

The Phenology of Gross Ecosystem Productivity and Ecosystem Respiration in Temperate Hardwood and Conifer Chronosequences

Asko Noormets, Jiquan Chen, Lianhong Gu, and Ankur Desai

Abstract The relative duration of active and dormant seasons has a strong influence on ecosystem net carbon balance and its carbon uptake potential. While recognized as an important source of temporal and spatial variability, the seasonality of ecosystem carbon balance has not been studied explicitly, and still lacks standard terminology. In the current chapter, we apply a curve fitting procedure to define seasonal transitions in ecosystem gross productivity (GEP) and respiration (ER), and we show that the temporal changes in these two fluxes are not synchronous, and that the transition dates and rates of change vary both across sites and between years. Carbon uptake period (CUP), a common phenological metric, defined from ecosystem net carbon exchange (NEE), is related to these periods of activity, but the differential sensitivities of GEP and ER to environmental factors complicate the interpretation of variation in CUP alone. On a landscape scale, differences in stand age represent a major source of heterogeneity reflected in different flux capacities as well as microclimate. In the current study, we evaluate age-related differences in the phenological transitions of GEP and ER using hardwood and conifer chronosequences. While a significant portion of variability in GEP seasonality was explained with stand age, the influence of interannual climatic variability exceeded these, and was the predominant factor affecting ER seasonality. The length of the

A. Noormets (✉)

Department of Forestry and Environmental Resources,
North Carolina State University, Raleigh, NC, USA
e-mail: anoorme@ncsu.edu

J. Chen

Department of Environmental Sciences, University of Toledo, Toledo, OH, USA
e-mail: jiquan.chen@utoledo.edu

L. Gu

Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA
e-mail: lianhong-gu@ornl.gov

A. Desai

Department of Atmospheric and Oceanic Sciences,
University of Wisconsin-Madison, WI, USA
e-mail: desai@aos.wisc.edu

active season (ASL) varied more due to differences in the timing of the end rather than the start of the active period. ASL of GEP was consistently greater in conifers than hardwoods, but the opposite was true for ER.

Abbreviations

Phenological stages and dates

ASL ^{AH}	length of active season (days)
ASL ^{BG}	length of active season (days)
ASL ^{x0}	length of active season (days)
EOS	end of active season (DOY)
x0	day of half-maximum flux (DOY)
LFD	length of flux development period (days)
LFR	length of flux recession period (days)
LPF	length of peak flux period (days)
RD	rate of development ($\text{g C m}^{-2} \text{ d}^{-1}$)
RR	rate of recession ($\text{g C m}^{-2} \text{ d}^{-1}$)
SOS	start of active season (DOY)

Subscripts appended to any of the above

GEP	index or date referring to gross ecosystem productivity
ER	index or date referring to ecosystem respiration

Site abbreviations

IH03	intermediate hardwood, 2003
IP03	intermediate red pine, 2003
MH02	mature hardwood, 2002
MH03	mature hardwood, 2003
MP02	mature red pine, 2002
MP03	mature red pine, 2003
YH02	young hardwood, 2002
YP02	young red pine, 2002

1 Introduction

Climate warming has now been recognized even in the popular media (Gore 2006) and the complexities of the mechanisms contributing to it are increasingly understood (Hansen et al. 1997; Houghton et al. 1998; IPCC 2007). Cues from sources as diverse as paleoclimatic proxies, surface and airborne observations, satellite remote sensing and meteorological models all indicate that land surface temperatures have been increasing globally at a rate of 0.2–0.25°C per decade over the last

30–100 years (Bogaert et al. 2002; IPCC 2007), caused by both natural and anthropogenic forcing (Hegerl et al. 1996; Santer et al. 1996; Stott et al. 2000). The association between the earlier start of the active season (SOS) for biological processes and warmer winter temperatures is particularly strong in the eastern US and Northern Europe. There, the trend of increasing mean temperatures is increasingly reflected in the seasonal development of plants (Linderholm 2006), as well as the expansion of the ranges of species (Chuine and Beaubien 2001; Tape et al. 2006).

Given the greater increase in the late winter and early spring temperatures than late spring and early summer temperatures (Groisman et al. 1994), the advance of spring phenology has been greater than the delay of fall (Menzel and Fabian 1999; Penuelas et al. 2002; Schwartz and Chen 2002). Also, the advance in the flowering time has been greater in early- than late-flowering species (Fitter and Fitter 2002; Lu et al. 2006), with contrasting effects between prairie plants flowering before and after the peak temperature (Sherry et al. 2007). Globally, the spring events in plant development, including times of flowering, bud break and leaf expansion, marking the SOS have been advancing at a rate of about 1.5–3 (but up to 5.4) days per decade (Ahas et al. 2002; Beaubien and Freeland 2000; Chmielewski and Rötzer 2001; Menzel and Fabian 1999; Schwartz et al. 2006; Schwartz and Reiter 2000; Smith et al. 2004), associated with increasing mean temperature (Menzel 2003), earlier retreat of snow cover (Aurela et al. 2004; Groisman et al. 1994; Lu et al. 2006) and decreasing occurrence of late freeze events (Penuelas and Filella 2001). These trends have been more pronounced in Eurasia than North America (Smith et al. 2004), and stronger in trees than shrubs and grasses (Parmesan 2007).

The ground observations of earlier and longer vegetation activity have been confirmed through global analyses of the magnitude and timing of the annual cycle of CO₂ concentration in the atmosphere (Keeling et al. 1996; Myneni et al. 1997). Remote sensing models have identified significant trends towards increased net primary productivity (NPP) in recent decades (Cao et al. 2004), which in some estimates can be a significant proportion of the annual total. For example, Jackson et al. (2001) proposed that the lengthening of the growing season by 5–10 days may increase the annual NPP of forest systems by as much as 30%. Such a large response can only be possible if gross ecosystem productivity (GEP) responds more to higher temperatures than ecosystem respiration (ER). Indeed, it has been confirmed through ground measurements that the lengthening of the growing season by a certain number of days in spring stimulates ecosystem C uptake more than a lengthening by the same number of days in the fall (Kramer et al. 2000; Piao et al. 2008). This has been attributed to greater radiative inputs and longer days, as well as better moisture availability as the result of snow melt and relatively lower evaporative demand in spring than in fall (Barr et al. 2004; Black et al. 2000).

While it is true that ecosystem C balance tends to be more sensitive to early spring than late fall, not all forests respond similarly. Early spring was found to stimulate GEP more than ER in some boreal stands (Black et al. 2000). In others, delayed fall stimulated ER more than GEP, leading to smaller net C uptake (Hollinger et al. 2004). It is likely that the degree of sensitivity of ER to spring and fall warming depends on the duration of these transition periods. With long fall, leaf litter can decompose to a greater extent before dormancy, and respond to variations in temperature, whereas

with short fall the litter primarily decays during the following growing season, exhibiting greater sensitivity to variations in spring temperature. In addition to direct effect on carbon fluxes, warm and late falls may have carry-over effects associated with plant development. Heide (2003) reported that delayed fall as the result of higher than average temperatures led to frost damage and subsequent delayed bud break the following spring, resulting in lower net carbon uptake. And then there are stands where prolonged GS in spring and fall has similar effect on ecosystem C balance (Goulden et al. 1996). In all, the trends are generally more consistent for spring phenology, whereas changes in the fall are more variable (Menzel 2002), varying by biome, species, and climatic variability (e.g. extreme events) during the preceding growing season (Walther et al. 2002). Later freeze (Smith et al. 2004) and leaf coloring (Menzel and Fabian 1999) have been reported primarily in the boreal forests in North America, but even there the trends in the fall are weaker than in the spring. Overall, recent trends in ecosystem CO₂ exchange and atmospheric fall-to-winter CO₂ build-up in the northern hemisphere suggest that as a general rule, warmer falls stimulate ER more than GEP, and lead to suppressed net productivity (Piao et al. 2008).

In addition to the spring-fall asymmetry, phenological stages close to one another may also have different sensitivity to increasing temperature. For example, in Central Europe the first leaf and last freeze dates have been advancing at about the same rate, whereas in Northern Eastern Europe the first leaf date has advanced faster than the last freeze date, and in East Asia, the last freeze date has advanced faster than the first leaf date (Schwartz et al. 2006). Such non-uniform responses are currently poorly understood, but may have major implications for plant vitality (Chuine and Beaubien 2001), synchrony with pollinators (Parmesan 2007) and ecosystem carbon balance (Oechel et al. 2000). Furthermore, the asymmetric changes in the ASL may also differentially affect GEP and ER. The different timing and magnitude of GEP and ER was invoked by Schaefer et al. (2005) to explain the increased amplitude of atmospheric CO₂ concentration (Myneni et al. 1997). It has recently been recognized that the feedback by vegetation on the physical and chemical properties of the atmosphere is not negligible, and the changes brought about in plant phenology may further trigger changes in the climate it responds to (Bonan et al. 2003; Lenton 2000; Meir et al. 2006). While the significance of feedback effects and interactive influences between temperature and other factors on phenology has been recognized (Norby et al. 2003), progress in this understanding is only beginning to be made. Despite the gaps in knowledge and the fact that the seasonality of ecosystem C exchange remains among the most significant uncertainties in land surface biogeochemical models (e.g. Kathuroju et al. 2007; Olesen et al. 2007), it is clear that it plays a major role in the interannual variability of ecosystem net carbon balance (e.g. Aurela et al. 2004; Barr et al. 2007; Carrara et al. 2003), and that global patterns in annual NEE strongly correlate with differences in growing season length (Fig. 1; Baldocchi et al. 2001).

