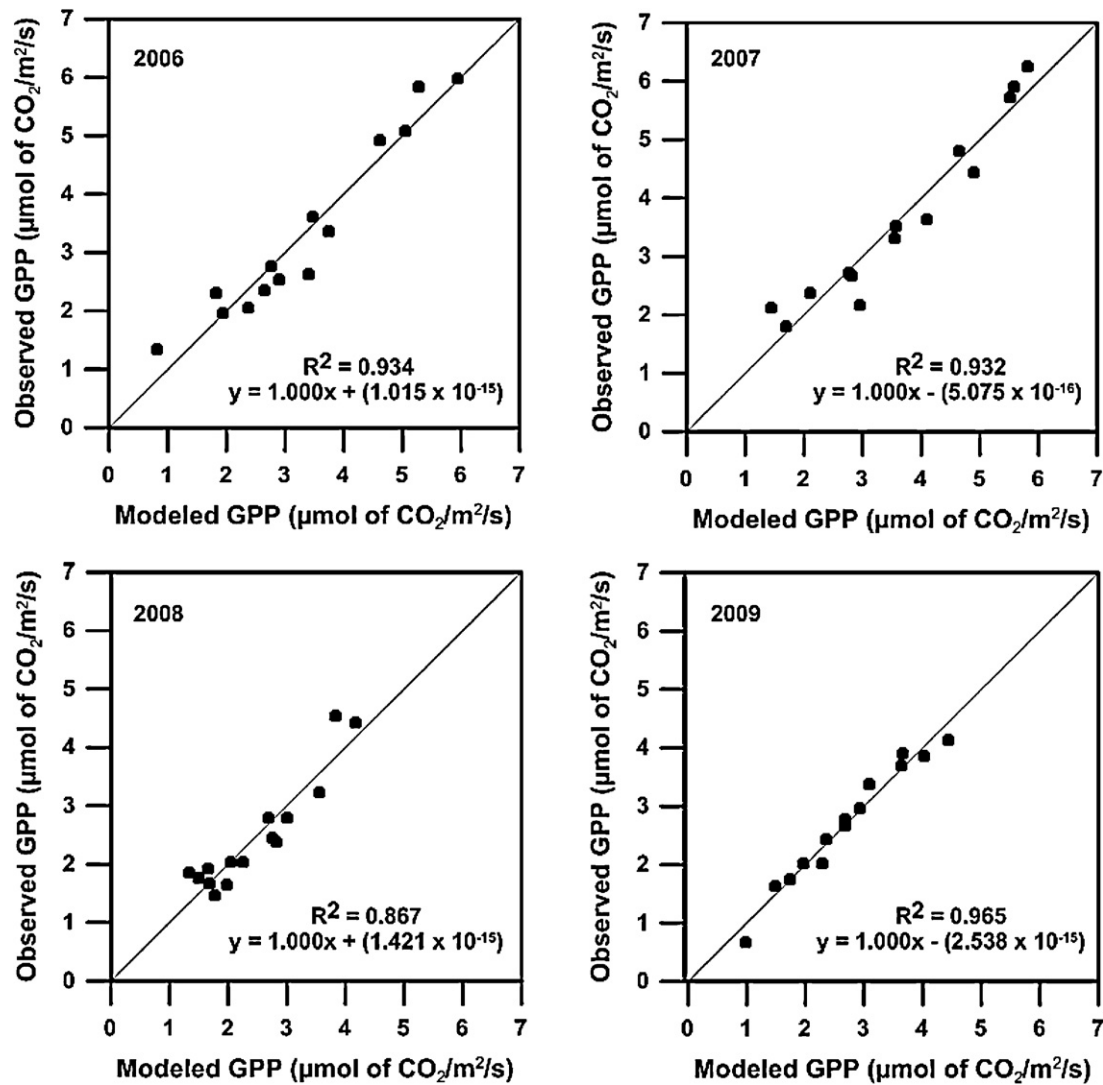


Fig. 7. Comparison of observed GPP and modeled GPP (based on phenology and climate) (the best-fit line represents the regression equation for each year).

days) as the sampling interval rose to 4 days ("2" on the x-axis) and rose to 0.46 days when the interval was further increased to 6 days ("3" on the x-axis). Additionally, species differences were present and consistent, with *A. rugosa* (ALRU) showing the least change, *A. saccharum* (ACSA) showing the most, and the other three major

species (*A. balsamea* [ABBA], *A. rubrum* [ACRU], and *P. tremuloides* [POTR]) displaying similar responses.

Our comparison of DBH and the 390, 490, and 590 stages for the major species did not reveal any consistent relationships between DBH and phenology during the 4 years studied. The amounts of

Table 5
Average 390, 490, 590 (phenological level) day-of-year dates for major deciduous tree species.

