Agricultural and Forest Meteorology 169 (2013) 156–173

Contents lists available at SciVerse ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Review

Climate change, phenology, and phenological control of vegetation feedbacks to the climate system

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ARTICLE INFO

Article history:
Received 14 June 2012
Received in revised form 3 September 2012
Accepted 11 September 2012

Keywords:
Autumn senescence
Biosphere–atmosphere interactions
Budburst
Carbon cycle
Climate change
Global warming
Models
Phenology
Seasonality
Spring onset

ABSTRACT

Vegetation phenology is highly sensitive to climate change. Phenology also controls many feedbacks of vegetation to the climate system by influencing the seasonality of albedo, surface roughness length, canopy conductance, and fluxes of water, energy, CO_2 and biogenic volatile organic compounds. In this review, we first discuss the environmental drivers of phenology, and the impacts of climate change on phenology, in different biomes. We then examine the vegetation-climate feedbacks that are mediated by phenology, and assess the potential impact on these feedbacks of shifts in phenology driven by climate change. We finish with an overview of phenological modeling and we suggest ways in which models might be improved using existing data sets. Several key weaknesses in our current understanding emerge from this analysis. First, we need a better understanding of the drivers of phenology, particularly in under-studied biomes (e.g. tropical forests). We do not have a mechanistic understanding of the role of photoperiod, even in well-studied biomes. In all biomes, the factors controlling senescence and dormancy are not well-documented. Second, for the most part (i.e. with the exception of phenology impacts on CO_2 exchange) we have only a qualitative understanding of the feedbacks between vegetation and climate that are mediated by phenology. We need to quantify the magnitude of these feedbacks, and ensure that they are accurately reproduced by models. Third, we need to work towards a new understanding of phenological processes that enables progress beyond the modeling paradigms currently in use. Accurate representation of phenological processes in models that couple the land surface to the climate system is particularly important, especially when such models are being used to predict future climate.

Contents

1. Introduction 157
2. Impacts of climate change on phenology 158
   2.1. Temperate forests 158
   2.2. Boreal and subalpine forests 159
   2.3. Subalpine meadows and Arctic and alpine tundra 160
   2.4. Tropical forests 160
   2.5. Mediterranean wood-, shrub- and grasslands 160
   2.6. Subtropical deserts 161
3. Feedbacks of vegetation to climate that are mediated by phenology 161
   3.1. Albedo 161
   3.2. Surface roughness length 162
   3.3. Canopy conductance 162

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0168-1923/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.agrformet.2012.09.012

3.4. Water and energy fluxes, and the surface energy budget 162
3.5. Photosynthesis and CO_2 fluxes 164
3.5.1. Phenological control of spatial patterns of C uptake 164
3.5.2. Phenological control of interannual patterns of C uptake 165
3.5.3. Climate change impacts on phenology: implications for C uptake 165
3.6. Fluxes of biogenic volatile organic compounds 166
4. Modeling and forecasting phenology 167
5. Conclusion 169
Acknowledgments 169
References 169

1. Introduction

The International Biological Program (IBP) defined phenology as "the study of the timing of recurrent biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species" (Lieth, 1974). This definition has been widely accepted, and repeated throughout the literature. It promotes a broad view of phenology, in that unlike other definitions (e.g. Rathcke and Lacey, 1985; Demaree and Rutishauser, 2009; Visser et al., 2010; see also Forrest and Miller-Rushing, 2010), it is not restricted solely to life cycle events (e.g. flowering of plants, breeding of animals), or to phenomena that are directly observable. Thus, the seasonality of photosynthesis in winter dormant/summer active ecosystems is also phenological in nature, as are the annual cycles of other ecosystem processes (e.g. Noormets et al., 2009). Explicit in this definition is an emphasis on understanding both the relationship of phenological events or transitions to environmental forcing, and the relationships of two or more phenological events to each other. Although almost 40 years old, the IBP definition of phenology is progressive and forward-thinking, placing phenology in the field of systems ecology (as noted by Lieth, 1976), as well as biometeorology, environmental biology, and physiological ecology. This broad interdisciplinary purview sets the stage for the rebirth of phenology, decades later, as a critical element of global change research.

As a field unto itself, phenology has historically been viewed with some disdain—perhaps the pursuit of amateur naturalists, but certainly not cutting-edge science. This perception is reinforced by the countless examples of phenological data that were recorded by individuals and families. For example, Henry David Thoreau (1817–1862) famously compiled a vast catalog of phenological observations in the woods around Concord, MA (Miller-Rushing and Primack, 2008). Notable also are the two centuries of Marsham family records (described in Sparks and Menzel, 2002). In the past, phenological research focused on the development of a "calendar of the seasons" (Leopold and Jones, 1947; Stoller, 1956). Even today, and perhaps because of the inherent human fascination with weather and the passing of the seasons, phenology is commonly referred to in lyrical terms—"the pulse of our planet" (www.usanpn.org) or "the rhythm of the seasons" (Morisette et al., 2009).

Over the last 15 years, the importance of phenology to the science of global change has been increasingly acknowledged. This shift began with modeling and empirical studies demonstrating that plant phenology, which was known to be sensitive to year-to-year variability in weather, could also serve as an indicator of the long-term biological impacts of climate change on terrestrial ecosystems (Schwartz, 1998; Bradley et al., 1999; Menzel and Fabian, 1999). Subsequent research, including numerous meta-analyses, gave strong support for this early work (Peñuelas et al., 2002; Badeck et al., 2004; Schwartz et al., 2006; Cleland et al., 2007; Parmesan, 2007). Thus, recent warming trends have been associated with earlier onset of vegetation activity in spring (e.g., leaf-out or flowering date) and an overall extension in the length of the active growing season (Linderholm, 2006). There is less of a consensus on how climate change is affecting autumn (or end-of-season) phenology, although many biological events are observed to be occurring later, as are climatological indicators such as first dates of autumn frost (Rosenzweig et al., 2008).

These trends have been observed across a diverse range of plant taxa, including herbs and grasses as well as trees and shrubs, and analogous patterns have been reported for amphibians, birds, fish, and mammals. Indeed, the 4th Assessment Report ("AR4", Parry et al., 2007) of the Intergovernmental Panel on Climate Change (IPCC)—which found that spring onset has been advancing at a rate of between 2.3 and 5.2 days per decade since the 1970s—emphatically concluded that phenology "is perhaps the simplest process in which to track changes in the ecology of species in response to climate change" (Rosenzweig et al., 2007).

Phenology varies greatly over broad geographic gradients, according to climate zone and vegetation type, and substantial interannual variability in the start and end of the growing season, and thus growing season length, is observed as a result of year-to-year variability in weather (Fig. 1). Phenology also varies within communities, and the phenology of individuals plays a key role in determining how ecosystems are structured and how they function (Cleland et al., 2007). For example, phenology is a factor in the fitness and reproductive success of both plants and animals, and in competitive interactions within and among species and across trophic levels, thereby driving species distribution (Chuine, 2010) and community assemblages (Gill et al., 1998; Augspurger et al., 2005). Furthermore, at scales from organs to ecosystems, many processes, particularly those related to the cycling of carbon (productivity and growth), water (evapotranspiration and runoff), and nutrients (decomposition and mineralization), are directly mediated by phenology, and the seasonality of these processes is implicitly phenological (Gu et al., 2003; Noormets et al., 2009). The sensitivity of phenology to climate change therefore has implications for land management (agriculture, forestry, invasive plants and pests) and human health (transport of allergens and disease vectors), as well as numerous ecosystem services (Schröter et al., 2005) on which society is dependent.

Phenology can influence microclimate in obvious ways (Fig. 2). Perhaps less well-appreciated are the multitude of ways in which phenology influences vegetation feedbacks to larger the climate system (Peñuelas et al., 2009). As a factor controlling the seasonal patterns of surface-atmosphere exchanges of energy (both short- and long-wave radiation), trace gases (most importantly water vapor and carbon dioxide), and other substances (e.g., biogenic volatile organic compounds, BVOCs), phenology has the potential to influence both regional-scale weather patterns and, in the longer term, global climate (Fig. 2). However, current-generation terrestrial biosphere models, including the land surface schemes used in earth system models that couple the land surface to the atmosphere, do not place sufficient emphasis on accurately modeling vegetation phenology or the seasonality of ecosystem processes

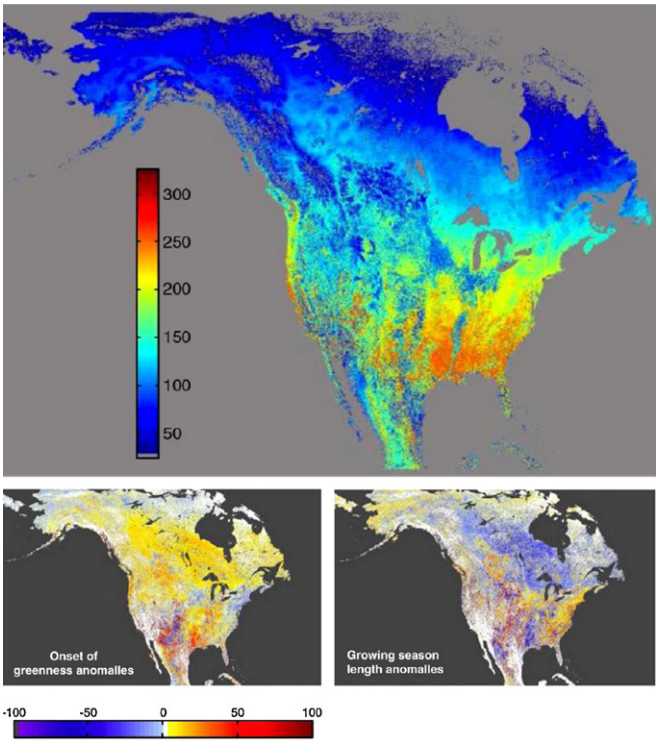

Fig. 1. The top panel shows mean growing season length, in days, for North America (2001–2006), as derived from satellite remote sensing data (the MODIS MLCD product, top). The bottom panels show anomalies for 2002, relative to the 2001–2006 mean, in the start of the growing season ("onset of greenness", bottom left) and growing season length (bottom right), also from MODIS data. Reproduced from Ganguly et al. (2010) (Remote Sensing of Environment 114:1805–1816).

(Richardson et al., 2012). One consequence is that many of the important feedbacks to the climate system that are affected by vegetation phenology are likely misrepresented in such models.