As of now, there is no standard terminology for assessing the seasonality of C exchange (or any other ecosystem process). The term “growing season” has been adopted from traditional phenology where it may mark different phases in the duration of deciduous canopy – from bud break to bud set, bud break to leaf fall, or from fully

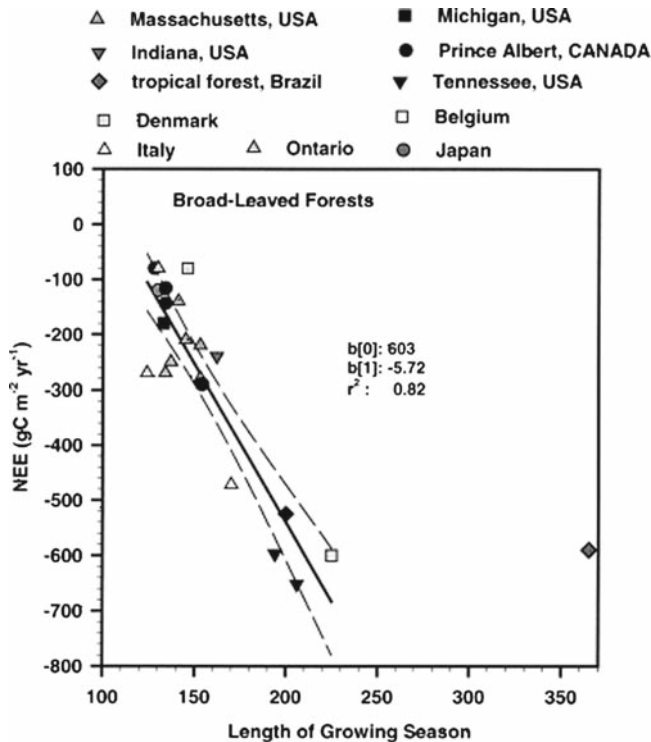


Fig. 1 Annual net ecosystem exchange of carbon (NEE) as a function of carbon uptake period (with permission, from Baldocchi et al. 2001). The $b[0]$ and $b[1]$ coefficients are the intercept and slope of the linear regression fitted to all sites, excluding the tropical forest in Brazil. The r^2 is the coefficient of determination, and the dashed lines are the 95% confidence intervals of the regression. Negative values indicate carbon uptake by vegetation.

expanded leaf to the beginning of leaf senescence. While all these dates are related, they may not always change similarly. Unlike traditional phenology of discrete events, the continuous scale of ecosystem biogeochemical fluxes (esp. ER) makes it more difficult to define the transition points. At this point, the science of phenology of ecosystem processes is still in the phase of trying to define the relevant transition points. However, the problem of identifying phases in a continuous data stream is not unique to ecology. Land surface phenology attempts to consolidate remotely sensed greenness indices (normalized difference vegetation index, NDVI, or enhanced vegetation index, EVI) with traditional phenological indices (Reed et al. 1994; White et al. 2005; White and Nemani 2003; Yang et al. 2007). Often, the transition from dormant to active periods has been defined by half-maximum greenness (Fisher et al. 2007; Schwartz et al. 2002). While there is little theoretical justification for this choice, especially as the relationship between satellite-based and ground observations of phenological changes is often poor (Badeck et al. 2004), this technique lends itself well to diverse streams of time series data. Finding the relevant transition points could be facilitated by existing

gas exchange models that have proven relatively accurate for delineating seasonal dynamics (e.g. Mäkelä et al. 2004, 2008).

For studying the phenology of ecosystem processes, the most promising recent development is the numerical method proposed by Gu et al. (2003) and developed further in the current volume (chapter “Characterizing the Seasonal Dynamics of Plant Community Photosynthesis Across a Range of Vegetation Types”). It isolates individual transitions between two periods of relatively stable fluxes, and fits a cumulative Weibull distribution function to this transition (Eqn. 1 in Methods). Similar approach was proposed for analyzing the seasonality of the remotely sensed normalized difference vegetation index (NDVI) time series data (Zhang et al. 2003), but was overlooked in a more recent study (Beck et al. 2006) that proposed a double logistic function instead. While the latter approach was superior to other fitting algorithms currently used in land surface phenology (second-order Fourier transform and asymmetric Gaussian function), Beck et al. (2006) did not develop the information as rigorously as Gu et al. (2003), who derived a full suite of phenological indicators (more details in Methods). Beck et al. (2006) only used the fitted curve to derive the inflection points, equivalent to the half-maximum points from sigmoid curve fits, commonly used in land surface phenology (Fisher et al. 2007; Schwartz et al. 2002). The transition points defined by Gu et al. (2003) are also significant because they allow to differentiate between ASL and C uptake potential of ecosystems, which, as we will discuss later, is a step towards deeper mechanistic understanding of land surface C exchange.

As an alternative to the somewhat ambiguous ASL, several eddy covariance (EC) studies (Baldocchi et al. 2005; Falge et al. 2002) and EC-remote sensing syntheses (Churkina et al. 2005; White and Nemani 2003) have adopted carbon uptake period (CUP) as the basis of delineating seasonality and comparing different ecosystems. This is particularly convenient, because EC measures the net balance of vegetation-atmosphere carbon exchange, and provides an accurate tool for among-stands comparison. However, the asynchronicity of GEP and ER, due to their sensitivity to different environmental drivers, makes CUP difficult to predict. For example, Kramer et al. (2002) found that while several models predicted the seasonal dynamics and annual total NEE correctly, the predictions of GEP and ER were wrong. Falge et al. (2002) reported that in temperate deciduous and boreal conifer forests, the seasonality of ER was generally delayed in relation to GEP. Depending on the relative juxtaposition of the seasonalities of these two fluxes, the onset of CUP may be advanced or delayed. Furthermore, it may be difficult to define CUP in conifers because ecosystem C balance may be positive (gaining C) throughout the year. Even if arbitrarily chosen thresholds (e.g. 20% of minimum NEE, as in Suni et al. 2003a) correlate well with cumulative temperature or model estimates (as it did for Suni et al. 2003a), it is difficult to apply these at different sites, or justify them on a mechanistic basis. Separating individual processes also makes the data available for studies beyond those of net carbon balance. For example, long-term C storage is closely tied to heterotrophic respiration (or ER, loosely speaking) and soil C (Field et al. 2007; Richter et al. 1999; Schlesinger and Lichten 2001), and understanding its seasonality independent of other confounding fluxes

would be of greater benefit than knowing the seasonality of NEE. For mechanistic understanding and prognostic power, we propose that the seasonality of ecosystem C exchange should be assessed on the basis of individual processes. In current study, working with eddy covariance data, we partition NEE to GEP and ER, acknowledging that ER itself represents a compound process and should ideally be partitioned further.

Variability in phenological changes occurs both globally, along broad environmental gradients (Baldocchi et al. 2001), as well as locally (Noormets et al. 2007). As a rule, ecosystem net productivity increases with the growing season length (Fig. 1) that generally decreases with latitude. However, forest stands may differ in their microclimate even when exposed to similar weather and soil conditions (Noormets et al. 2008), and these differences are expected to affect the seasonal development of photosynthetic and respiratory capacities. Across different forest types, there is a consistent trend for lower mean soil temperature in older stands with more closed canopy compared to younger open-canopied stands (Fig. 2; Bond-Lamberty et al. 2005a, b). Besides temperature, the differences also manifest in net radiation and vapor pressure deficit (VPD) (Amiro et al. 2006; Ewers et al. 2005). The age-related differences in annual carbon balance may be in the order of 500 g C m^{-2} (Noormets et al. 2007), and accounting for these is crucial for accurate representation of regional integrated carbon balance (Desai et al. 2008). Stand age may influence C exchange through the interacting influences of canopy cover, the amount of live and dead biomass, understory composition, radiation balance and microclimate. While there may be considerable variation among young stands due to diverse post-harvest management practices that control the amount of harvest residue (Devine and Harrington 2007), young stands typically tend to lose snow and warm up earlier than mature stands (Amiro 2001; Bergeron et al. 2008; Noormets et al. 2007). When the concept of chronosequence is treated more loosely, allowing for species succession throughout the stand development, like in a fire chronosequence (Goulden et al. 2006), the differences in phenology and carbon

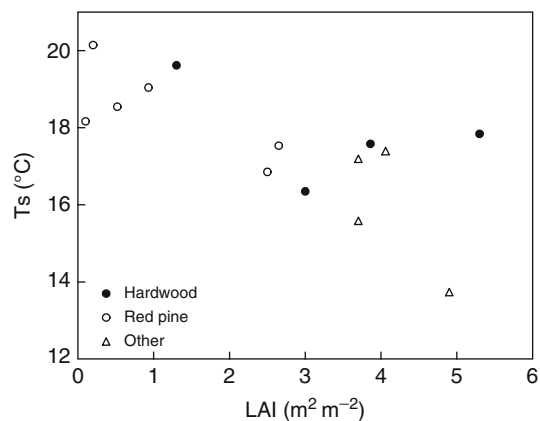


Fig. 2 Growing season (May–September) average soil temperature (T_s) as a function of canopy leaf area index (LAI) in different boreo-temperate forest types. Re-drawn, with permission, from Noormets et al. (2008).

exchange become even more pronounced, with CUP varying from as short as 65 days in young stands with primarily herbaceous vegetation to 130 days in old stands with coniferous vegetation. Understanding the mechanism of age-related differences in C fluxes could potentially provide an additional constraint to regional C cycle models by combining the information about the phenological dynamics of one stand with the age composition of stands in the area of interest. In earlier studies we have shown the significance of considering stand age and forest type-related variability for regional upscaling of C budgets (Desai et al. 2008). Thus, consistent differences with stand age could prove helpful in applications from continental data assimilation systems (e.g. AmeriFlux Data Assimilation System) to monitoring issues of practical interest (e.g. the Early Warning System; Hargrove and Hoffman 2005).

The goals of the current study were to (1) apply consistent criteria for defining the seasonality of GEP and ER, and (2) evaluate the phenology of these fluxes in relation to each other, and across two chronosequences – three deciduous and three coniferous stands – to evaluate the effect of different canopy duration and different microclimate on the seasonal development of C fluxes. We will also evaluate the relationship of the seasonality of GEP and ER with CUP, and discuss additional phenological metrics that affect ecosystem carbon balance.