Year	<i>Acer rubrum</i>	<i>Alnus rugosa</i>	<i>Acer saccharum</i>	<i>Populus tremuloides</i>
2006				
(nhs)	122 ^a , 127 ^a , 139	123 ^a , 128, 140	122 ^a , 126, 138	123 ^a , 126 ^a , 133 ^a
(n+s)	122, 127, 138	123, 129, 139	121, 126, 137	123, 126, 133
2007				
(nhs)	125, 129, 134	122, 127, 134	124, 127, 133	127, 131, 134
(n+s)	125, 129, 134	122, 128, 134	123, 128, 133	127, 131, 134
2008				
(nhs)	138, 141, 149 ^b	135, 140, 149 ^b	136, 142, 150 ^b	137 ^b , 139 ^b , 144 ^b
(n+s)	137, 141 ^b , 148 ^b	134 ^b , 140 ^b , 148 ^b	137, 143 ^b , 148 ^b	137 ^b , 140 ^b , 145 ^b
2009				
(nhs)	136, 138, 142	131, 135, 141	136, 138, 144	130, 133, 138
(n+s)	135, 138, 142 ^b	131, 137, 141 ^b	136, 138, 142 ^b	130, 133, 137

nhs = northern half of the south study area; n+s = both study areas (estimated dates in italics).

^a The phenophase occurred prior to the observation period for some trees. In these cases the dates for the affected trees were set to the first day of observation.

^b The phenophase occurred after the observation period for some trees.

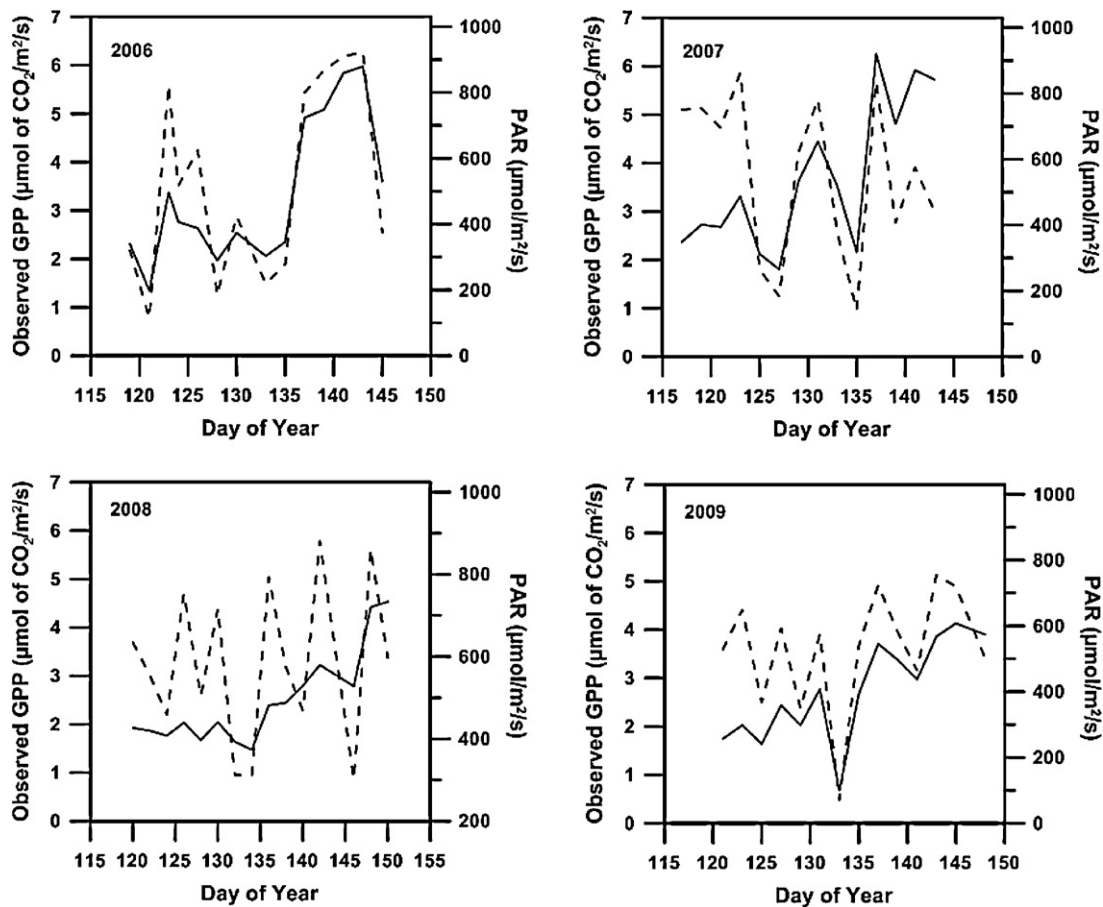


Fig. 8. Time series of observed GPP (solid line) and PAR (dotted line).