The main objective of this review is to highlight the diverse ways in which phenology mediates feedbacks of terrestrial vegetation to the global climate system. We begin with a review of climate change impacts on phenology in different ecosystem types, paying special attention to phenological shifts that are expected, or projected, to occur in the future. We then explore those climate system feedbacks in which phenology plays a key role, and examine how these feedbacks might be affected by future phenological shifts. Finally, we provide an overview of different approaches to modeling phenology, and suggest ways in which the uncertainties in forecasts of phenological shifts, and the impact of these shifts on ecosystem processes and climate system feedbacks, might be reduced.

2. Impacts of climate change on phenology

The phenological literature is increasing at a rapid rate. Many of these publications focus on the impact of global change factors on plant phenophases such as leaf-out, flowering, fruiting, senescence and abscission (e.g. Morisette et al., 2009; Tooke and Battey, 2010; Pau et al., 2011; Polgar and Primack, 2011). As noted by the IPCC's AR4 (Rosenzweig et al., 2007), these studies provide incontrovertible evidence of some of the biological impacts of climate change, particularly as related to warmer temperatures, on terrestrial ecosystems. In this section, we (1) review the recent literature on climate change impacts on phenology, emphasizing work published since the AR4 and concentrating on phenological transitions that are most important in the context of the feedbacks shown in Fig. 2 (i.e., favoring leaf phenology over reproductive phenology); (2) identify the key environmental drivers for phenology in major biomes: how does the importance of temperature, photoperiod and precipitation/soil moisture vary among plant functional types, and are there other biome-specific drivers?; and (3) highlight knowledge gaps with respect to forecasting future shifts in phenology.

2.1. Temperate forests

The longest known phenological records assembled to date track the flowering of Japanese cherry trees back to the 9th century. Analysis of these data provides insight into phenological variability on annual, decadal, and century+ time scales, and also provides a pre-Industrial context for recent phenological shifts. Spring blooming is now occurring earlier than at any other point in the past 1200 years (Aono and Kazui, 2008; Primack et al., 2009a). Numerous other studies have documented advances, particularly over the last four decades, in the timing of spring onset in temperate trees. These trends have been unequivocally attributed to

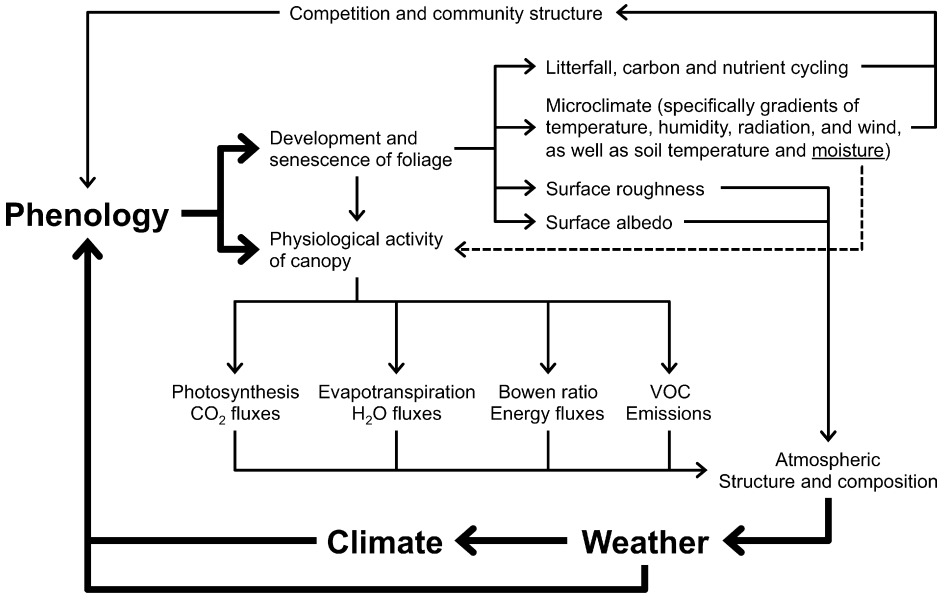

Fig. 2. Conceptual model illustrating the primary feedbacks between vegetation and the climate system that are influenced by vegetation phenology.

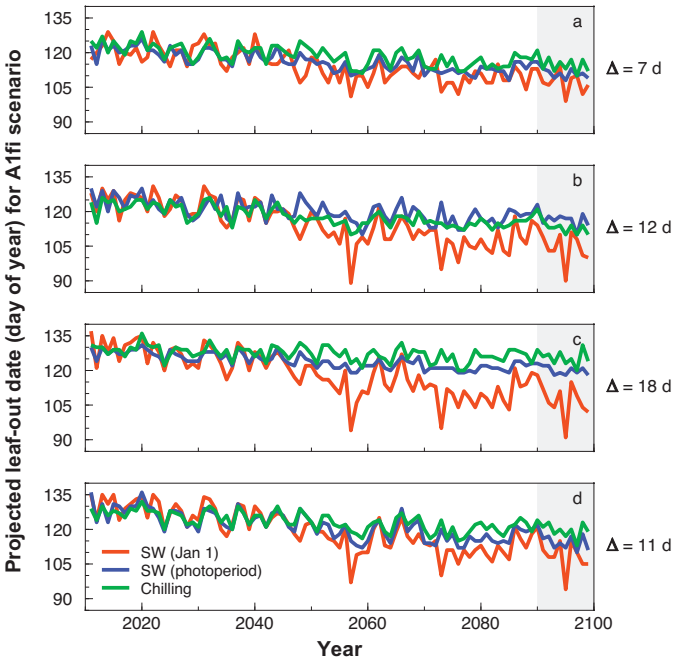

Fig. 3. Projections of leaf-out phenology, 2010–2099, for four different New England species: (a) *Acer saccharum*, sugar maple; (b) *Betula papyrifera*, paper birch; (c) *Fagus grandifolia*, American beech; (d) *Quercus rubra*, red oak. Three different types of models are shown: the red line shows a standard "spring warming" (SW) model, with accumulation of forcing units beginning on January 1; the blue line shows a modified spring warming model, with accumulation of forcing units commencing when an empirically-determined photoperiod threshold is reached; the green line shows a model which incorporates both cold-weather chilling and warm-weather forcing. Chilling and photoperiod requirements result in a smaller advancement of leaf-out by the end of the century, compared to the spring warming model. Models were parameterized using ground observations (1990–2009) from the Harvard Forest (central Massachusetts, USA) and run forward using statistically downscaled NOAA GFDL CM2 model projections (IPCC A1fi scenario). The *y*-axis range is identical in all four panels. "Delta values" on far right indicate the mean difference, over the period 2090–2099 (light shading), between "earliest" and "latest" model predictions. Data are from Migliavacca et al. (2012). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

warming temperatures. For example, long term (century+) records of tree leaf-out from England (Thompson and Clark, 2008) and flowering by a range of herbaceous and woody forest species in the northeastern U.S. (Miller-Rushing and Primack, 2008) have chronicled phenological advances of approximately 3–8 days for each 1 °C increase in air temperature. Other studies in temperate forests, using modeling and remote sensing, suggest rapid rates of advance (1.8–7.8 days/decade) of spring leaf-out in recent decades, although considerable variability among species and studies has been reported (Richardson et al., 2006; Vitasse et al., 2009; Jeong et al., 2011).

In some temperate trees species, photoperiod and winter chilling requirements are also known to play a role in spring phenology. Strong photoperiod control may limit the degree to which leaf-out can advance in the future, while if chilling requirements are not met before the end of winter, leaf-out may be delayed in spite of continued warming (Fig. 3; Zhang et al., 2007; Morin et al., 2009; Korner and Basler, 2010; Migliavacca et al., 2012).

Changes in the timing of autumn phenology of temperate forests in response to climate change are not as well documented as changes in spring phenology. Still, most published studies have reported delays in leaf coloring and abscission, and these trends have typically been linked to increases in late summer or early fall temperatures (Estrella and Menzel, 2006; Doi and Takahashi, 2008; Delpierre et al., 2009). Conversely, Menzel et al. (2008) attributed delays in fall coloring to high temperatures in late spring. Complementing these ground-based studies, satellite remote sensing data from the Advanced Very High Resolution Radiometer (AVHRR) indicate a trend in delayed autumn senescence (3–4 days/decade) in European and North American temperate forests since 1982 (Jeong et al., 2011).

Combined with advances in spring onset, delays in autumn senescence have worked to increase growing season length (trend of 2.1–4.2 days/decade) in Eurasian and North American temperate forests over the several last decades (Menzel et al., 2008; Jeong et al., 2011). Continuing trends of rising air temperatures in temperate zones (Christensen et al., 2007) suggest increasingly earlier spring leaf-out (potentially tempered by photoperiod or chilling requirements in some species) (Lebourgeois et al., 2010; Migliavacca et al., 2012), delayed senescence (Vitasse et al., 2011), and consequently longer growing seasons in the decades to come.

Rising atmospheric CO_2 is not expected to have significant impacts on spring leaf-out of temperate tree species (Badeck et al., 2004; Asshoff et al., 2006), although some studies have suggested that elevated CO_2 may delay autumn coloration and senescence (Taylor et al., 2008).

2.2. Boreal and subalpine forests

In the boreal forest, recent trends are similar to those observed in temperate forests, and these shifts have also been attributed to a warming climate. For example, over the past 160 years, leaf-out of six deciduous boreal tree species in Norway has advanced at a mean rate of between 0.3 and 1.1 days/decade (Linkosalo et al., 2009). Other boreal studies, focused on phenological shifts in more recent decades, have reported considerably higher rates of change (advancement of 2–14 days/decade) in spring onset (Delbart et al., 2008; Nordli et al., 2008; Pudas et al., 2008).

Variability in the timing of spring onset in northern Europe has been linked to the strength of the North Atlantic Oscillation Index (NAOI). Positive NAOI conditions are characterized by warmer winters with more precipitation in northern Europe and cooler, drier winters in southern Europe and the Mediterranean. A strongly positive NAOI has been associated with earlier leaf-out (Maignan et al., 2008), although it has also been suggested that when the NAOI is positive, heavy snow (Shutova et al., 2006) or insufficient winter chilling (Nordli et al., 2008) may cause delays in spring onset in some parts of boreal Europe.

Climate change impacts on autumn senescence in boreal forests are more uncertain, as trends appear to be spatially variable and the associated mechanisms are not fully identified. Satellite data indicate trends towards later senescence in boreal Eurasia, but towards earlier senescence in northern Canada and Alaska, over the period 1982–2008 (Jeong et al., 2011). While ground observations of birch trees at sites across Finland (1997–2006) do not indicate any significant trends in autumn phenology (Pudas et al., 2008), data from three sites in northwestern Russia indicate consistent, but not statistically significant, trends towards earlier ($\approx$−1.5 days/decade) autumn yellowing of birch over the period 1964–2003 (Shutova et al., 2006). In the latter study, these patterns were in agreement with both satellite data and local temperature trends.