2 Methods

2.1 Study Area and Site Characteristics

The study area is located in northern Wisconsin, USA ($46^{\circ}30'–46^{\circ}45'N$, $91^{\circ}2'–91^{\circ}22'W$) and belongs to the northern coniferous-deciduous biome. The climate is humid-continental with 30-year temperature normals from $-16^{\circ}C$ in January to $25^{\circ}C$ in July, and annual precipitation over the same period ranged from 660 to 910 mm. The dominant vegetation types are second-growth hardwood stands with aspen, birch and maple as the predominant species, and red pine and jack pine plantations. We measured ecosystem carbon exchange in a pair of different-aged hardwood and a pair of conifer stands each in 2002 and 2003. The mature stands were measured in both years, whereas the young stands were sampled for only 1 year. The paired sampling scheme was designed to provide information about age-related differences in C exchange in the two predominant forest types in the area. The predominant species and main site characteristics are given in Table 1, and further details about the study area, measurement and gapfilling protocols can be found in Noormets et al. (2007). The mature stands had a well developed understory, and the young stands had a significant herbaceous-grassy component, whereas the intermediate-aged stands had very dense overstory canopy and very limited understory. While differences in the understory composition could potentially affect ecosystem C fluxes (Heijmans et al. 2004), we did not detect obvious signs of it in the current study and do not address this pos-

Table 1 Site properties, including dominant species, age, leaf area index (LAI), canopy cover and basal area. Further site information available in Noormets et al. (2008a). Site abbreviations: *MH* mature hardwood, *IH* intermediate-aged hardwood, *YH* young hardwood, *MP* mature red pine, *IP* intermediate-aged red pine, *YP* young red and jack pine

Site	Dominant species	Age (years)	LAI (m ² m ⁻²)	Canopy cover (%)	Basal area (m ² ha ⁻¹)
MH	<i>Populus grandidentata</i> , <i>Betula papyrifera</i> , <i>Quercus rubra</i> , <i>Acer rubrum</i> , <i>Acer saccharum</i>	65, 66	3.9	97	33.5
IH	<i>Populus grandidentata</i> , <i>Populus tremuloides</i>	17	3.0	92	11.8
YH	<i>Acer rubrum</i> , <i>Populus grandidentata</i> , <i>Populus tremuloides</i>	3	1.2–1.4	2	1.5
MP	<i>Pinus resinosa</i> , <i>Populus grandidentata</i>	63, 64	2.5–2.8	73	26.9
IP	<i>Pinus resinosa</i>	21	2.8	60	18.2
YP	<i>Pinus banksiana</i> , <i>Pinus resinosa</i>	8	0.5	17	4.7

sibility further. However, as the understory phenology is often shifted in relation to overstory (Richardson and O’Keefe, current volume) it should be considered as a potential source of variation on a site-by-site basis.

As ER is extrapolated from nighttime data, and GEP is calculated as the sum of NEE and ER, it is possible (at least, in principle) that gapfilling protocols may affect the phenological parameters. While our gapfilling protocols include tests for bias and have been validated against other commonly used gapfilling approaches (Moffat et al. 2007), the procedures for producing defensible ER and GEP estimates are beyond the scope of this chapter. Please see Falge et al. (2001) and Moffat et al. (2007) for further details.

2.2 Phenological Transitions

To distinguish periods of relatively high activity from those of relatively low activity or dormancy, we use cumulative Weibull distribution function to delineate the “active season” for GEP and ER (Gu et al. 2003). It is a generalization of the commonly used “growing season”. Gu et al. (2003) defined seasonal transitions in GEP by fitting cumulative Weibull distribution function to daily maximum photosynthesis. In the current study, we use daily flux totals for both GEP and ER. Monitoring changes in flux capacity (light-saturated) may often be preferential to integrals, but it also has limitations. For example, eddy covariance data, recorded every 30–60 min has limited number of observations per day, and sometimes estimating capacities from such datasets may be

difficult (especially for ER). However, both scales reflect the same trends and could be analyzed, and both data types may be sensitive to extended periods of adverse weather suppressing the fluxes of interest. The Weibull cumulative distribution function is given by:

$$y = y_0 + \beta_1 \left[1 - e^{-\left(\frac{x - x_0 + \beta_2 \ln(2)^{\frac{1}{\beta_3}}}{\beta_2} \right)^{\beta_3}} \right] \quad (1)$$

where y is the daily integral of the flux of interest, y_0 is the base-value of y during the dormant season, x is day-of-year (DOY) for the first half of the year, and days until the end of the year for the second half of the year, x_0 is the DOY at half-maximum y (fitted), β_1 is the difference between peak and base y , β_2 is the difference between 75th and 25th percentiles of the time from base to peak y , and β_3 is a shape parameter. Parameters y_0 , x_0 , β_1 , β_2 and β_3 are estimated in model fitting. The universality of Eqn. (1) allows defining relatively simple transitions between a single active period and a single dormant period per year, but would also work in situations where multiple active periods or multiple levels of activity are the norm (please see Gu et al., in current volume).

Once the model parameters for spring development and fall recession are determined, the first and second derivatives of predicted fluxes can be used to singularly identify the turning points. The maximum and minimum of the first derivative identify the midpoints for spring and fall as the days with greatest change in the fluxes of interest (points C and F in Fig. 3). The period CF corresponds to the active season length according to the half-maximum (crossing x_0 , Eqn. 1) thresholding method used in remote sensing (see Sect. 1). The spring and fall maxima of the second derivative mark flux upturn date (point B, this and other names of the transition dates follow the nomenclature suggested by Gu et al. 2003) and flux retardation date (point G), whereas the minima mark the flux saturation date (point D) and flux downturn date (point E). Periods between BD, DE and EG mark the length of flux development, peak flux, and flux recession periods (LFD, LPF and LFR, respectively). Active season length can be defined in different ways, as the period between points A and H (e.g. as suggested by Gu et al. 2003), B and G, or C and F. In the current study we found greater and more consistent differences in the period defined by half-maximum points (C and F) and the extended active season (period BG) than the one defined by AH. We will denote the respective active season lengths as ASL^{x_0} , ASL^{BG} , and ASL^{AH} . The slopes of regressions fitted to the predicted fluxes during phases BD and EG give us the rate of flux development (RD) and the rate of flux retardation (RR), respectively. To illustrate the range of variability of various phenological turning points, the duration of different stages, and the differences between GEP and ER at the same stand, Fig. 4 depicts the seasonal dynamics of the fluxes, the fitted Weibull distribution function and its first and second derivatives in the conifer chronosequence.

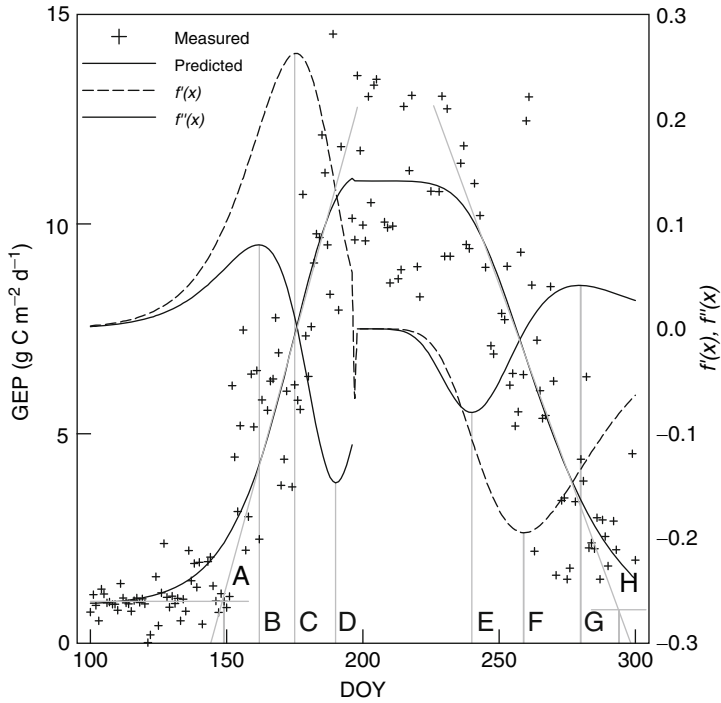


Fig. 3 Seasonal course of gross ecosystem productivity (GEP), and the phenological transition points (denoted with letters, A–H) as defined by the extremes of the first and second derivatives of the fitted cumulative Weibull functions Eqn. (1). The scale of the second derivative is enhanced tenfold for visual clarity. See text for details.