Table 6

Coefficients of determination (R^2) representing the amount of variation in GPP explained by phenology, climate (combined) and individual meteorological variables.

Variables	2006	2007	2008	2009
Phenology	0.456	0.547	0.716	0.634
Climate	0.821	0.602	0.324	0.678
Phenology and Climate	0.934	0.932	0.867	0.965
PAR	0.803	0.116	0.203	0.596
VPD	0.457	0.003	0.170	0.424
Air temperature	0.137	0.065	0.121	0.213

variation in leaf phenology explained by DBH were low, with the exception of sugar maple trees in 2007. During the spring of 2007, DBH explained 54% and 44% of the variation in the 390 and 490 stages for sugar maple, respectively.

In all of the years studied, phenology and climate together explained at least 86.7% of the variation in average daily daytime GPP (Fig. 7). Based on the results from the analyses of the separate effects of phenology and climate on GPP, there is substantial interannual variability in the strength of the relationship between phenology and GPP (Table 6). GPP exhibited greater day-to-day variability during the 3 years when climate explained more of the variation than phenology (2006, 2007, and 2009). The variability in GPP during these three spring seasons was caused by large day-to-day variability in PAR (seasonal range of PAR received >600 $\mu\text{mol}/\text{m}^2/\text{s}$). The close correspondence between PAR and GPP during these 3 years is shown in Fig. 8. During 2008, the amount of PAR received was less variable and had a seasonal range less than 600 $\mu\text{mol}/\text{m}^2/\text{s}$. Consequently, GPP varied less during this year

and was better explained by the phenology of the dominant forest species than climate.

In contrast to PAR, fluctuations in the other climatic variables (air temperature and VPD) did not have a large influence on GPP. Based on the R^2 values representing the relationships among GPP and the three meteorological variables, it is evident that air temperature and VPD did contribute partially to the total amount of variation in GPP explained by climate (Table 6).

4. Discussion

One of the inherent advantages of recording phenology using a continuous measurement scale at high temporal and spatial resolution (as in this study), is the ability to easily look at within or between year variability aggregated across multiple species or for specific species in selected locations. An example of this approach for multiple species is shown in Fig. 3 (phenology data from the 2010 spring field campaign were added to this figure for comparative purposes, but not included in any other analyses).

Our results suggest that phenology and climate are indeed the primary factors controlling GPP, which is typically the primary determinant of NEE during the spring season. A comparison of the variation in GPP explained by the phenology of the dominant species and the variation in GPP explained by climate suggests that this interannual variability can be attributed to climate variability. These findings suggest that PAR governs the strength of the relationship between the phenological development of the dominant species and GPP. When PAR varies substantially, the relationship between phenology and GPP is weaker than the relationship between climate and GPP. When PAR does not vary substantially,

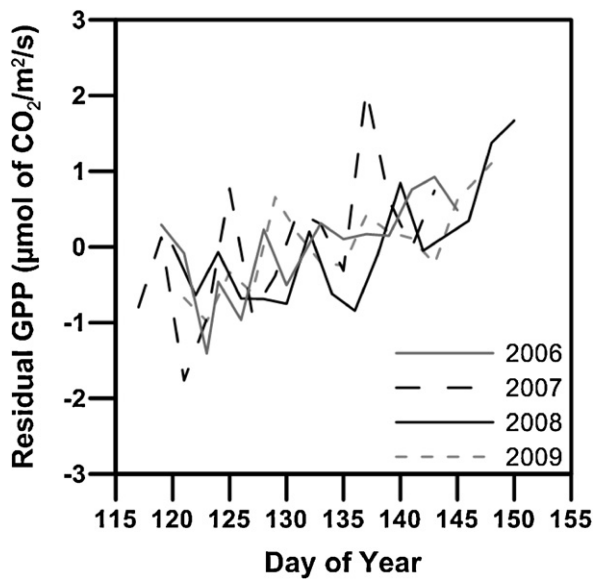


Fig. 9. Residuals of modeled GPP based on climate.

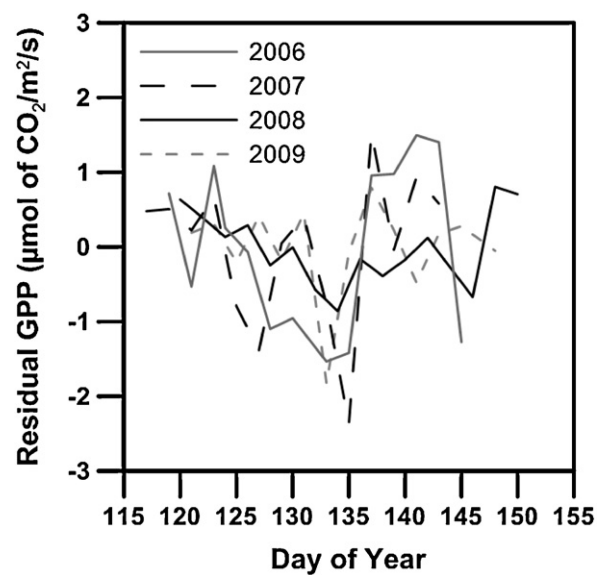


Fig. 10. Residuals of modeled GPP based on phenology.