Future warming of the boreal zone (Christensen et al., 2007) will most likely result in continuing trends towards earlier spring onset, although the influence of the NAO will be super-imposed on this long-term trend. There is considerable uncertainty about future changes in fall coloring and senescence, and it is possible that photoperiod control may limit the potential for growing season extension in autumn.

With respect to factors other than temperature, there is little evidence that precipitation has a significant influence on boreal forest phenology, although spring onset may be delayed by high winter snowfall (Shutova et al., 2006). Experimental work suggests

that leaf-out of Norway spruce is not sensitive to elevated CO_2 (Hänninen et al., 2007).

There are fewer studies concerning phenological changes in subalpine forests. Based on elevational patterns, Busetto et al. (2010) reported that leaf-out of European larch growing in the Alpine region of northern Italy was advanced at a rate of 7 days for each 1 °C increase in spring air temperature. In another study looking at the European Alpine region, Ziello et al. (2009) found that flowering of both grasses and a variety of woody species, including some trees, had advanced at rates between 1 and 5 days/decade over the period 1971–2000. These patterns were linked to warming trends over the same period.

2.3. Subalpine meadows and Arctic and alpine tundra

In high latitude and high altitude ecosystems (Wielgolaski and Inouye, 2003; Inouye and Wielgolaski, 2003), there are typically two critical factors that regulate the spring onset of growth and flowering: the timing of snowmelt (which is often spatially highly variable), and the temperatures that follow snowmelt. The nature of climate-change driven shifts in phenology will depend on both factors (Høye et al., 2007a).

The timing of snowmelt is determined both by the depth of the winter snowpack, and by springtime temperatures. The presence of snow is a barrier to the phenological development of the low-stature vegetation that characterizes subalpine meadows and Arctic and alpine tundra. However, if the snow is thin and melts early, plants may be exposed to cold air temperatures that inhibit rates of development or cause frost damage (Wipf et al., 2006). In meadows of the Rocky Mountains, for example, recent trends towards earlier snowmelt have been associated with an increase in the frequency of frost damage to buds and flowers of several frost-sensitive perennial herbaceous species (Inouye, 2008).

A number of studies have documented a threshold response of phenology to the date of snowmelt (e.g., Høye et al., 2007a; Steltzer et al., 2009), which may indicate strong photoperiod control as a frost-avoidance mechanism. By comparison, a deep snowpack invariably delays plant development and shortens the growing season (Borner et al., 2008), but has the advantage of providing protection for the buried plants, such that by the time the deep snow has melted in late spring or early summer, air temperatures are usually favorable for plant growth.

With respect to the magnitude of shifts in phenology that could result from climate change, one study that merged results from both experimental warming treatments and naturally occurring gradients concluded that flowering time of subalpine meadow species would advance by up to 11 d as a result of either a two-week advancement in snowmelt date, or a 2 °C increase in mean temperature (Dunne et al., 2003). In the Arctic, observational studies indicate trends towards earlier spring emergence (advancing trend, 3 days/decade 1993–2006, Post and Forchhammer, 2008) and flowering (advancing trend, 14 days/decade 1996–2005, Høye et al., 2007b) of plants in Greenland since the mid-1990s. These trends have been linked to warmer temperatures (see also the passive warming experiment described by Post et al., 2008, and more generally the results from the International Tundra Experiment, ITEX, in which warming treatments were applied at more than two dozen Arctic and alpine research sites worldwide, Henry and Molau, 1997, Arft et al., 1999) and shifts towards earlier snowmelt, respectively. However, although future warming is forecast to be largest at high latitudes, it is also expected that winter precipitation will increase across the Arctic (Christensen et al., 2007), making the timing of snowmelt, and hence future predictions of phenological shifts, uncertain.

In Arctic and alpine tundra ecosystems, the factors controlling autumn senescence, and the impacts of climate change on senescence, have not been extensively studied with ground observations. However, one experiment in Greenland showed that warming treatments both increased the cover of green vegetation and delayed autumn senescence by more than two weeks (Marchand et al., 2004). Results from ITEX also suggested that warming might delay senescence of herbaceous tundra species (Arft et al., 1999).

2.4. Tropical forests

Tropical dry, wet, and rain forests are differentiated by the amount and seasonal variability of precipitation, and community-level differences in phenology tend to be driven by the duration of the dry season (Reich, 1995). Thus, in tropical dry forests, many species are deciduous and the dropping of old leaves, and production of new leaves, tends to coincide with the start and end of the dry season. However, solar radiation (either total insolation, peak irradiance, or photoperiod) has also been implicated as a major cue for phenology (Wright and van Schaik, 1994), in both seasonal (Xiao et al., 2006; Doughty and Goulden, 2008; Bradley et al., 2011) and aseasonal (Zimmerman et al., 2007; Zalamea and Gonzalez, 2008) tropical forests.

We are not aware of any long-term, multi-species or multi-site studies that have used ground observations to investigate the causes of interannual variability in tropical forest phenology, or to document shifts in phenology that can be attributed to climate change. However, Reich (1995) predicted that climate change impacts would vary among tropical forest types, according to the degree to which the site water balance was influenced. Thus, little change was predicted for rain forests that will remain wet. In dry forests, by comparison, Reich (1995) proposed that rising CO_2 could enhance leaf longevity, whereas rising temperatures and reduced precipitation would exacerbate dry season water-limitation.

The impacts of climate change on tropical forests will likely vary across regional-to-continental scales. Decreasing precipitation and reduced cloudiness (enhancing insolation) in Amazonia may result in different phenological shifts than, for example, in central Africa where precipitation is projected to increase. Projections of future El Niño oscillations, which induce drought in Southeast Asia, are highly uncertain (Christensen et al., 2007).

2.5. Mediterranean wood-, shrub- and grasslands

Mediterranean vegetation includes a diverse range of plant functional types, and phenological responses to environmental cues vary accordingly. Temperature is a key driver for most species, but precipitation, through its influence on soil moisture, is also in many cases important (e.g., Peñuelas et al., 2002; Gordo and Sanz, 2010).

Long term (1943–2003) observational data on 29 perennial species, collected at over 1500 monitoring sites across Spain, give insight into the impacts of recent climate change on Mediterranean phenology (Gordo and Sanz, 2009, 2010). Key phenological events such as leaf-out, flowering, and fruiting have advanced by 4.8, 5.9 and 3.2 days/decade, respectively, while there is also a modest trend towards delayed (1.2 day/decade) leaf abscission since the 1970s (Gordo and Sanz, 2009).

Many manipulative experiments have been conducted to characterize the sensitivity of Mediterranean flora to global change factors, particularly temperature. In a multi-factor experiment, the warming treatment (+1.5 °C) advanced flowering of annual species by 2–5 days, while the phenological response to elevated CO_2 and N treatments varied among functional groups (Cleland et al., 2006). Both deciduous and evergreen oak species responded to experimental warming treatments of +1.5 °C and +3.0 °C by advancing leaf-out by 8 and 13 days, respectively (Morin et al., 2010).

However, in another study, only one of three Mediterranean shrubs advanced leaf-out in response to experimental warming (Prieto et al., 2009).

Summer drought is a defining characteristic of Mediterranean ecosystems. Seasonal changes in moisture availability control vegetation activity, and typically most plant growth occurs during the cooler but wetter part of the year (e.g. Rambal et al., 2003; Xu and Baldocchi, 2004). The phenology of Mediterranean shrub species appears to be particularly sensitive to water availability; drought treatment advanced the timing of late-spring flowering in one study (Matesanz et al., 2009), while drought treatment delayed autumn flowering in another study (Prieto et al., 2008). The annual green-up and die-back cycle of shallow-rooting savanna grasses is driven by surface soil moisture, whereas trees can sustain photosynthetic activity longer than grasses because they are able to tap deeper soil water (Baldocchi et al., 2004; Ma et al., 2007). This deep rooting may explain why Morin et al. (2010) found that leaf-out and senescence dates of Mediterranean oaks did not respond to precipitation manipulation (see also the multifactor experiment by Cleland et al., 2006; cf. Misson et al., 2011).

Climate projections indicate that increasing aridity (both reduced annual precipitation and prolonged summer drought) and rising temperatures (which will increase evaporation and further reduce soil water content) are likely for most of the world's Mediterranean ecosystems (Christensen et al., 2007). Together these factors will probably result in a shift of the active season, with earlier onset of winter-spring growth being offset to some degree by an earlier, and longer lasting, summer drought period.

2.6. Subtropical deserts

In semi-arid and arid desert ecosystems, phenological shifts resulting from climate change may occur both as a result of changes in the timing and amount of precipitation, and increases in temperature. Major precipitation events trigger the end of dormancy, while temperature controls the rates of subsequent plant growth and development. Bowers (2007) used climate data and two simple models to predict changes in the flowering time of Sonoran desert shrubs over the last century. The photoperiod-temperature model predicted flowering had advanced at a rate of 1.1 days/decade, while the precipitation-temperature model predicted a rate of change of 3.7 days/decade.

Shifts in the timing and frequency of precipitation can, through phenology, result in shifts in community structure of arid ecosystems. For example, the American southwest has become both warmer and drier over the last 25 years. In particular, winter rains, which once arrived in October, now begin in December. Kimball et al. (2010) reported that this has caused a shift towards desert annuals that are adapted to colder conditions, as these are the species that are best adapted to growth following December rain. The amount of rainfall during the southwestern summer monsoon is also correlated with timing of the seasonal peak in vegetation greenness as observed from MODIS satellite data (Jenerette et al., 2010).

Therefore, vegetation in semi-arid and arid regions is anticipated to respond strongly to future decreases in subtropical precipitation (Christensen et al., 2007) as plant phenology shifts to utilize this limited resource.

3. Feedbacks of vegetation to climate that are mediated by phenology

It has long been known that vegetation can influence climate, and that phenology plays a role in regulating these feedbacks. In *Weather Prediction by Numerical Process*, Richardson (1922) wrote, "Leaves, when present, exert a paramount influence on the interchanges of moisture and heat. They absorb the sunshine and screen the soil beneath. Being very freely exposed to the air they very rapidly communicate the absorbed energy to the air, either by raising its temperature or by evaporating water into it." Our understanding of these vegetation-atmosphere feedbacks has advanced greatly over the last century (Pielke et al., 1998; Pitman, 2003; McPherson, 2007; Bonan, 2008), and the importance of phenology as a regulating factor is receiving increased attention (Peñuelas et al., 2009), largely because of the observed sensitivity of phenology itself to climate change and variability.

In this section, we focus on the following mechanisms through which vegetation influences the climate system, and discuss the role of phenology in these feedbacks: albedo, surface roughness length, canopy conductance, water and energy fluxes, photosynthesis and CO_2 fluxes, and fluxes of BVOCs. Where possible, we attempt to quantify the degree to which shifts in phenology may influence the strength of these feedbacks.