2.3 Requirements for Data Quality and Level of Integration

The seasonality of fluxes can be assessed from different types of daily data – daily maximum values, daily totals or normalized flux capacities (e.g. maximum photosynthetic capacity, P_{max} , or temperature-normalized base respiration, R_{10}). In the current study, we use daily integrals because of their greater robustness, whereas earlier studies have analyzed the changes in daily maximum values (Falge et al. 2002; Gu et al. 2003). Daily integrals require prior gapfilling and may potentially be affected by model assumptions, but such bias can be evaluated using established procedures (Moffat et al. 2007). Both data types may be sensitive to extended periods of adverse weather if it suppresses flux capacities. However, brief periods of a few days that do not reverse flux development, as well as periods of missing data do not significantly affect the phenological parameters. The parameters can be

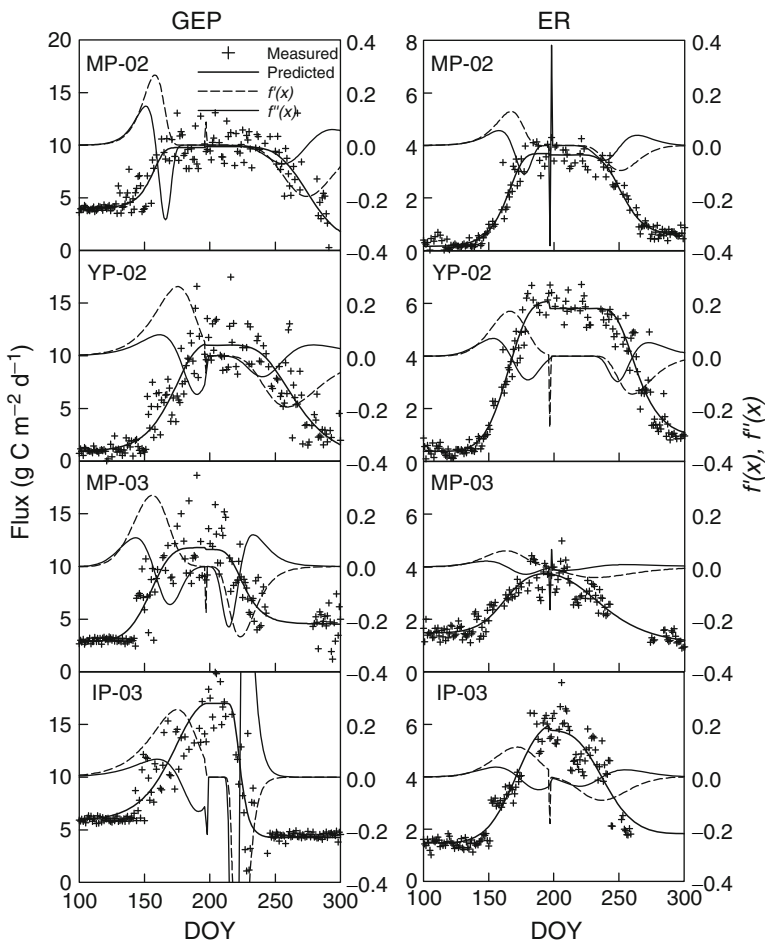


Fig. 4 Seasonal dynamics of GEP and ER in three different red pine stands, measured in 2002 and 2003. Overlaid with daily fluxes are the fitted Weibull function, and its 1st and 2nd derivatives.

estimated even with a sizeable proportion of missing data, as long as the transition points are represented.

Theoretically, the flux capacities should minimize the influence of environmental variability, providing the smoothest seasonal change curve. However, our tests of using normalized flux capacities (P_{\max} , R_{10}) to evaluate the seasonality of ecosystem carbon exchange showed that these parameters were not robust. For example, estimating ASL from changes in R_{10} resulted in significantly shorter ASL (by nearly 2 months; data not shown) than when estimating it from daily total ER. Other weaknesses of the parameter-based approach include that R_{10} is not estimable independently, but is closely related to the temperature sensitivity parameter of the

temperature response model (Noormets et al. 2008), and the data must often be grouped by more than a single day to achieve stable parameter estimates. Therefore, we can not recommend that the parameters of the light and temperature response models commonly used in gapfilling eddy covariance data be used for evaluating phenological transitions. It should also be emphasized that diurnal changes in fluxes may confound with detecting phenological changes, and their influence on the analysis should be minimized.

2.4 Robustness of Parameter Estimates

The robustness of the phenological parameter estimates was evaluated using Monte Carlo analysis. We treated the first fitted model as the ideal data, and added noise by sampling with replacement from the observed population of residuals. Fitting new Weibull functions to 1,000 of these synthetic datasets gave us 95% confidence intervals for the derived phenological parameters on the scale of 0.1–0.4 days. While tightly constrained, the parameters were sensitive to the temporal structure of the synthetic error. The variance in C fluxes increases with increasing flux magnitude (Hollinger and Richardson 2005) and therefore, overestimating the variance during low fluxes, i.e. during the dormant period, could lead to unrealistic seasonal dynamics in the synthetic data. To avoid this, the error must be sampled from the appropriate subpopulation. This, however, leads to a circular approach because we want to use the synthetic data to draw inferences about the seasonality, but we must define the seasons in order to sample the residuals.

2.5 Statistical Analyses

The parameters of the Weibull function were estimated with a nonlinear curve fitting procedure (PROC NLIN, SAS 9). The significance of forest type and year on the phenological parameters was evaluated with Tukey's post-hoc tests on least squares means in ANOVA framework (PROC MIXED), and the effects of stand age, leaf area index (LAI) and basal area (BA) were evaluated with regression analysis (PROC REG). All significant effects we defined at $p < 0.05$ level, unless noted otherwise. The relative effects of age, year and forest type were determined with a stepwise regression (PROC REG), with both entry and staying p-values at 0.15. It should be noted that measuring the younger sites in separate years in the face of large year-to-year variation restricts the level of confidence with which the conclusions can be drawn about age-related changes. However, some strong trends that emerge in the current study can be further tested on longer data series when they become available.

3 Results

3.1 Main Sources of Variation

The fitted model explained the spring and fall changes better for ER (average R^2 across sites 0.92 in spring and 0.93 in fall) than GEP (average $R^2 = 0.87$ (spring) and 0.89 (fall)). No difference was observed among age classes. The primary source of variability of phenological parameters among the eight site-years was interannual difference in weather conditions (Table 2), leading to 29 ± 10 days longer ASL_{GEP}^{x0} ($t_{1,6} = 3.0$, $P = 0.024$) and 24 ± 5 days longer ASL_{ER}^{x0} ($t_{1,6} = 4.65$, $P = 0.004$) in 2002 than 2003. This was attributed to warmer autumn and later leaf fall in the former, whereas the differences in SOS were small (2.0 ± 3.8 and 0.6 ± 5.9 days for SOS_{GEP} and SOS_{ER} , respectively) and not statistically significant (Fig. 5). Interestingly, significant differences between the 2 years were also observed in LPF and ASL^{BG} , whereas those in ASL^{AH} varied by site. The age-related trends were significant for LFD_{GEP} and LPF_{GEP} indicating that mature stands developed faster and maintained peak GEP longer than the young stands. ASL_{ER} , however, started later and ended more gradually in mature than young stands (Table 2). Our initial hypothesis of longer ASL in young than mature stands did not prove true (Fig. 5), even though RD_{ER} , RR_{ER} and RR_{GEP} were greater in the young than mature stands. These change rates and ASL_{ER}^{x0} and EOS_{ER} were narrowly constrained in the mature but not young stands. The expected dichotomy between the deciduous and conifer stands was observed only for GEP (mean ASL_{GEP}^{x0} of 80 ± 3 days in hardwoods and 87 ± 3 days in conifers), whereas ASL_{ER}^{x0} was 15 ± 6 days longer in hardwood than conifer stands. No other consistent differences were detected between the forest types.

Partitioning the relative contributions of age and year using a stepwise regression showed that the most significant source of variation for GEP seasonality was stand age, whereas interannual weather variability dominated the seasonality of ER (Table 3). Most age-related differences were also significant when expressed on

Table 2 Probability of type I error of significant difference in phenological parameters among age classes and years (both direct and interactive effects). Model denominator degrees of freedom = 6

	GEP			ER		
	Age	Year	Age \times Year	Age	Year	Age*Year
SOS	0.120	0.534	0.142	0.023	0.885	0.032
EOS	0.329	0.059	0.839	0.071	0.023	0.015
ASL^{x0}	0.055	0.012	0.281	0.875	0.001	0.009
ASL^{AH}	0.163	0.055	0.526	0.406	0.029	0.002
ASL^{BG}	0.087	0.024	0.414	0.669	0.009	0.006
LPF	0.043	0.012	0.525	0.298	0.0004	0.205
LFD	0.042	0.501	0.171	0.184	0.305	0.024
LFR	0.450	0.689	0.905	0.407	0.001	0.050
RD	0.704	0.218	0.198	0.094	0.466	0.206
RR	0.053	0.085	0.178	0.027	0.518	0.456

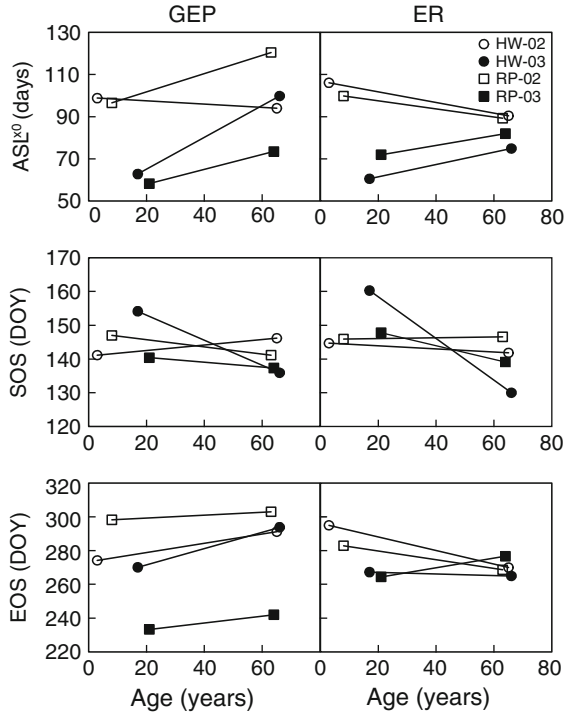


Fig. 5 Active season length (ASL^{x0}), start of active season (SOS), and end of active season (EOS) for gross ecosystem productivity (GEP) and ecosystem respiration (ER) in different-aged hardwood (HW) and conifer (RP) stands during 2 years (2002 and 2003). The 95% confidence intervals for all phenological indices were 0.1–0.4 days, as estimated with Monte Carlo analysis. That is, all visual differences on the figures are statistically significant in terms of precision of calculation. The significance of interannual and age-related differences, however, was derived from the mean parameters for every site-year.

Table 3 Adjusted coefficients of determination (and corresponding P-values) of stepwise regression models for the dependence of phenological parameters on age and year

	GEP		ER	
	Age	Year	Age	Year
SOS			0.35 (0.13)	
EOS	0.42 (0.08)			
ASL ^{x0}				0.73 (<0.01)
ASL ^{AH}	0.39 (0.10)			
ASL ^{BG}		0.48 (0.06)		0.38 (0.10)
LPF	0.21 (0.10)	0.52 (0.04)		0.91 (<0.01)
LFD	0.42 (0.08)			
LFR				0.86 (<0.01)
RD				
RR	0.98 (<0.01)		0.59 (0.03)	

LAI or BA basis (not shown). However, sometimes age integrated the site characteristics better than the other properties. For example, the intermediate and mature stands had comparable LAI, and it was a poor scalar for resolving their functional differences.