Table 7

Slope and R^2 of the residuals of modeled GPP based (separately) on climate and phenology.

Year	Slope	R^2
2006		
Climate	0.048	0.404
Phenology	0.010	0.006
2007		
Climate	0.066	0.335
Phenology	0.004	0.001
2008		
Climate	0.057	0.487
Phenology	−0.002	0.001
2009		
Climate	0.049	0.525
Phenology	−0.002	<0.001

the relationship between phenology and GPP is stronger than the relationship between climate and GPP. Such variability in PAR is caused by intermittent cloud cover in the atmosphere (Goulden et al., 1996; Gough et al., 2008). That PAR is the most influential meteorological variable is not surprising considering that it is an integral component of photosynthesis. It is likely that air temperature and VPD accounted for less of the variation in GPP because they did not reach levels that heavily constrained photosynthesis.

Although meteorological conditions explained more of the variation in GPP during three of the 4 years studied, phenology did capture the positive trend in GPP that occurred during each spring season. Climate did not capture this increase as well as phenology. This is evident when examining the residuals from the regression analyses. In each year, the residuals from the modeled GPP values based on climate exhibit an increase throughout most of the spring season (Fig. 9, slopes and R^2 of the best-fit lines of the residuals are listed in Table 7). This indicates that climate alone failed to adequately explain the increase/positive trend in GPP during spring in each year. In contrast, the residuals from the modeled GPP values based on phenology do not exhibit any strong, discernible positive or negative trend (Fig. 10, slopes and R^2 of the best-fit lines of the residuals are listed in Table 7). These findings suggest that the phenological development of the dominant tree species is responsible for the overall positive trend in GPP and climate is the cause of day-to-day variation.

5. Conclusions

High spatial and temporal resolution phenological measurements have already shown their usefulness in connecting remote sensing measures to ground observations through spatial scaling (Liang and Schwartz, 2009; Liang et al., 2011). In this study we began to explore their ability to reveal relationships among in situ (possibly biological/genetic), microclimatic, and sampling factors in determining the variation and representativeness of cumulative phenological measures within and across species in a specific mesoclimate. In addition, our comparison of these phenological measurements with eddy covariance flux measurements highlights the relationship between tree phenology and carbon exchange.

One of the most important findings is that even though phenological variations are large between individual trees in a specific microclimate, they are not spatially autocorrelated, and thus can be adequately represented with a sample of 30 or more (Fig. 5). These variations cannot be explained by the DBH of the observed trees, which suggests that the phenology of the major species is not dependent on tree age. Further, visual phenological observations can be generally related to under-canopy light levels (Fig. 6), and for spring phenology measurements in similar microclimates, a sampling interval of every 4 days appears to be the “sweet spot” in the northern mixed forest environment, which minimizes data uncertainty and field work expenses (Fig. 7).

Our study provides an example approach for collecting high resolution (spatial and temporal scale) phenological data in relation to climatic and environmental variations. The analysis has unveiled detailed patterns of plant phenology in a spatially and temporally concentrated setting. Our tests for sampling size and frequency should provide a useful reference to planning future data collection campaigns. The comparison with carbon flux data specifically demonstrated that phenology is a more direct predictor of average daily daytime GPP than weather conditions. Follow-up works should include comparisons with tree physiology data (canopy stomatal conductance) and extension of a similar approach for autumn tree phenology. The potential utility of this high-resolution dataset entails a further understanding of the biophysical processes within heterogeneous vegetation during the critical time of growing season onset. Knowledge gained through high-resolution measurements, as demonstrated in this study, are useful for revealing details of biosphere–climate interactions within

the atmospheric boundary layer and for calibrating large scale ecosystem measures, which are needed to enhance global change studies.

Author contributions

Mark D. Schwartz developed the ideas for the study, wrote the majority of the manuscript, and took the lead in editing toward the final version of the paper. Jonathan Hanes contributed to editing the entire manuscript, processed and analyzed data, and wrote the sections of the manuscript that concern the relationships among phenology, climate, and carbon flux. Liang Liang contributed to the initial design and data collection of high-resolution phenology for this study and provided comments on drafts of the manuscript as it was prepared.

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