We will not discuss in detail the ways in which phenological transitions influence microclimate, e.g. gradients of temperature, humidity, radiation (particularly shading), and wind speed, in addition to atmospheric deposition, precipitation throughfall, and soil temperature and moisture (Fig. 2; see also Hutchison and Matt, 1977; Wilson et al., 2000; Staelens et al., 2007; Ryu et al., 2008; Richardson and O'Keefe, 2009). However, we note that by affecting microclimate in this manner, phenological patterns can also influence competition among individuals, and thus community structure, which may feed back to larger-scale biosphere–atmosphere interactions.

3.1. Albedo

Albedo (α) is the proportion of incident solar radiation that is reflected by the land surface. Thus albedo plays a critical role in the surface energy budget and is a direct feedback of vegetation to the climate system (Pitman, 2003; Bala et al., 2007; Bonan, 2008). Albedo varies substantially among different vegetation types. Typical growing season albedo values for different ecosystems are as follows: broadleaved deciduous forest, $\alpha \approx 0.15$; needleleaf evergreen forest, $\alpha \approx 0.08$; grasslands, $\alpha \approx 0.18$; and agricultural crops, $\alpha \approx 0.19$ (Hollinger et al., 2010).

Albedo changes with the development and senescence of the canopy. More specifically, the seasonal course of albedo is determined by the combined effect of seasonal changes in reflectance of photosynthetically active (PAR, 400–700 nm wavelengths) and near-infrared (NIR) radiation. For example, canopy PAR reflectance quickly decreases with leaf-out as the canopy absorbs an increasing amount of PAR for photosynthesis (Moore et al., 1996; Burba and Verma, 2001; Ryu et al., 2008). In contrast, canopy NIR reflectance generally increases with canopy development due to increased multiple scattering within the canopy (Gates, 1965).

For evergreen vegetation types located in snow-free regions, albedo is relatively constant throughout the year, because seasonal variation in both PAR and NIR reflectance tends to be low (Jackson et al., 2008). Other ecosystems tend to be more variable. In deciduous ecosystems, the observed seasonal patterns are influenced by background albedo, which varies substantially, e.g. bare ground $\alpha \approx 0.1$–0.35, snow $\alpha \approx 0.40$–0.95, and understory green vegetation $\alpha \approx 0.05 - 0.25$ (Campbell and Norman, 1998). In deciduous forests, snow on the forest floor may result in winter $\alpha \approx 0.2$–0.3, compared with $\alpha \approx 0.1$ after snowmelt but before leaf-out. Leaf-out by canopy tree species causes albedo to increase by 20–50% (e.g., from $\alpha \approx 0.10$ to $\alpha \approx 0.15$ in the study of Moore et al., 1996) between spring minima and growing season maxima (Hollinger et al., 2010), as the increase in NIR reflectance is larger than the decrease in PAR reflectance. However, leaf aging results in a gradual decrease of NIR

reflectance, but little change in PAR reflectance, over the summer (Jenkins et al., 2007). This is followed by a rapid decrease in overall albedo during senescence (Hollinger et al., 2010) as NIR reflectance decreases sharply when leaves are shed.

In grassland ecosystems, albedo decreases with green-up and the onset of new growth, and then increases with senescence (Ryu et al., 2008; Hollinger et al., 2010). This pattern is largely driven by seasonality in the PAR reflectance of live (low reflectance) vs. dead (high reflectance) grass. In agricultural ecosystems, the seasonal patterns are influenced not only by plant phenology and growth, but also the specifics of agricultural management, particularly the timing of sowing and harvest. There are four typical phases: snow (high albedo) in winter, bare ground (high albedo when the soil is dry, low albedo when it is moist) in spring, green vegetation (low albedo when the canopy is closed), and crop residue (high albedo) in autumn. Note that in ecosystems with open canopies, such as northern peatlands, the spectral characteristics of background materials are important for the overall albedo of the ecosystem throughout the year (Sonnentag et al., 2007).

Climate change feedbacks through phenological impacts on albedo will vary among ecosystem types. A longer growing season will itself likely have little or no impact on evergreen forest albedo, although a reduction in the duration of canopy snow cover would decrease winter albedo. Reduced precipitation and warmer temperatures in water-limited grassland ecosystems will likely shorten the growing season, but cause an overall increase in annual albedo because of the high reflectivity of dead grasses. In temperate and boreal deciduous forests, a warmer climate may result in both less snow (which will decrease albedo) and longer canopy duration (which will increase albedo). We are not aware of studies where the total impact of these shifts on annual surface energy budgets has been quantified.

3.2. Surface roughness length

Surface roughness length is the height above the surface where mean wind speed extrapolates to zero. It was shown that surface roughness length is related to canopy height (Shaw and Pereira, 1982) and leaf area index (Lindroth, 1993; Raupach, 1994). The surface roughness length has a direct link with the climate system by influencing the degree of coupling between the land surface and the atmosphere, thereby modulating land surface energy fluxes (Xue et al., 1996, Pitman, 2003). For example, increases in surface roughness are associated with an increase in the efficiency with which sensible heat is transferred from the surface to the atmosphere (Rotenberg and Yakir, 2010; Lee et al., 2011). Hoffmann and Jackson (2000) also show how by reducing convection, reductions in surface roughness length can also reduce precipitation and influence larger-scale circulation patterns.

Surface roughness length varies according to seasonal changes in canopy structure, specifically leaf area and canopy height. For agricultural crops and some other short canopies, surface roughness length increases substantially over the course of the growing season, as there is a transition from bare ground to tall plants (e.g., Sonnentag et al., 2011). This increase in surface roughness length increases the coupling between the vegetation and the atmosphere.

For deciduous forests, the impact of the development and shedding of leaves on surface roughness appears to be surprisingly small. Schmid et al. (2000) reported that surface roughness length did not differ between leaf-off and leaf-on periods in a temperate, oak-dominated forest. By comparison, Blanken and Black (2004) concluded that the canopy of a boreal aspen forest was "aerodynamically smoother" when leaves were present. In the Simple Biosphere Model (SiB), surface roughness length of deciduous broadleaf forest increases from ≈50 cm (leaf-off) to ≈100 cm (leaf-on) (Dorman and Sellers, 1989). The seasonality of surface roughness length is even less variant for evergreen needleleaf and evergreen broadleaf forests where canopy structure changes little on seasonal time scales.

Climate system feedbacks resulting from phenological shifts influencing the seasonal course (cf. Lee et al., 2011) of surface roughness length have not, to our knowledge, been fully quantified. It seems likely that these feedbacks would, in most ecosystem types, be quite small compared to potential impacts on surface roughness length of shifts in vegetation cover resulting from climate change (e.g. Hoffmann and Jackson, 2000).

3.3. Canopy conductance

Canopy conductance is the product of the amount of leaf area present and the stomatal conductance per unit leaf area. It is an important parameter because of its role in regulating rates of transpiration and CO_2 uptake by plants. Thus the factors controlling the seasonality of canopy conductance are similar to those controlling the seasonality of latent heat flux and photosynthesis. The impacts of shifts in phenology on these flux feedbacks are discussed in more detail in the sections that follow.

In a boreal deciduous forest, Blanken and Black (2004) reported that the spring increases in canopy conductance occurred simultaneously with leaf-out, and canopy conductance increased linearly, and in parallel, with leaf area. The strong dependence of canopy conductance on leaf-out and expansion, given ample soil moisture in spring, has been described for a variety of ecosystem types (grassland, Ripley and Saugier, 1978; boreal deciduous forest, Blanken et al., 1997; temperate deciduous forest, Sakai et al., 1997; Wilson and Baldocchi, 2000; see also Zha et al., 2010). However, as moisture becomes limiting, drought responses can cause reductions in canopy conductance that are unrelated to changes in leaf area. In other words, phenology has first-order control over canopy conductance, but other factors can serve to modify this relationship.

In a boreal conifer forest, results of Hollinger et al. (1999) show that canopy conductance increased at the same time as daytime temperatures rose above freezing in spring (April), and dropped off dramatically with the first frosts in autumn (October). Hollinger et al. (1999) also reported that with the annual flush of new foliage in June, canopy conductance increased by roughly 50%. Thus, the main seasonal dynamics of canopy conductance in winter-dormant/summer-active evergreen ecosystems are largely, but not completely, decoupled from changes in leaf area.

3.4. Water and energy fluxes, and the surface energy budget

As described above, seasonal variation in the amount and physiological activity of plant leaf area results in corresponding changes in albedo, surface roughness length, and canopy conductance for water vapor. These biophysical properties influence the surface energy balance, and the partitioning of the net radiation into latent, sensible, and ground heat fluxes (Pielke et al., 1998; McPherson, 2007). The turbulent heat fluxes in turn influence the composition and structure of the planetary boundary layer (McNaughton and Spriggs, 1986; Pielke et al., 1998; Raupach, 1998) and thus atmospheric processes, including transport.

Moore et al. (1996) showed that in temperate deciduous forests the seasonal patterns of sensible and latent heat fluxes are in large part driven by changes in leaf area index. Sensible heat fluxes peak in spring and autumn, whereas latent heat fluxes peak in midsummer. In spring, the Bowen ratio (the ratio of sensible to latent heat) drops rapidly as leaves become fully expanded and transpiration rates increase. In autumn, the reverse occurs with leaf senescence and abscission. The corresponding patterns in boreal deciduous forests (Barr et al., 2007) and Mediterranean grasslands (Ryu et al., 2008) have also been described. The seasonal patterns of