3.2 *Start, End and Length of Active Season (ASL)*

The among-stand differences in ASL_{GEP}^{x0} were greatest by year (in conifers over 50 days) and by forest type (Figs. 4 and 5). There were large year-to-year differences in the ASL_{ER}^{x0} in young stands in both forest types, whereas the mature stands were relatively consistent both between years and between forest types. In both years, SOS_{ER} (but not SOS_{GEP}) was earlier in mature hardwood than conifer stands. Whether this is due to the more open canopy and faster surface warming or greater metabolic activity associated with foliage development in hardwood than conifer stands remains to be elucidated. In young stands, SOS_{ER} was more consistent than SOS_{GEP} . The contiguous CUP (not shown) was longer in mature than young hardwood stands.

The EOS_{GEP} was similar between years in the hardwood stands, and showed consistent age-related differences, with 5–10 days earlier EOS_{GEP} in young than mature stands. However, the contrast between different years was big in the conifer stands, where EOS_{GEP} differed by over 2 months. This also contrasts with the consistency of EOS_{ER} in all mature stands. EOS_{ER} was within 5 days between the 2 years in both mature hardwood and conifer stands. Overall, SOS was earlier and EOS later (with the exception of EOS_{ER} in 2002) in mature than young stands.

3.3 *The Duration and Rate of Change of Flux Transitions*

The length of the flux development period decreased with age for GEP (LFD_{GEP} ; Fig. 6), whereas the age-related trends in LFD_{ER} varied by year (Table 2). Both GEP and ER had significantly longer LPF in 2002 than 2003, and LPF_{GEP} also increased with stand age (Table 2). The length of flux recession period (LFR) exhibited significant interannual differences for ER, but not for GEP (Table 2), whereas the rate of recession (RR) differed among years in GEP. Both RR_{GEP} and RR_{ER} were greater in young than mature stands.

The rates of flux development in spring were relatively constant for both GEP (RD_{GEP}) and ER (RD_{ER} ; Fig. 7; Table 2), with the exception of IH which had nearly threefold higher RD_{ER} than the other stands. The rates of recession (RR) were consistently greater in the young than mature stands. The $|RD|$ were greater than $|RR|$ in the mature but not in the young stands. Both RD and RR were about twofold greater for GEP than ER, likely because of the greater change of magnitude from winter- to summertime fluxes. However, if this was the sole reason, the pattern should have

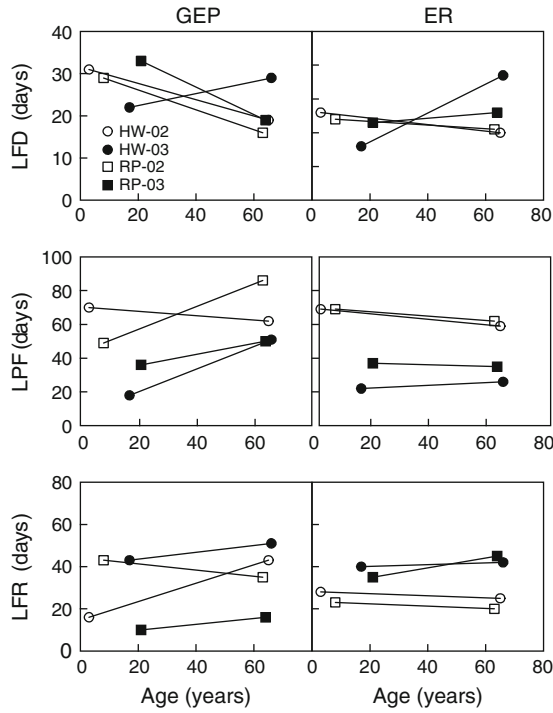


Fig. 6 Lengths of flux development (LFD), peak flux (LPF) and flux recession (LFR) periods of GEP and ER in different-aged hardwood (HW) and conifer (RP) stands during 2 years (2002 and 2003).

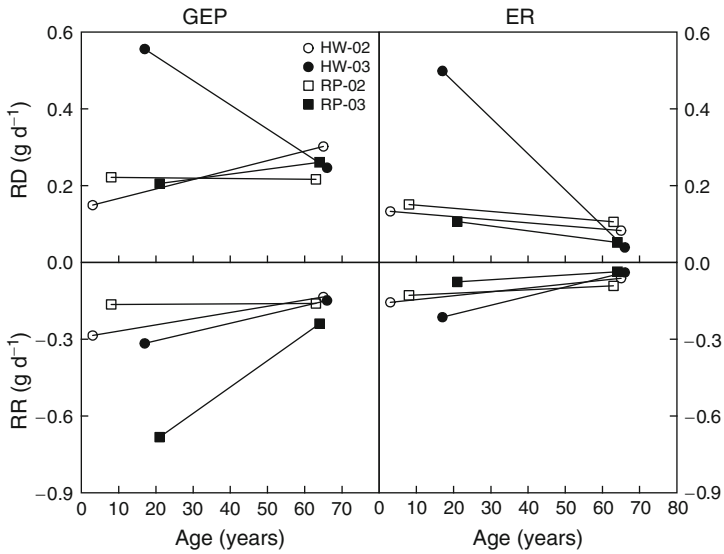


Fig. 7 Rates of development (RD, spring) and recession (RR, fall) of GEP and ER in different-aged- hardwood (HW) and conifer (RP) stands during 2 years (2002 and 2003).

Table 4 Regression parameters of ASL^{x0} vs. SOS, ASL^{x0} vs. EOS, RD vs. LFD, RR vs. LFR, LFR vs. LFD and RR vs. RD relationships

	GEP		ER	
	ASL = $\alpha + \beta \times \text{SOS}$	ASL = $\alpha + \beta \times \text{EOS}$	ASL = $\alpha + \beta \times \text{SOS}$	ASL = $\alpha + \beta \times \text{EOS}$
P-value	0.525	0.009	0.511	0.016
R ²	0.071	0.705	0.075	0.649
β	-0.95 ± 1.41	0.68 ± 0.18	-0.48 ± 0.69	1.14 ± 0.34
	RD = $\alpha + \beta \times \text{LFD}$	RR = $\alpha + \beta \times \text{LFR}$	RD = $\alpha + \beta \times \text{LFD}$	RR = $\alpha + \beta \times \text{LFR}$
P-value	0.376	0.062	0.094	0.685
R ²	0.132	0.466	0.397	0.029
β	-0.0070 ± 0.0073	0.0079 ± 0.0034	-0.015 ± 0.008	0.0011 ± 0.0026
	LFR = $\alpha + \beta \times \text{LFD}$	RR = $\alpha + \beta \times \text{RD}$	LFR = $\alpha + \beta \times \text{LFD}$	RR = $\alpha + \beta \times \text{RD}$
P-value	0.542	0.935	0.392	0.005
R ²	0.065	0.001	0.124	0.764
β	-0.62 ± 0.96	0.05 ± 0.60	0.54 ± 0.59	-0.37 ± 0.08

been consistently stronger in hardwood than conifer stands, which was not the case (Fig. 7). It is curious that the intermediate-aged stands exhibited the greatest deviation from otherwise relatively conservative RD and RR (Fig. 7). We hypothesize that the rapid change in the intermediate-aged stands could be related to their high homogeneity in species composition compared to other stands (Table 1), leading to highly synchronized on- and offset of vegetation activity.

The expected inverse relationship between the duration of the transition periods (LFD and LFR) and the rates of change (RD and RR) was seen for GEP (Table 4), but not for ER. This, along with the notable consistency of RD_{ER} and RR_{ER} in the mature stands, and their tight relationship with each other (Table 4) suggests that these change rates are under strong physiological control. Yet, the RD_{GEP} and RR_{GEP} did not exhibit clear relationship nor did LFD and LFR (Table 4).

4 Discussion

4.1 Variability of Phenological Phases

It is obvious that of the sources of variation considered in this study, the year-to-year differences dominated over those related to stand age (LAI and BA) and forest type on the seasonality of GEP and ER. The interannual differences were far greater than suggested by temperature sums. Although there were age-related differences in degree-day accumulation, consistent with Fig. 2, the much larger differences between years than individual sites did not lead to a comparable phenological response in each of the years and the parameterization of degree-day models (Chuine

2000) across years proved difficult (data not shown). The large interannual variability corroborates the observations of large year-to-year variability (up to 30 days) of SOS (Sun et al. 2003b) and ASL (Zha et al. 2008) in boreal forests. However, in the current study, among-stand differences in ASL^{x0} were more related to differences in EOS than SOS (Table 4). It has been found, however, that earlier SOS tends to stimulate GEP more than ER (e.g. Black et al. 2000; Jackson et al. 2001), whereas later EOS has the opposite effect (Piao et al. 2008), thus increasing and decreasing net productivity, respectively. Although the effect of EOS on ecosystem C balance may be smaller than that of SOS on per day basis, its effect can still be significant when the interannual variability of EOS exceeds that in SOS (Fig. 5). Furthermore, given that ASL_{ER} was more consistent in the mature than young stands (Fig. 5), whereas the magnitude of ER decreased with age in these systems (Noormets et al. 2007), the effect on net ecosystem C balance may be determined primarily by the changes in ASL_{GEP} . It is important to note that the expected differences in the SOS and ASL between the deciduous and conifer stands were not observed.