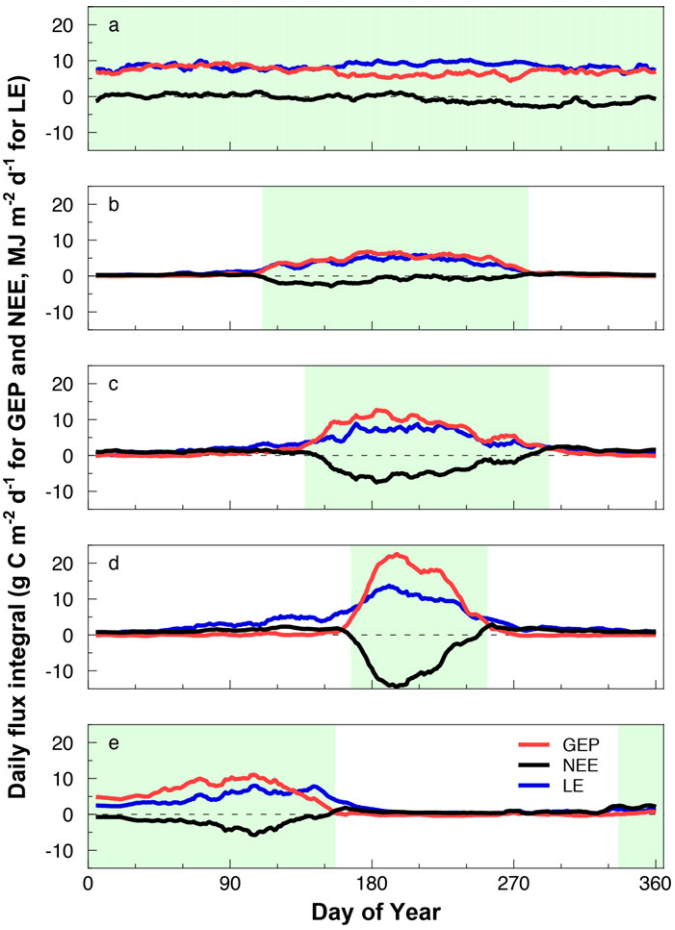

Fig. 4. Seasonality of gross ecosystem photosynthesis (GEP) and net ecosystem exchange (NEE) of CO_2 (both in g C m^{-2} d^{-1}), and latent heat flux (LE, MJ m^{-2} d^{-1}), across a range of FLUXNET sites. Data have been smoothed with a 7-day running mean; green shading indicates the typical growing season at each site. (a) Santarem, Brazil (2002): evergreen tropical forest; (b) Thompson, Manitoba, Canada (2002): evergreen boreal forest; (c) Harvard Forest, MA, USA (1995): temperate deciduous broadleaf forest; (d) Mead, NE, USA (2003): rainfed agricultural crop (maize/soybean rotation; data shown for maize); (e) Vaira, CA, USA (2005): Mediterranean grassland. The *y*-axis range is identical in all five panels. Data are courtesy of FLUXNET and individual site PIs.

latent heat flux tend to parallel those of gross ecosystem photosynthesis (GEP) (e.g., Fig. 4), reflecting the fact that water loss through transpiration is an inevitable consequence of opening stomata to allow CO_2 uptake for photosynthesis.

Phenologically-driven increases in latent heat flux, and concurrent decreases in sensible heat flux, result in several impacts on climate at local-to-regional scales (Schwartz, 1992; Fitzjarrald et al., 2001). During spring, the rate of increase in the daily maximum temperatures is substantially lower immediately after leaf-out than prior to leaf-out. This occurs because the increased transpiration that follows leaf-out not only causes surface cooling but also puts large amounts of water vapor into the lower atmosphere, thereby raising its heat capacity (Schwartz and Karl, 1990).

The increase in evapotranspiration that accompanies leaf-out influences the climate system in other ways as well. In areas where soil moisture is adequate and vegetation is extensive (e.g., the forests of New England, see Freedman et al., 2001), the movement of large quantities of water from the soil column to the atmosphere greatly increases the frequency of cumulus clouds during the growing season. Clouds moderate surface temperatures and increase the diffuse fraction of incident solar radiation, both of which contribute to enhanced photosynthesis (clouds also make the atmosphere more reflective; this may result in larger impacts on planetary albedo than the previously-discussed effects of phenology on surface albedo: see, for example, Donohoe and Battisti, 2011). Similarly, Hogg et al. (2000) suggested that boreal aspen forests also appear to modify regional-scale climate, through their influence on evapotranspiration and energy partitioning, in two ways that enhance forest growth: first, by warming temperatures in early spring and late autumn, thereby extending the length of the growing season, and second, by moderating temperatures and enhancing precipitation during the summer months, thereby reducing moisture stress.

At seasonal-to-annual time scales, phenological controls on latent heat fluxes play an important role in influencing the overall ecosystem water budget, including both runoff and soil water availability. For example, at both a boreal aspen forest and a prairie grassland in western Canada, warmer spring temperatures advanced spring leaf-out, enhanced springtime evapotranspiration, and increased annual evapotranspiration (Zha et al., 2010). At a Mediterranean grassland, the length of the growing season was a strong control on annual evapotranspiration ($r^2 = 0.81$, $n = 6$), with each one-day increase in growing season length increasing annual evapotranspiration by 1.6 mm (Ryu et al., 2008). At these sites, relationships between phenology and water fluxes are analogous to those between phenology and carbon fluxes (see below) (Zha et al., 2010). Such patterns are not universal, however. Reanalysis of the FLUXNET data used by Richardson et al. (2010) shows little correlation between interannual variation in growing season length and annual evapotranspiration ($r^2 = 0.03$, $n = 58$ years for 9 deciduous broadleaf forest sites; $r^2 = 0.09$, $n = 78$ years for 12 evergreen needleleaf forest sites). By comparison, the relationship between interannual variation in growing season length and annual GEP ($r^2 = 0.42$ and 0.47, respectively) is much stronger. Similarly, modeling runs conducted for a temperate deciduous forest under current climate conditions (Harvard Forest, 1960–2000) show little correlation between leaf-out date and modeled annual evapotranspiration ($r^2 = 0.03$, Fig. 5B), despite a comparatively strong relationship between leaf-out date and modeled annual GEP ($r^2 = 0.32$, Fig. 5A) (Migliavacca et al., 2012).

The differing sensitivities of evapotranspiration and photosynthesis to phenology may be attributed to several factors. First, annual evapotranspiration represents the aggregate flux of evaporation and transpiration. In years with an "early" spring the resulting increases in transpiration may be partially offset by simultaneous decreases in soil evaporation. Second, evapotranspiration can be supply-limited, whereas the atmospheric supply of CO_2 is essentially unlimited. With respect to the second explanation, there are a number of routes by which water might become limiting in years with early spring onset. For example, if early spring onset is the result of a thin snowpack, and early snowmelt, plants may enter the growing season with smaller than usual soil water reserves, enhancing the likelihood of summer drought (e.g. Hu et al., 2010). Alternatively, if early spring results from warm temperatures that enhance evapotranspiration, soil water may simply be drawn down earlier in the growing season (Kljun et al., 2006), again resulting in dry soils by mid-summer. In either case, years with early spring will not result in increased annual evapotranspiration if summer evapotranspiration is limited by soil water availability. In extreme cases, e.g. where a warm, early spring is followed by a pronounced summer drought, the reductions in summer evapotranspiration may lead to large increases in surface temperature that exacerbate the already-dry conditions. Indeed, Fischer et al. (2007) used simulation models to show that by reducing latent heat fluxes, the soil water feedback increased temperature anomalies by up to 40%, and also influenced continental-scale atmospheric circulation patterns, during the 2003 European summer heat wave.

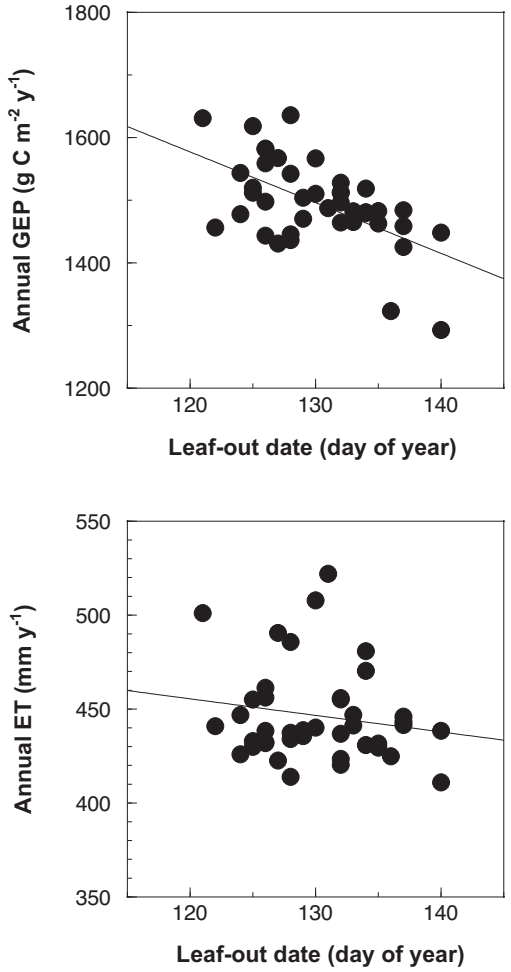

Fig. 5. Correlation between budburst date and (a) annual gross ecosystem photosynthesis (GEP) and (b) evapotranspiration (ET), based on model runs (1960–2000) for a temperate deciduous forest (Harvard Forest, MA, USA) with BEPS (the Boreal Ecosystem Process Simulator) and a spring phenology model that incorporates both winter chilling and spring warming requirements. In (a), the regression line has a slope of -8.1 ± 1.9 g C m^{-2} d^{-1} ($p < 0.001$, $n = 41$, $r^2 = 0.32$); in (b), the regression line has a slope of -0.9 ± 0.8 mm H_2O d^{-1} ($p = 0.30$, $n = 41$, $r^2 = 0.03$). Data are from model runs reported by Migliavacca et al. (2012).

Therefore, the abrupt changes in water and energy fluxes that occur simultaneously with spring onset (and by extension, other phenological transitions) cause important feedbacks to the climate system (Schwartz and Crawford, 2001). These include changes in local surface layer properties as well as larger-scale effects, such as changes in precipitation and atmospheric circulation. These feedbacks cannot be properly represented in land surface models unless phenology is itself properly represented and dynamically coupled to climate (Schwartz, 1992; Levis and Bonan, 2004). The timing and nature of these feedbacks will obviously be affected by climate-change driven shifts in phenology, although concurrent changes in precipitation and soil water availability will make accurate prediction of these impacts challenging.

3.5. Photosynthesis and CO_2 fluxes

One of the most important feedbacks between vegetation and the climate system is the influence of vegetation on atmospheric CO_2 and thus global temperature. Gross productivity by terrestrial vegetation is estimated to be 123 Pg C y^{-1} (Beer et al., 2010), and the total land sink is 2–4 Pg C y^{-1}, compared with anthropogenic emissions of 8 Pg C y^{-1} (Le Quéré et al., 2009). Interannual variability in terrestrial ecosystem metabolism influences the annual growth rate of atmospheric CO_2 (Houghton, 2000), and the seasonal cycle of atmospheric CO_2 observed at monitoring sites such as Mauna Loa is largely driven by the phenology of vegetation activity in the Northern hemisphere (Keeling et al., 1976). Changes in the phasing of this cycle (i.e., trends in the "downward zero crossing" date in spring) have been attributed to climate change impacts of phenology, specifically warming trends triggering an earlier spring onset of vegetation activity (Keeling et al., 1996). At several high-latitude monitoring sites, more recent data also suggest a surprising trend towards an earlier "upward zero crossing" date in autumn. Piao et al. (2008) have proposed that this is the result of warmer temperatures enhancing autumn respiration more than autumn photosynthesis in northern ecosystems. A direct consequence of this would be that these ecosystems switch from CO_2 sinks to CO_2 sources earlier in autumn, despite warmer temperatures enabling a longer growing season and prolonged photosynthetic activity.

The phenology of the exchange of CO_2 varies among ecosystem types (Fig. 4; see also Falge et al., 2002; Baldocchi, 2008), according to shifts in the balance between canopy photosynthesis and ecosystem respiration. In deciduous ecosystems, the development of new foliage (leaf-out) is a prerequisite for photosynthetic uptake to occur at the start of the growing season, and photosynthetic rates decline as foliage progresses through senescence at the end of the growing season. In strongly seasonal evergreen ecosystems (e.g. boreal conifer forests), leaves are present year-round, but photosynthetic activity is limited by one or more environmental factors during the dormant season. Recovery of conifer photosynthesis occurs when environmental conditions are favorable (Monson et al., 2005; Tanja et al., 2003; Ensminger et al., 2004), but before new foliage is produced (Richardson et al., 2009a). In aseasonal evergreen ecosystems (e.g. tropical rain forests), vegetation activity may remain high throughout the year.

In this section, we examine how phenology influences variation in surface-atmosphere fluxes of CO_2. We focus on the spatial patterns in C uptake that are driven by phenology, the role of phenology in governing interannual variability in C uptake, and the potential for future climate change impacts.

3.5.1. Phenological control of spatial patterns of C uptake

How well does variation in phenology explain spatial variability (across sites) in annual net C uptake, as determined from eddy covariance measurements? Baldocchi (2008) reported that the relationship between net C uptake (y) and growing season length (x) had a slope of about 5.6 g C m^{-2} d^{-1} in deciduous broadleaf forests. For savannas, the value was 3.7 g C m^{-2} d^{-1}. This analysis drew on data from sites across a wide range of climate zones; growing season length varied from 100 to 200 days in deciduous forests, and from 200 to 365 days in savannas. Using a somewhat different definition of growing season length, but still analyzing relationships across sites, Churkina et al. (2005) nevertheless calculated an almost identical slope for broadleaf forests (5.8 g C m^{-2} d^{-1}). However, annual net C uptake of grasslands and crops (7.9 g C m^{-2} d^{-1}) was more sensitive to growing season length, while net C uptake of evergreen needle-leaf forests (3.4 g C m^{-2} d^{-1}) was less sensitive.

These spatial patterns are driven by the influence of growing season length on the annual integral of GEP: other factors being equal, the longer that plants are active, the more their leaves can photosynthesize. While some of the extra photosynthesis resulting from a longer growing season tends to be offset by concurrent increases in ecosystem respiration, this effect tends to be smaller than the increase in GEP, which explains why net C uptake is generally greater at sites with a longer, rather than shorter growing season (Richardson et al., 2010).

3.5.2. Phenological control of interannual patterns of C uptake

Interannual variability in long-term data records can also be used as a natural experiment to investigate relationships between phenology and productivity. In other words, how much more carbon is taken up in years when spring onset is early, or autumn senescence is delayed, compared to a normal year? Combining long-term ground observations of spring phenology with tower-based CO_2 flux measurements at a deciduous broadleaf forest and an evergreen needleleaf forest, Richardson et al. (2009b) estimated that in years with earlier spring leaf-out, the springtime integral of GEP was increased by about 5 g C m^{-2} d^{-1}, while the annual integral of GEP was increased by almost 10 g C m^{-2} d^{-1}. The larger impact of earlier spring on the annual integral compared to the springtime integral was taken as evidence for lagged or indirect effects of the timing of spring onset on ecosystem function.

Richardson et al. (2010) conducted a similar analysis using a larger dataset, 153 years of data from 21 FLUXNET sites. Because phenological transition dates such as spring leaf-out and autumn senescence have not been routinely observed or recorded at most sites, spring onset and autumn dormancy dates were derived from remote sensing and the CO_2 flux time series themselves. Interannual variability (1 s.d.) in onset and dormancy dates was typically on the order of ±5–10 d, and thus growing season length was less variable than in the across-sites analysis of Baldocchi (2008) or Churkina et al. (2005). Nevertheless, Richardson et al. (2010) showed that earlier spring onset and delayed autumn dormancy both resulted in increased GEP, and that the effect was generally larger for deciduous forests (mean 8 g C d^{-1}, with some variability depending on the phenological indicator used e.g., Fig. 6), than evergreen needle-leaf forests (4 g C d^{-1}). This increase was again partially offset by concurrent increases in ecosystem respiration, particularly in autumn, and particularly for evergreen needle-leaf sites. As a result, the sensitivity of net C uptake to interannual variability in growing season length was only about half as large as for GEP (Fig. 6).

Interannual variability in net C uptake has also been related to growing season length in both Mediterranean savanna (2 g C m^{-2} d^{-1}) and grassland (4 g C m^{-2} d^{-1}) ecosystems (Ma et al., 2007). Data in Flanagan and Adkinson (2011) suggest that interannual variability in GEP of a semi-arid continental grassland is also linked to growing season length (5 g C m^{-2} d^{-1}).

The patterns described above are generalizations. At individual sites, other factors may come into play, and lagged or indirect effects of phenological anomalies may modify these relationships. It has already been pointed out that concurrent enhancement of ecosystem respiration typically tends to offset, by about 50%, the increased GEP that results from a longer growing season (Richardson et al., 2010). In peat-rich boreal sites, the same factors that lead to a longer growing season and enhanced GEP may also result in earlier or deeper soil thaw, and improved soil drainage, further increasing decomposition to the point where there is no relationship between growing season length and net C uptake (Dunn et al., 2007). Alternatively, Kljun et al. (2006) found that earlier spring onset of photosynthesis in a boreal aspen forest was also correlated with increased springtime transpiration, which depleted soil moisture and resulted in reductions in mid-summer respiratory fluxes, which further contributed to anomalously high net C uptake. By comparison, Hu et al. (2010) combined an ecosystem model with CO_2 flux measurements from a subalpine conifer site, and reported that earlier spring onset of photosynthesis generally occurred in years with warmer winter temperatures and a shallower snowpack. This meant that soil water reserves were reduced to drought levels by late summer, and that photosynthesis was inhibited. For this ecosystem, net C uptake was in fact reduced in years with a longer growing season. Finally, in years where leaves emerge unusually early, the likelihood of frost damage, which may incur a significant C cost (Gu et al., 2008; Hufkens et al., 2012), increases in temperate and boreal ecosystems. Thus, the relationship between growing season length and GEP or net C uptake is not necessarily linear and predictable.

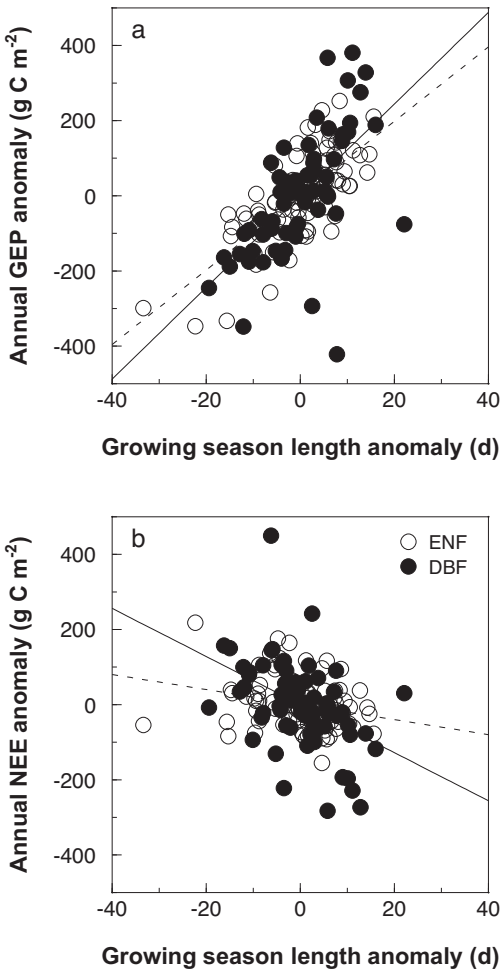

Fig. 6. Relationship between anomalies in length of the growing season (defined in terms of the duration of photosynthetic activity, estimated from eddy covariance measurements of net ecosystem exchange [NEE] of CO_2), and annual integrals of (a) GEP (gross ecosystem photosynthesis) and (b) NEE, a measure of net carbon storage, across 153 years of data from 22 FLUXNET sites (data from Richardson et al., 2010). Lines show best-fit linear regressions; solid line and filled symbols for deciduous broadleaf forest (DBF) sites, dotted line and open symbols for evergreen needle-leaf forest (ENF) sites. Regression statistics: for (a) DBF, slope = 12.2 ±1.9 g C m^{-2} d^{-1} (r^2 = 0.38, n = 67, p < 0.001), ENF, slope = 9.9 ± 1.0 g C m^{-2} d^{-1} (r^2 = 0.52, n = 86, p < 0.001); (b) DBF, slope = −6.4 ± 1.6 g C m^{-2} d^{-1} (r^2 = 0.19, n = 67, p < 0.001), ENF, slope = −2.0 ± 0.9 g C m^{-2} d^{-1} (r^2 = 0.06, n = 86, p = 0.02). Note that in (b), slopes are negative because the micrometeorological sign convention is that a flux from the atmosphere to the land surface is negative.

3.5.3. Climate change impacts on phenology: implications for C uptake

Shifts in temperature and precipitation driven by climate change will likely cause shifts in the phenology of CO_2 exchange, and annual C uptake, in many ecosystems. For example, warming temperatures will almost certainly extend the period of active canopy photosynthesis in ecosystems where winter temperatures are limiting, potentially increasing annual C sequestration (e.g. Black et al., 2000; Delpierre et al., 2009). In the FLUXNET analysis described above, Richardson et al. (2010) evaluated relationships between spring temperature anomalies and interannual variability in CO_2 fluxes. This study found that a +1 °C anomaly in spring air temperature advanced the spring onset of photosynthesis

by ≈3 days. Temperature anomalies in spring increased GEP by $35 \pm 5\,g\,C\,m^{-2}$ per °C in deciduous forests, and by $20 \pm 3\,g\,C\,m^{-2}$ per °C in evergreen needle-leaf forests. At the same time, however, concurrent increases in ecosystem respiration partially offset the photosynthetic gains, resulting in increases in net C uptake during spring of 20 ± 3 and $9 \pm 2\,g\,C\,m^{-2}$ per °C, respectively.