Although typically classified as northern temperate forests, the spring and fall transition dynamics of both GEP and ER suggest greater similarity with boreal than temperate forests. For temperate forests, LFD_{GEP} is usually found to be greater than LFR_{GEP} (Falge et al. 2002; Morecroft et al. 2003). For example, Morecroft et al. (2003) observed that the increase in leaf photosynthetic capacity (P_{max}) in an oak forest took longer (50–70 days after bud break) than the decline in the fall (14 days). In a study of forests from different climate zones, Falge et al. (2002) observed a similar pattern among temperate forests, whereas in the boreal zone $LFD_{GEP} < LFR_{GEP}$. Likewise, in the current study the mean $LFD < LFR$ for both GEP and ER ($LFR = 32.2 \pm 3.1$ and $LFD = 24.4 \pm 1.5$ days, $F_{1,38} = 2.29$, $p = 0.029$), although for a given site LFD and LFR were not well correlated (Table 4). Furthermore, the often proposed (e.g. DeForest et al. 2006; Falge et al. 2002) later cessation of ER in the fall compared to GEP was not observed in this study (Fig. 5). Likewise, the $|RD|$ and $|RR|$ did not systematically differ although there were individual stands exhibiting seasonal asymmetry in flux development (e.g. IP; Fig. 4). While RD_{ER} and RR_{ER} were highly correlated (Table 4), RD_{GEP} and RR_{GEP} were not. The latter contrasts with the findings of Gu et al. (2003), and might be related to the current study reflecting local variability, whereas Gu et al. addressed a broader latitudinal gradient. Comparing the relatively large differences in the flux change rates (RD and RR) in the young stands to the relative stability in the duration of the transition periods (LFD and LFR) suggests that any observed correlation might be mostly a reflection of the difference between the dormant season base flux and peak flux, as the LFD and LFR were strongly controlled by weather conditions (Table 2). It is unclear what controls the notable consistency of RD and RR as well as EOS_{ER} and ASL^{x0}_{ER} in the mature stands. Further research in this area is warranted, as ER plays a key role in affecting ecosystem net carbon balance, and its response to climate variability can be expected to be greater in the early stages of stand development (Fig. 5; Noormets et al. 2007).

4.2 Differences Between GEP and ER

The temporal dynamics of GEP and ER development were related, but clearly responded to different cues. The phenological indices of GEP exhibited consistent age-related variability, whereas differences in ER seasonality were mostly explained with those in weather (Table 3). The hypothesized systematic difference between ASL_{GEP} and ASL_{ER} due to later EOS_{ER} was not observed, because the temporary increase in ER following leaf fall did not affect points E and G (Fig. 3) and RR_{ER} derived from them. However, RD and RR were consistently about twofold greater for GEP than ER. This could partly be an artifact due to the greater absolute value of the GEP, but the longer LFD_{GEP} than LFD_{ER} suggested that this was not the only cause (Fig. 6). The variability of observed fluxes during the transition period was smaller in ER than GEP, but could be related to the considerable gapfilling of night-time data (Noormets et al. 2008).

4.3 Various Definitions of ASL

The variety and vagueness of the definitions of “growing season” could easily lead to the comparison of studies that use different approaches for delineating seasonality. In the current study, we have presented four different measures of ASL for each flux (ASL^{x0} , ASL^{AH} , ASL^{BG} , LPF). Some additional possibilities are described by Barr et al. in chapter “Climatic and Phenological Controls of the Carbon and Energy Balances of Three Contrasting Boreal Forest Ecosystems in Western Canada” in the current volume. Of the different measures of ASL, ASL^{x0} explained the most variation among stands, offering encouragement that the popular measures of half-maximum NDVI or EVI in remote sensing studies (Fisher et al. 2007; Schwartz et al. 2002) might also suit well for analyzing surface carbon fluxes.

Figure 8 shows that the different measures of ASL were generally well correlated, but the small-scale age-related differences did not always transfer. The carbon uptake period (CUP), the most commonly used measure of ASL in eddy covariance studies (Baldocchi et al. 2005; Churkina et al. 2005; Falge et al. 2002), was 79 (YH02), 133 (IH03), 131 (MH02) and 140 (MH03) days, and similar in scale to ASL^{AH} . However, YH02 had much shorter CUP than ASL^{AH}_{GEP} because of large ER and alternating sink and source periods during the ASL (see Noormets et al. 2007). The inclusion or exclusion of this site significantly affected the correlation coefficients between CUP and other measures of ASL (Table 5). The change in R^2 was smallest for LPF_{ER} indicating that the among-site differences in sink strength were strongly affected by the duration of peak respiration. We have discussed this in greater detail in the past (Noormets et al. 2007, 2008). As the discontinuity of CUP makes comparisons with ASL (which is continuous by definition) difficult to interpret, it is important that uniform standards be adopted for delineating the seasonality of different processes that would allow comparisons among studies. Currently, it is often not clearly defined if CUP includes source days ($NEE > 0$) during otherwise active canopy.

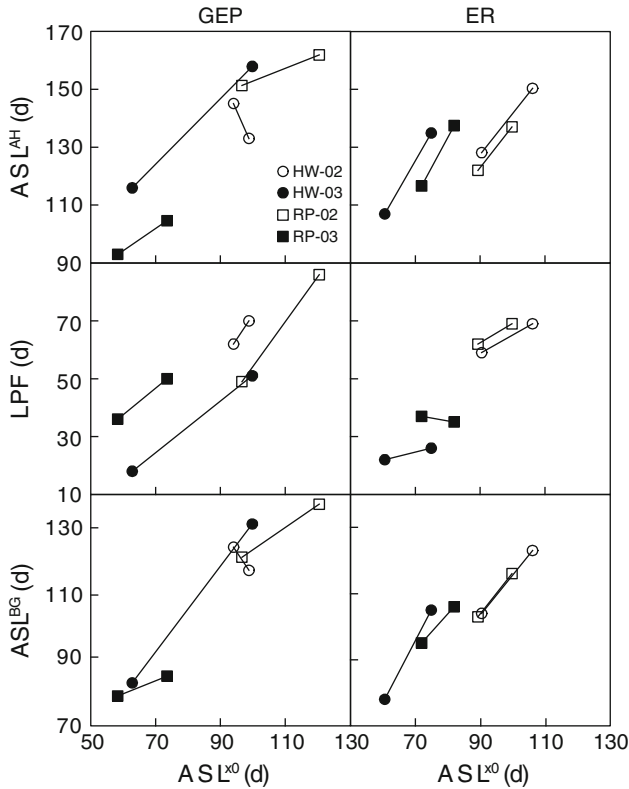


Fig. 8 Relationships between different measures of growing season length.

Table 5 Correlation coefficients between the contiguous carbon uptake period (CUP) and four measures of active season length for GEP and ER. Correlations were calculated for all hardwood stands and without YH02

	GEP		ER	
	All deciduous	w/o YH	All deciduous	w/o YH
ASL ^{x0}	-0.32	0.44	-0.80	-0.24
ASL ^{AH}	0.26	0.58	-0.70	0.52
ASL ^{BG}	-0.38	0.31	-0.76	-0.25
LPF	-0.56	0.07	-0.76	-0.60

4.4 Predicting Responses to Climate Change

The timing of phenological transitions and phases could affect ecosystem C budget when ER and GEP are affected differentially by the changing weather dynamics. The greatest proportion of variability was explained by interannual climate differences, far exceeding the influence of stand age and forest type. Given that the influence of

year was greater on the seasonality of ER than of GEP, it appears that the immediate implications for the regional carbon balance may be constrained by the stability of ASL_{ER} . While the literature suggests strong negative relationship between SOS and annual NEP (i.e. the later the SOS, the lower the NEP), in the current study most of the variability in ASL originated from EOS. Yet, detecting even the more conservative 7–10 day difference observed in the mature stands between the 2 years may require 10–12 year data record, assuming the 3.3–3.7 days per decade advance rate observed for trees (Estrella et al. 2007; Parmesan 2007). While several flux sites have attained such record, the analysis is further facilitated by the coordination and standardization under the global FLUXNET monitoring network. Given that interannual variation exceeds local among-sites differences, a network of sites with shorter individual record length is still well suited for the analysis of trends.

5 Conclusions

The largest proportion of variation in GEP and ER seasonality was explained by interannual variations in weather. The among-site differences in ASL were due to different EOS rather than SOS, with the latter being more consistent among sites, and less responsive to interannual climatic differences. However, this does not contradict the earlier conclusions of greater effect of unit change in SOS than EOS on annual carbon balance.

The seasonalities of GEP and ER differed in both timing and sensitivity to external factors. The age-related differences were stronger in the seasonality of GEP, whereas that of ER was dominated by interannual weather variability. The development and recession rates of fluxes were proportional to the difference between winter base and summer peak fluxes (i.e. $RD_{GEP} \approx 2 \times RD_{ER}$ and $RR_{GEP} \approx 2 \times RR_{ER}$).

The differences between deciduous and evergreen forest types were minimal, with marginally longer ASL_{GEP} in evergreen than deciduous stands, whereas ASL_{ER} was longer in the latter. The phenology of gas exchange suggests that these forests, typically classified as northern temperate stands, actually resemble boreal forests in terms of their flux development and recession dynamics.

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References

- Ahas, R., Aasa, A., Menzel, A., Fedotova, V.G. and Scheifinger, H. (2002) Changes in European spring phenology. *Int. J. Climatol.*, 22, 1727–1738.
- Amiro, B.D. (2001) Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest. *Global Change Biol.*, 7, 253–268.