In arid ecosystems, changes in precipitation may impact phenology and C exchange more than changes in temperature. For example, Ma et al. (2007) reported that a 1 mm increase in precipitation during April and May was associated with a $2\,g\,C\,m^{-2}$ increase in grassland GEP, presumably because enhanced soil moisture extended the growing season of the shallow-rooting grasses. However, in arid ecosystems, changes in the timing of precipitation are just as important as changes in the total amount of precipitation (Xu and Baldocchi, 2004), which makes forecasts of climate change impacts highly uncertain.

There may also be interacting effects of shifts in temperature and precipitation on relationships between phenology and C exchange. Barr et al. (2007) concluded that when a boreal aspen forest received adequate precipitation, annual GEP was largely controlled by how long the deciduous canopy had leaves, as this governed the amount of solar radiation that was intercepted. Under drought conditions, however, photosynthetic light-use efficiency was diminished, although the canopy's capacity for light interception was unchanged. Extreme drought reduced light-use efficiency by 20%, and annual GEP by $300\,g\,C\,m^{-2}$, compared to what would have been expected on the basis of canopy duration alone. Thus, even in regions where phenology is predominantly determined by temperature, future shifts in precipitation may modify these relationships, and potentially offset C gains associated with warming and extension of the growing season (see also Angert et al., 2005).

Can future responses of ecosystem C cycling to climate change impacts on phenology be inferred from either spatial or temporal patterns under current conditions? Richardson et al. (2010) argued that spatial relationships between phenology and CO_2 uptake should differ from those inferred from interannual patterns, because spatial patterns reflect mean conditions, whereas temporal patterns are driven by transient dynamics. Neither approach may be an ideal model for gradual shifts in climate over decades-to-centuries. However, the results described above are largely consistent with studies of long-term trends at individual sites. For example, Dragoni et al. (2011) reported that growing season length in a temperate deciduous forest in the Midwestern U.S. increased at the remarkable rate of about $3\,d\,y^{-1}$ over the period 1998–2008, as rising late-summer temperatures delayed autumn senescence. A trend towards increasing annual net C uptake was observed over the same period. Changes in growing season length were found to explain roughly 50% of the C uptake trend, at a rate ($3\,g\,C\,m^{-2}\,d^{-1}$) that is slightly lower than in the other studies cited above. Pilegaard et al. (2011) reported comparable results for a temperate deciduous forest in Denmark, with a trend in C uptake over the 1996–2009 period being partially attributed to a concurrent trend, $1.9\,d\,y^{-1}$, towards increases in the duration of photosynthetic activity. In response to prolonged photosynthetic activity, annual net C uptake increased by $4.9\,g\,C\,m^{-2}\,d^{-1}$.

3.6. Fluxes of biogenic volatile organic compounds

Non-methane BVOCs represent a large class of reactive hydrocarbons (isoprene, monoterpenes, and sesquiterpenes). They are emitted from green foliage by most of the world's terrestrial plants, although there is large variability among species. For example, eucalypt and oaks trees emit considerably more BVOCs than maple and elm trees. BVOCs are known to play multiple ecological roles related to plant protection (Peñuelas and Llusia, 2004). They serve in defense against high radiative loads (Sharkey and Singsaas, 1995), high temperatures (Peñuelas et al., 2005), and both biotic (van Poecke and Dicke, 2004) and oxidative (Loreto et al., 2001) stress. As described below, environmental (Grote and Niinemets, 2008) and phenological (Peñuelas and Llusia, 2001) factors are the dominant controls on BVOC emissions.

BVOCs play a variety of roles in the photochemistry of the lower atmosphere, and control various feedback mechanisms within the climate system (Kulmala et al., 2004; Laothawornkitkul et al., 2009; Pacifico et al., 2009). The products of BVOC reactions directly affect the radiative forcing of the atmosphere. They increase the concentration of cloud condensation nuclei through aerosol production (O'Dowd et al., 2002; Laaksonen et al., 2008; Mentel et al., 2009), reduce the oxidation capacity of the troposphere (Laothawornkitkul et al., 2009), and change ozone levels (Curci et al., 2009). BVOC induced changes in the concentration of cloud condensing nuclei can change local radiative forcing by about $-4 \pm 2.5\,W\,m^{-2}$ by altering cloud albedo (Spracklen et al., 2008; Goldstein et al., 2009). Aerosols produced by BVOC reactions also increase the amount of diffuse light, which provides an indirect feedback to the climate system by increasing canopy-scale light use efficiency of photosynthesis (Niyogi et al., 2004). By reducing atmospheric oxidation through reactions with the OH radical (Pacifico et al., 2009), BVOCs can indirectly lead to an increase in the lifetime of atmospheric methane (Poisson et al., 2000). Ozone, an important greenhouse gas, is a direct product of BVOC degradation (Curci et al., 2009), although BVOCs also readily react with ozone. Each of the above-mentioned processes is directly affected by seasonal cycles in BVOC production, constituting a further indirect feedback between phenology and climate.

Enzyme kinetics responsible for the production of foliar BVOCs are governed by instantaneous temperature and radiation, recent weather conditions (including precipitation), and the physiological status of the leaf (Mayrhofer et al., 2005). For example, there is an exponential relationship between instantaneous BVOC emissions and temperature; a 10 °C rise is associated with a 3–6× increase in emissions (Peñuelas and Staudt, 2010). At slower (e.g. seasonal-to-annual) time scales, however, phenology plays an important role. For example, Kuhn et al. (2004) found that the BVOC emission potential for the tropical tree *Hymenaea courbaril* varied substantially over the course of the season, as foliage developed from immature to fully-formed, and progressed through senescence. In a meta-analysis of two evergreen species, Keenan et al. (2009b) found significant seasonal variation in the emission potential, which led to large reductions in regional emissions inventories when compared to previous estimates. Recent efforts by Grote et al. (2010) have linked seasonal dynamics of the leaf level emissions potential to those of enzyme activity, thus providing a mechanistic approach for scaling to the canopy.

Estimates of the timing and extent of global BVOCs fluxes vary widely. Isoprene global emissions have been estimated at 412–601 Tg C y^{-1} and monoterpenes at 30–128 Tg C y^{-1} (Arneth et al., 2008). This large range is in part due to differences in the emissions algorithms used for scaling from the leaf to the landscape. The models used have different responses to the canopy microclimate (Arneth et al., 2007; Keenan et al., 2011), and different assumptions regarding phenology (Keenan et al., 2009b; Grote et al., 2010). Through temperature effects on emission rates, global BVOC emissions are estimated to have increased by 10% over the past 30 years. Future temperature increases are forecast to further increase BVOC emissions by an additional 30% or more (Peñuelas and Staudt, 2010), though large uncertainties exist with regard to the future response of emissions to changes in temperature (Keenan et al., 2009a) and atmospheric CO_2 (Arneth et al., 2007). Although current emissions inventories account for vegetation phenology and growing season length, future projections of emissions are uncertain because phenology models themselves diverge under future

climate change (e.g., Migliavacca et al., 2012). We are not aware of studies where the climate system feedbacks, and uncertainties, associated with phenologically-driven changes in BVOC emissions have been explicitly quantified.

4. Modeling and forecasting phenology

Models to predict phenological transition dates are needed for a variety of applications, including (1) inferring the physiological mechanisms or environmental thresholds and drivers that control phenology (Migliavacca et al., 2012); (2) forecasting (and hindcasting) of climate change impacts on phenology (Morin et al., 2009; Ibanez et al., 2010); and (3) representing the seasonal trajectory of vegetation development and senescence, and associated physiological activity, in large-scale models (Richardson et al., 2012). Here we provide a very brief overview of phenological modeling, and suggest ways in which future modeling efforts might best make progress.

Most work to date has focused on developing predictive models for flowering and leaf-out in temperate and boreal ecosystems. Recent examples include Linkosalo et al. (2008, 2009), Richardson and O'Keefe (2009), Kaduk and Los (2011), Fu et al. (2012), and Migliavacca et al. (2012). By comparison, few modeling analyses of autumn senescence have been published (Richardson et al., 2006). There is, however, increasing recognition that this is an area where additional work is needed (Delpierre et al., 2009; Vitasse et al., 2011).

Phenology models for other biomes have also received considerably less attention, although Knorr et al. (2010) and Stöckli et al. (2011) used satellite data to constrain model parameters for a range of climate zones and plant functional types, including grasslands and both evergreen and deciduous tropical forests. Similarly, Archibald and Scholes (2007) used satellite data to constrain a green-up model, based on soil moisture and photoperiod, for African savanna. Choler et al. (2010) developed an ecohydrology model, calibrated to satellite data, to predict phenology in a semi-arid tropical grassland. It is not surprising, perhaps, that these four studies all used satellite observations as model constraints, because in many biomes the ground observations that are needed for model development, calibration, and testing are simply not available.

Important advances in phenological modeling have also been made using observations on cloned plants growing in different environments. For example, data on the phenology of lilac (*Syringa*) and honeysuckle (*Lonicera*) clones were recorded, for several decades, by a cooperative network of observers across North America. Schwartz and Marotz (1986) and Schwartz and Reiter (2000) used these data to develop a set of "Spring Index" models, which have most recently been used to assess the impact of recent warming trends on spring onset across the northern hemisphere (Schwartz et al., 2006). In Europe, the International Phenological Gardens (IPG) program was established beginning in 1959. This is a network of common gardens, now spanning more than 30° of latitude, at which observations on genetically identical clones of over 20 common temperate species are recorded using a standardized protocol. At present, there are 89 gardens in 19 different countries. Data from the IPG have been used to develop temperature-based models with which the impact of climate variability and change on spring phenology (Menzel and Fabian, 1999), and spatial patterns in spring onset (Rötzer and Chmielewski, 2001) have been studied. The main advantage of using cloned plants is that genetic variability (both within and among populations) can be minimized. This enables stronger inference about the environmental controls on phenology. At the same time, however, the lack of genetic variability in the plants being observed is also a significant drawback. Genetically identical clones (particularly of ornamental plants) cannot be considered representative of wild-grown native plants, which may be locally adapted to environmental conditions (e.g. population-level differences in thermal forcing requirements for budburst). Accounting for genetic variability in phenological models remains an outstanding challenge, as is the development of generalizable phenological models (discussed more fully below).

Fig. 7. Digital camera images can be analyzed and used to obtain quantitative data on the seasonal patterns of development and senescence of terrestrial vegetation in different ecosystems. The top image, from the Harvard Forest (Massachusetts, USA) Little Prospect Hill tower, shows the onset of autumn coloring in a temperate deciduous forest. The bottom image, from the Konza Prairie (Kansas, USA) Natural Area, shows the greenup of tallgrass prairie in early summer. Images courtesy of the PhenoCam network (http://phenocam.unh.edu/).