- Amiro, B.D., Orchansky, A.L., Barr, A.G., Black, T.A., Chambers, S.D., Chapin III, F.S., Goulden, M.L., Litvak, M., Liu, H.P. and McCaughey, J.H. (2006) The effect of post-fire stand age on the boreal forest energy balance. *Agric. For. Meteorol.*, 140, 41–50.
- Aurela, M., Laurila, T. and Tuovinen, J.P. (2004) The timing of snow melt controls the annual CO₂ balance in a subarctic fen. *Geophys. Res. Lett.*, 31, art. no. L16119.
- Badeck, F.W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J. and Sitch, S. (2004) Responses of spring phenology to climate change. *New Phytol.*, 162, 295–309.
- Baldocchi, D.D., Black, T.A., Curtis, P.S., Falge, E., Fuentes, J.D., Granier, A., Gu, L., Knohl, A., Pilegaard, K., Schmid, H.P., Valentini, R., Wilson, K., Wofsy, S., Xu, L. and Yamamoto, S. (2005) Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data. *Int. J. Biometeorol.*, 49, 377–387.
- Baldocchi, D.D., Falge, E., Gu, L.H., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K.J., Evans, R., Fuentes, J.D., Goldstein, A.H., Katul, G., Law, B.E., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K. and Wofsy, S. (2001) FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull. Am. Meteorol. Soc.*, 82, 2415–2434.
- Barr, A.G., Black, T.A., Hogg, E.H., Griffis, T.J., Morgenstern, K., Kljun, N., Theede, A. and Nestic, Z. (2007) Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. *Global Change Biol.*, 13, 561–576.
- Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K. and Nestic, Z. (2004) Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agric. For. Meteorol.*, 126, 237–255.
- Beaubien, E.G. and Freeland, H.J. (2000) Spring phenology trends in Alberta, Canada: links to ocean temperature. *Int. J. Biometeorol.*, 44, 53–59.
- Beck, P.S.A., Atzberger, C., Hogda, K.A., Johansen, B. and Skidmore, A.K. (2006) Improved monitoring of vegetation dynamics at very high latitudes: A new method using MODIS NDVI. *Remote Sens. Environ.*, 100, 321–334.
- Bergeron, O., Margolis, H.A., Coursolle, C. and Giasson, M.-A. (2008) How does forest harvest influence carbon dioxide fluxes of black spruce ecosystems in eastern North America? *Agric. For. Meteorol.*, doi:10.1016/j.agrformet.2007.10.012, 148, 537–548.
- Black, T.A., Chen, W.J., Barr, A.G., Arain, M.A., Chen, Z., Nestic, Z., Hogg, E.H., Neumann, H.H. and Yang, P.C. (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophys. Res. Lett.*, 27, 1271–1274.
- Bogaert, J., Zhou, L., Tucker, C.J., Myneni, R.B. and Ceulemans, R. (2002) Evidence for a persistent and extensive greening trend in Eurasia inferred from satellite vegetation index data. *J. Geophys. Res. (D Atmos.)*, 107, 10.1029/2001JD001075.
- Bonan, G.B., Levis, S., Sitch, S., Vertenstein, M. and Oleson, K.W. (2003) A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. *Global Change Biol.*, 9, 1543–1566.
- Bond-Lamberty, B., Gower, S.T., Ahl, D.E. and Thornton, P.E. (2005a) Reimplementation of the Biome-BGC model to simulate successional change. *Tree Physiol.*, 25, 413–424.
- Bond-Lamberty, B., Wang, C.K. and Gower, S.T. (2005b) Spatiotemporal measurement and modeling of stand-level boreal forest soil temperatures. *Agric. For. Meteorol.*, 131, 27–40.
- Cao, M.K., Prince, S.D., Small, J. and Goetz, S.J. (2004) Remotely sensed interannual variations and trends in terrestrial net primary productivity 1981–2000. *Ecosystems*, 7, 233–242.
- Carrara, A., Kowalski, A., Neiryck, J., Janssens, I.A., Yuste, J.C. and Ceulemans, R. (2003) Net ecosystem CO₂ exchange of mixed forest in Belgium over 5 years. *Agric. For. Meteorol.*, 119, 209–227.
- Chmielewski, F.M. and Rötzer, T. (2001) Response of tree phenology to climate change across Europe. *Agric. For. Meteorol.*, 108, 101–112.
- Chuine, I. (2000) A unified model for budburst of trees. *J. Theor. Biol.*, 207, 337–347.
- Chuine, I. and Beaubien, E.G. (2001) Phenology is a major determinant of tree species range. *Ecol. Lett.*, 4, 500–510.

- Churkina, G., Schimel, D., Braswell, B.H. and Xiao, X. (2005) Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biol.*, 11, 1777–1787.
- DeForest, J.L., Noormets, A., Tenney, G., Sun, G., McNulty, S.G. and Chen, J. (2006) Phenophases in an oak-dominated forest alter the soil respiration-temperature relationship. *Int. J. Biometeorol.*, 51, 135–144.
- Desai, A.R., Noormets, A., Bolstad, P.V., Chen, J., Cook, B.D., Davis, K.J., Euskirchen, E.S., Gough, C., Martin, J.M., Ricciuto, D.M., Schmid, H.P., Tang, J. and Wang, W. (2008) Influence of vegetation type, stand age and climate on carbon dioxide fluxes across the Upper Midwest, USA: Implications for regional scaling of carbon flux. *Agric. For. Meteorol.*, 148, 288–308.
- Devine, W.D. and Harrington, C.A. (2007) Influence of harvest residues and vegetation on micro-site soil and air temperatures in a young conifer plantation. *Agric. For. Meteorol.*, 145, 125–138.
- Estrella, N., Sparks, T.H. and Menzel, A. (2007) Trends and temperature response in the phenology of crops in Germany. *Global Change Biol.*, 13, 1737–1747.
- Ewers, B.E., Gower, S.T., Bond-Lamberty, B. and Wang, C.K. (2005) Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant Cell Environ.*, 28, 660–678.
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jensen, N.-O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B.E., Meyers, T., Moncrieff, J., Moors, E., Munger, J.W., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K. and Wofsy, S. (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. For. Meteorol.*, 107, 43–69.
- Falge, E., Baldocchi, D.D., Tenhunen, J., Aubinet, M., Bakwin, P.S., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K.J., Elbers, J.A., Goldstein, A.H., Grelle, A., Granier, A., Guddmundsson, J., Hollinger, D., Kowalski, A.S., Katul, G., Law, B.E., Malhi, Y., Meyers, T., Monson, R.K., Munger, J.W., Oechel, W., Paw U, K.T., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Valentini, R., Wilson, K. and Wofsy, S. (2002) Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agric. For. Meteorol.*, 113, 53–74.
- Field, C.B., Lobell, D.B., Peters, H.A. and Chiariello, N.R. (2007) Feedbacks of terrestrial ecosystems to climate change. *Annu. Rev. Environ. Res.*, 32, 1–29.
- Fisher, J.I., Richardson, A.D. and Mustard, J.F. (2007) Phenology model from surface meteorology does not capture satellite-based greenup estimations. *Global Change Biol.*, 13, 707–721.
- Fitter, A.H. and Fitter, R.S.R. (2002) Rapid Changes in Flowering Time in British Plants. *Science*, 296, 1689–1691.
- Gore, A. (2006) *An Inconvenient Truth: The Planetary Emergency of Global Warming and What We Can Do About It*. Rodale Books: New York.
- Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C. and Wofsy, S.C. (1996) Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science*, 271, 1576–1578.
- Goulden, M.L., Winston, G.C., McMillan, A.M.S., Litvak, M.E., Read, E.L., Rocha, A.V. and Elliot, J.R. (2006) An eddy covariance mesonet to measure the effect of forest age on land-atmosphere exchange. *Global Change Biol.*, 12, 2146–2162.
- Groisman, P.Y., Karl, T.R. and Knight, R.W. (1994) Observed impact of snow cover on the heat balance and the rise of continental spring temperatures. *Science*, 263, 198–200.
- Gu, L., Post, W.M., Baldocchi, D., Black, T.A., Verma, S.B., Vesala, T. and Wofsy, S.C. (2003). Phenology of vegetation photosynthesis. In: Schwartz, M.D. (Ed.) *Phenology: An Integrated Environmental Science*. Kluwer; Dordrecht, pp. 467–485.
- Hansen, J., Sato, M., Lacis, A. and Ruedy, R. (1997) The missing climate forcing. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 352, 231–240.
- Hargrove, W.W. and Hoffman, F.M. (2005) Potential of multivariate quantitative methods for delineation and visualization of ecoregions. *Environ. Manage.*, 34, S39–S60.