In recent years, some novel approaches to modeling phenology have been proposed (e.g. the "promoter-inhibitor" model of Schaber and Badeck, 2003; the "growing season index" model of Jolly et al., 2005; and the carbon-gain-based model of Arora and Boer, 2005). However, most recent analyses continue to be based around paradigms that have been in wide use for several decades (Sarvas, 1972; Cannell and Smith, 1983; Hunter and Lechowicz, 1992; Kramer, 1994; Chuine et al., 2003; Hänninen and Kramer, 2007). These models are all based around the degree-day concept, although in some cases photoperiod controls or chilling requirements are incorporated as well. Even the "unified model" proposed by Chuine (2000) is essentially an extension of earlier work, in that various configurations and functional forms for accumulation of chilling (cold temperatures required to break dormancy) and forcing (warm temperatures required for bud-burst) are generalized to a single model with 9 parameters. While none of these examples is really "process-based" in the literal sense, these models are more mechanistic (and more complex, as they require that developmental states be tracked through time) than wholly empirical

regression models that are based on the average environmental conditions over a specific time window (e.g., average temperature during spring months of April–June) (Estrella and Menzel, 2006; Primack et al., 2009b; Ibanez et al., 2010; Lebourgeois et al., 2010).

A limitation of many existing approaches is that while many different model structures can all provide adequate fits to observational data for a single site (Hunter and Lechowicz, 1992), over-fitting is common, and models often perform poorly when tested against data that were not used to constrain the model (e.g. Chuine et al., 1998). Validation is thus essential. This can be done in a variety of different ways, including (1) dividing the available data into two groups, e.g. odd years for the calibration group, even years for the validation group (Chuine et al., 1998); (2) using *k*-fold cross-validation, e.g. leave-one-out approaches (Melaas et al., 2012); or (3) using wholly independent data sets, e.g. site A for calibration, site B for validation (Chuine et al., 1999; Richardson et al., 2006; Morin et al., 2009). In addition to validation, we also recommend that uncertainties in model predictions be fully propagated. Migliavacca et al. (2012) provide a framework by which three different sources of uncertainty (related to uncertainty in model parameters, uncertainty in model structure, and uncertainty in model drivers) can be quantified. Finally, we suggest that formal model selection procedures (e.g., Akaike's Information Criterion) be adopted in future studies, and that "Akaike weights" be used for averaging across an ensemble of models (Turkheimer et al., 2003; Migliavacca et al., 2012).

The ideal phenology model should be generalizable. By this we mean that it should perform well beyond the specific conditions to which the model parameters were tuned. Thus, the model should function across the entire native range of a species (or plant functional type, if that is the level at which modeling is being conducted), and make good predictions under both current conditions and future climate scenarios. For these conditions to be met, it is essential that observational data come from as wide a range of environmental or climatic conditions as possible. For example, the analysis by Schaber and Badeck (2003) used a vast (1500 or more observations, for each of five different species) database compiled by the German Weather Service, while Lebourgeois et al. (2010) used a decade of observations from a network of forest plots from the French RENECOFOR network. Few data sets like these are available to modelers. However, the eddy covariance measurements of surface-atmosphere exchanges of CO_2 from FLUXNET can be mined to obtain valuable insights into phenology at hundreds of research sites around the globe, and these data are just starting to be exploited for phenological modeling purposes (Baldocchi et al., 2005; Melaas et al., 2012). Near-surface remote sensing data, including measurements of canopy reflectance and transmittance (Jenkins et al., 2007; Ryu et al., 2010; Garrity et al., 2010), as well as digital imagery from "PhenoCams" (Fig. 7; Richardson et al., 2009b; Sonnentag et al., 2012; http://phenocam.unh.edu/), could also be leveraged for model development and testing. Finally, data from warming experiments are potentially valuable (but see Wolkovich et al., 2012) because the experimental treatment can push species into novel climate spaces that are beyond the range of natural variability under current conditions. Experimental data can thus provide greater power to falsify model predictions and distinguish among candidate model structures (Hänninen, 1995).

With respect to the three modeling applications mentioned above, and in the context of the present review, the representation of phenology in state-of-the art terrestrial biosphere models tends to be poor. This causes large biases in the modeled seasonality of processes and climate system feedbacks that are phenologically-mediated (Levis and Bonan, 2004; Kucharik et al., 2006; Randerson et al., 2009). For example, the analysis by Richardson et al. (2012) showed that existing models tend to substantially over-estimate the length of the growing season in temperate deciduous forests, with spring onset of photosynthesis coming too early, and autumn dormancy too late (Fig. 8). This finding is particularly surprising—or discouraging—given the focus that has historically been placed on studying deciduous forest phenology. Richardson et al. (2012) concluded that if models are unable to predict phenology successfully under current climate scenarios, it is highly unlikely that they be able to make good predictions under future climate scenarios. Furthermore, in addition to causing errors in modeling CO_2 exchange, it is probable that other key feedbacks of vegetation to climate are also misrepresented because of errors in phenology. Related to this, we note that the analysis by Keenan et al. (2012) demonstrated that failure to accurately predict phenology is a key reason why many of these types of models are unable to predict interannual variability in either GEP or net CO_2 uptake.

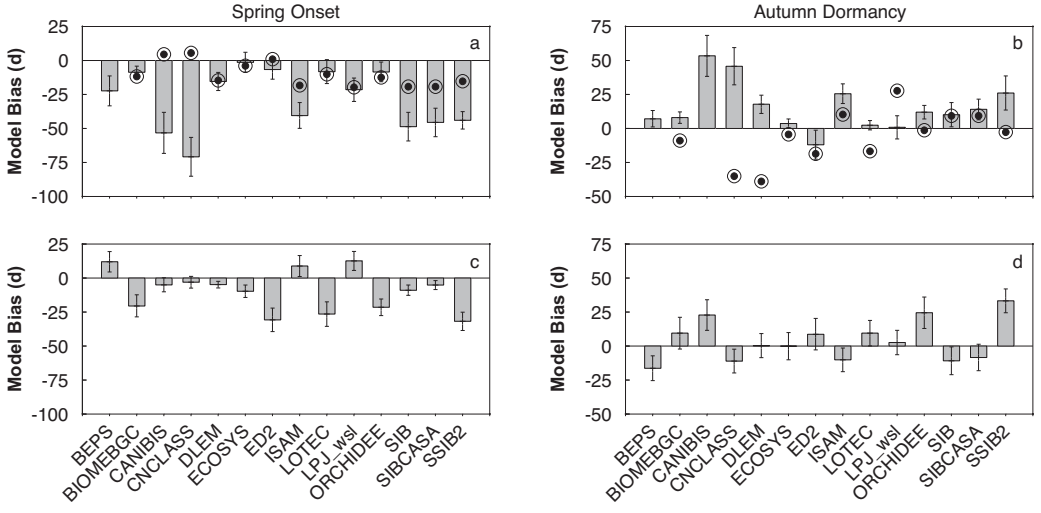

Fig. 8. State of the art terrestrial biosphere models (14 models, arranged along the *x*-axis) consistently predict that spring onset of photosynthesis occurs too early, and autumn dormancy too late, in North American deciduous broadleaf forests (data for Harvard Forest, Massachusetts, USA, shown in panels a, b), while there is no consistent bias for evergreen needleleaf forests (data for Howland Forest, Maine, USA, shown in panels c, d). The sign convention is that a negative bias means that the model predicted the event occurred before it was observed to occur. Spring onset and autumn dormancy were determined from time series of gross ecosystem photosynthesis (GEP), derived from eddy covariance measurements of net ecosystem exchange (NEE) of CO_2. For deciduous sites, circular symbols indicate corresponding bias in the seasonality of leaf area index dynamics. North American Carbon Program Site Synthesis data are from Richardson et al. (2012).

Improvements to models of phenology, especially the switches that control leaf-out, development and senescence, and the interactions between phenology and surface-atmosphere exchanges of carbon, water, and energy, are therefore needed. Better predictions of the future impacts of climate change on phenology are required to reduce uncertainties of prognostic earth system models (Randerson et al., 2009), and are also a key to predicting shifts in interspecific competition and species range (Morin et al., 2008; Chuine, 2010). The importance of getting phenology "right" in these large scale models, particularly those with dynamic vegetation, cannot be under-estimated (Schwartz, 1992; Levis and Bonan, 2004). The brief summary presented here underscores the need for additional work towards this goal.

5. Conclusion

In recent years, there has been surge of interest in the field of phenology. Scientists now recognize the relevance of phenology to global change science. For example, documented shifts in phenology serve as robust indicators of the impacts of climate change and variability on natural and managed ecosystems. Furthermore, climate change impacts on both community structure and ecosystem function will be partially controlled by the response of the phenology of individual organisms to climate change.

In this review, we have emphasized the importance of phenology as a factor that mediates vegetation feedbacks to the atmosphere and climate system through a diverse set of processes and mechanisms including albedo, surface roughness length, canopy conductance, water and energy fluxes, photosynthesis and CO_2 fluxes, and fluxes of BVOCs. We have identified several critical knowledge gaps that are in need of further research:

(1) In many ecosystems, but particularly in the tropics, we need to better understand the environmental drivers controlling phenology. Even in well-studied temperate and boreal ecosystems, the role of photoperiod is not yet fully understood. Finally, most attention to date has focused on phenological events at the start of the growing season. More work is needed to understand how phenological events at the end of the growing season are being affected by climate change.
(2) The ways in which feedbacks of vegetation to the climate system are mediated by phenology is quite well understood. However, despite a conceptual understanding of how these feedbacks may be influenced by climate change, we are in most cases unable to provide quantitative estimates of the magnitude of these shifts (CO_2 fluxes are an exception). Thus, we lack an understanding of exactly how much a one-week shift in spring onset or autumn senescence may impact the annual surface energy budget, surface temperatures, or regional precipitation. We need to be able to quantify these impacts, and identify the common patterns across different biomes and climate zones.
(3) Improved modeling of phenology, and phenologically mediated feedbacks to the climate system, is an essential prerequisite for improving the current-generation of global-scale models that couple the atmosphere and the biosphere. This relies on progress towards (1) and (2).

Acknowledgments

The Richardson Lab acknowledges support from Northeastern States Research Cooperative, the National Science Foundation's Macrosystem Biology program (award EF-1065029), the US National Park Service Inventory and Monitoring Program and the USA National Phenology Network (grant number G10AP00129 from the United States Geological Survey), and the NOAA Climate Program Office, Global Carbon Cycle Program (award NA11OAR4310054). We thank the PIs of sites used in Fig. 4 for making their data publicly available. The contents of this paper are solely the responsibility of the authors and do not necessarily represent the official views of NSF or USGS.

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