- Hegerl, G.C., vonStorch, H., Hasselmann, K., Santer, B.D., Cubasch, U. and Jones, P.D. (1996) Detecting greenhouse-gas-induced climate change with an optimal fingerprint method. *J. Clim.*, 9, 2281–2306.
- Heide, O.M. (2003) High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiol.*, 23, 931–936.
- Heijmans, M.M.P.D., Arp, W.J. and Chapin, F.S. (2004) Carbon dioxide and water vapour exchange from understory species in boreal forest. *Agric. For. Meteorol.*, 123, 135–147.
- Hollinger, D.Y., Aber, J.D., Dail, B., Davidson, E.A., Goltz, S.M., Hughes, H., Leclerc, M.Y., Lee, J.T., Richardson, A.D., Rodrigues, C., Scott, N.A., Achuatavariar, D. and Walsh, J. (2004) Spatial and temporal variability in forest-atmosphere CO₂ exchange. *Global Change Biol.*, 10, 1689–1706.
- Hollinger, D.Y. and Richardson, A.D. (2005) Uncertainty in eddy covariance measurements and its application to physiological models. *Tree Physiol.*, 25, 873–885.
- Houghton, R.A., Davidson, E.A. and Woodwell, G.M. (1998) Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance. *Global Biogeochem. Cycles*, 12, 25–34.
- IPCC (2007). *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Pachauri, R.K. and Reisinger, A. (Eds.), IPCC, Geneva, Switzerland, pp.104.
- Jackson, R.B., Lechowicz, M.J., Li, X. and Mooney, H.A. (2001). Phenology, growth, and allocation in global terrestrial productivity. In: Saugier, B., Roy, J. and Mooney, H.A. (Eds.), *Terrestrial Global Productivity: Past, Present, and Future.* Academic: San Diego, CA, pp. 61–82.
- Kathuroju, N., White, M.A., Symanzik, J., Schwartz, M.D., Powell, J.A. and Nemani, R.R. (2007) On the use of the advanced very high resolution radiometer for development of prognostic land surface phenology models. *Ecol. Model.*, 201, 144–156.
- Keeling, C.D., Chin, J.F.S. and Whorf, T.P. (1996) Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature*, 382, 146–149.
- Kramer, K., Leinonen, I., Bartelink, H.H., Berbigier, P., Borghetti, M., Bernhofer, C., Cienciala, E., Dolman, A.J., Froer, O., Gracia, C.A., Granier, A., Grünwald, T., Hari, P., Jans, W., Kellomäki, S., Loustau, D., Magnani, F., Markkanen, T., Matteucci, G., Mohren, G.M.J., Moors, E., Nissinen, A., Peltola, H., Sabate, S., Sanchez, A., Sontag, M., Valentini, R. and Vesala, T. (2002) Evaluation of six process-based forest growth models using eddy-covariance measurements of CO₂ and H₂O fluxes at six forest sites in Europe. *Global Change Biol.*, 8, 213–230.
- Kramer, K., Leinonen, I. and Loustau, D. (2000) The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *Int. J. Biometeorol.*, 44, 67–75.
- Lenton, T.M. (2000) Land and ocean carbon cycle feedback effects on global warming in a simple Earth system model. *Tellus B*, 52, 1159–1188.
- Linderholm, H.W. (2006) Growing season changes in the last century. *Agric. For. Meteorol.*, 137, 1–14.
- Lu, P., Yu, Q., Liu, J. and Lee, X. (2006) Advance of tree-flowering dates in response to urban climate change. *Agric. For. Meteorol.*, 138, 120–131.
- Mäkelä, A., Hari, P., Berninger, F., Hänninen, H. and Nikinmaa, E. (2004) Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. *Tree Physiol.*, 24, 369–376.
- Mäkelä, A., Pulkkinen, M., Kolari, P., Lagergren, F., Berbigier, P., Lindroth, A., Loustau, D., Nikinmaa, E., Vesala, T. and Hari, P. (2008) Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. *Global Change Biol.*, 14, 92–108.
- Meir, P., Cox, P. and Grace, J. (2006) The influence of terrestrial ecosystems on climate. *Trends Ecol. Evol.*, 21, 254–260.
- Menzel, A. (2002) Phenology: Its importance to the global change community – An editorial comment. *Clim. Change*, 54, 379–385.
- Menzel, A. (2003) Plant phenological anomalies in Germany and their relation to air temperature and NAO. *Clim. Change*, 57, 243–263.

- Menzel, A. and Fabian, P. (1999) Growing season extended in Europe. *Nature*, 397, 659–659.
- Moffat, A.M., Papale, D., Reichstein, M., Hollinger, D.Y., Richardson, A.D., Barr, A.G., Beckstein, C., Braswell, B.H., Churkina, G., Desai, A.R., Falge, E., Gove, J.H., Heimann, M., Hui, D., Jarvis, A.J., Kattge, J., Noormets, A. and Stauch, V.J. (2007) Comprehensive comparison of gap filling techniques for eddy covariance net carbon fluxes. *Agric. For. Meteorol.*, 147, 209–232.
- Morecroft, M.D., Stokes, V.J. and Morison, J.I.L. (2003) Seasonal changes in the photosynthetic capacity of canopy oak (*Quercus robur*) leaves: the impact of slow development on annual carbon uptake. *Int. J. Biometeorol.*, 47, 221–226.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. and Nemani, R.R. (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, 386, 698–702.
- Noormets, A., Chen, J. and Crow, T.R. (2007) Age-dependent changes in ecosystem carbon fluxes in managed forests in northern Wisconsin, USA. *Ecosystems*, 10, 187–203.
- Noormets, A., Desai, A.R., Cook, B.D., Euskirchen, E.S., Ricciuto, D.M., Davis, K.J., Bolstad, P.V., Schmid, H.P., Vogel, C.V., Carey, E.V., Su, H.B. and Chen, J. (2008) Moisture sensitivity of ecosystem respiration: Comparison of 14 forest ecosystems in the Upper Great Lakes Region, USA. *Agric. For. Meteorol.*, 148, 216–230.
- Norby, R.J., Hartz-Rubin, J.S. and Verbrugge, M.J. (2003) Phenological responses in maple to experimental atmospheric warming and CO₂ enrichment. *Global Change Biol.*, 9, 1792–1801.
- Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Zulueta, R.C., Hinzman, L. and Kane, D. (2000) Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, 406, 978–981.
- Olesen, J.E., Carter, T.R., Diaz-Ambrona, C.H., Fronzek, S., Heidmann, T., Hickler, T., Holt, T., Quemada, M., Ruiz-Ramos, M., Rubaek, G.H., Sau, F., Smith, B. and Sykes, M.T. (2007) Uncertainties in projected impacts of climate change on European agriculture and terrestrial ecosystems based on scenarios from regional climate models. *Clim. Change*, 81, 123–143.
- Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biol.*, 13, 1860–1872.
- Penuelas, J. and Filella, I. (2001) Responses to a Warming World. *Science*, 294, 793–794.
- Penuelas, J., Filella, I. and Comas, P. (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biol.*, 8, 531–544.
- Piao, S.L., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luysaert, S., Margolis, H., Fang, J.Y., Barr, A., Chen, A.P., Grelle, A., Hollinger, D.Y., Laurila, T., Lindroth, A., Richardson, A.D. and Vesala, T. (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, 451, 49–53.
- Reed, B.C., Brown, J.F., VanderZee, D., Loveland, T.L., Merchant, J.W. and Ohlen, D.O. (1994) Measuring phenological variability from satellite imagery. *J. Veg. Sci.*, 5, 703–714.
- Richter, D.D., Markewitz, D., Trumbore, S.E. and Wells, C.G. (1999) Rapid accumulation and turnover of soil carbon in a re-establishing forest. *Nature*, 400, 56–58.
- Santer, B.D., Taylor, K.E., Wigley, T.M.L., Johns, T.C., Jones, P.D., Karoly, D.J., Mitchell, J.F.B., Oort, A.H., Penner, J.E., Ramaswamy, V., Schwarzkopf, M.D., Stouffer, R.J. and Tett, S. (1996) A search for human influences on the thermal structure of the atmosphere. *Nature*, 382, 39–46.
- Schaefer, K., Denning, A.S. and Leonard, O. (2005) The winter Arctic oscillation, the timing of spring, and carbon fluxes in the Northern Hemisphere. *Global Biogeochem. Cycle*, 19.
- Schlesinger, W.H. and Lichten, J. (2001) Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. *Nature*, 411, 466–469.
- Schwartz, M.D., Ahas, R. and Aasa, A. (2006) Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biol.*, 12, 343–351.
- Schwartz, M.D. and Chen, Z.Q. (2002) Examining the onset of spring in China. *Clim. Res.*, 21, 157–164.
- Schwartz, M.D., Reed, B.C. and White, M.A. (2002) Assessing satellite-derived start-of-season measures in the conterminous USA. *Int. J. Climatol.*, 22, 1793–1805.

- Schwartz, M.D. and Reiter, B.E. (2000) Changes in North American spring. *Int. J. Climatol.*, 20, 929–932.
- Sherry, R.A., Zhou, X., Gu, S., Arnone, J.A., III, Schimel, D.S., Verburg, P.S., Wallace, L.L. and Luo, Y. (2007) Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences*, 104, 198–202.
- Smith, N.V., Saatchi, S.S. and Randerson, J.T. (2004) Trends in high northern latitude soil freeze and thaw cycles from 1988 to 2002. *J. Geophys. Res.*, 109.
- Stott, P.A., Tett, S.F.B., Jones, G.S., Allen, M.R., Mitchell, J.F.B. and Jenkins, G.J. (2000) External control of 20th century temperature by natural and anthropogenic forcings. *Science*, 290, 2133–2137.
- Suni, T., Berninger, F., Markkanen, T., Keronen, P., Rannik, Ü. and Vesala, T. (2003a) Interannual variability and timing of growing-season CO₂ exchange in a boreal forest. *J. Geophys. Res.*, 108, No. D9, 4265. doi:10.1029/2002JD002381, 2.1–2.8.
- Suni, T., Berninger, F., Vesala, T., Markkanen, T., Hari, P., Mäkelä, A., Ilvesniemi, H., Hanninen, H., Nikinmaa, E., Huttula, T., Laurila, T., Aurela, M., Grelle, A., Lindroth, A., Arneth, A., Shi-bistova, O. and Lloyd, J. (2003b) Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biol.*, 9, 1410–1426.
- Tape, K., Sturm, M. and Racine, C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biol.*, 12, 686–702.
- Walther, G.-R., Post, E., Convey, P., Menzels, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. and Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, 416, 389–395.
- White, M.A., Hoffman, F., Hargrove, W.W. and Nemani, R.R. (2005) A global framework for monitoring phenological responses to climate change. *Geophys. Res. Lett.*, 32, Art. No. L04705.
- White, M.A. and Nemani, A.R. (2003) Canopy duration has little influence on annual carbon storage in the deciduous broad leaf forest. *Global Change Biol.*, 9, 967–972.
- Yang, F., Ichii, K., White, M.A., Hashimoto, H., Michaelis, A.R., Votava, P., Zhu, A.X., Huete, A., Running, S.W. and Nemani, R.R. (2007) Developing a continental-scale measure of gross primary production by combining MODIS and AmeriFlux data through Support Vector Machine approach. *Remote Sens. Environ.*, 110, 109–122.
- Zha, T., Barr, A.G., Black, T.A., McCaughey, H., Bhatti, J.S., Hawthorne, I., Krishnan, P., Kidston, J., Saigusa, N., Shashkov, A. and Nesic, Z. (2008) Carbon sequestration in boreal Jack pine stands following harvesting. *Global Change Biol.*, 15, 1475–1487.
- Zhang, X.Y., Friedl, M.A., Schaaf, C.B., Strahler, A.H., Hodges, J.C.F., Gao, F., Reed, B.C. and Huete, A. (2003) Monitoring vegetation phenology using MODIS. *Remote Sens. Environ.*, 84, 471–475.