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Leaf-out phenology of temperate woody plants: from trees to ecosystems

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Summary

Leafing-out of woody plants begins the growing season in temperate forests and is one of the most important drivers of ecosystem processes. There is substantial variation in the timing of leaf-out, both within and among species, but the leaf development of almost all temperate tree and shrub species is highly sensitive to temperature. As a result, leaf-out times of temperate forests are valuable for observing the effects of climate change. Analysis of phenology data from around the world indicates that leaf-out is generally earlier in warmer years than in cooler years and that the onset of leaf-out has advanced in many locations. Changes in the timing of leaf-out will affect carbon sequestration, plant–animal interactions, and other essential ecosystem processes. The development of remote sensing methods has expanded the scope of leaf-out monitoring from the level of an individual plant or forest to an entire region. Meanwhile, historical data have informed modeling and experimental studies addressing questions about leaf-out timing. For most species, onset of leaf-out will continue to advance, although advancement may be slowed for some species because of unmet chilling requirements. More information is needed to reduce the uncertainty in predicting the timing of future spring onset.

I. Introduction

The emergence of leaves on deciduous trees signals the transition from winter to spring and the onset of the growing season in temperate forests. The timing of this transition – from leafless, dormant trees to branches tinged with green – has enormous implications across ecological scales ranging from individual trees to the global climate. The study of the annual timing of developmental events is known as phenology (Badeck *et al.*, 2004; Forrest & Miller-Rushing, 2010). Extensive evidence has shown that over the past few decades, global climate change has been responsible for forcing rapid changes in the phenology of many species and communities, including the leaf-out of temperate and boreal woody plants (Myneni *et al.*, 1997; Menzel, 2000; Parmesan, 2006; Primack *et al.*, 2009). Understanding the mechanisms and controls regulating leaf-out, how these mechanisms differ among species, and how the timing of leaf-out in plant species, populations, and communities will be affected by climatic changes, would be helpful in the management and conservation of natural areas and in forecasting future changes in the carbon budgets of ecosystems.

Although the exact physiological mechanisms and interactions that control leaf-out are still not known for most plant species, it is understood that leaf development in most species is extremely sensitive to temperature (Perry, 1971; Linkosalo *et al.*, 2006). This close relationship to temperature leads to large year-to-year variation in the timing of spring onset. Differences in responses to regulating mechanisms account for variation in leaf-out times among species (Lechowicz, 1984). While interannual variation is expected, anthropogenic global climate change has led to significant directional changes in the onset of spring across the world that cannot be attributed solely to normal year-to-year variation (Schwartz & Reiter, 2000; Parmesan, 2006; Ibanez *et al.*, 2010). This shift in leaf-out timing results from the dominant role that temperature plays in vegetative development, making plants highly responsive to, and an excellent indicator of, changes in climate. Monitoring plant phenology, especially flowering time, is a popular approach through which to study the biological effects of recent climate change (Menzel & Fabian, 1999; Menzel *et al.*, 2006).

How plants respond to climate change has significant consequences for world ecosystems. Changes in the length and timing of the growing season, and shifts in the habitat ranges of plant species, can have substantial effects on ecosystem dynamics such as carbon and water cycling and plant–animal interactions (White *et al.*, 1999; Parmesan, 2006; Piao *et al.*, 2008), as well as possible economic effects for industries relying on tree species, such as apple, peach, and maple sugar production (Chmielewski *et al.*, 2004; Eccel *et al.*, 2009). The timing of leaf-out may affect individual plants by allowing for greater rates of photosynthesis, influencing production of biomass, or by putting the plant at risk of damage from a late frost (Menzel & Fabian, 1999; Doi & Katano, 2008). The enormity of the effect that leaf-out timing has on so many processes of temperate forests makes understanding the processes and responses of bud-burst critical both for understanding current ecology and for accurately modeling future forest and tree-crop dynamics (Wesolowski & Rowinski, 2006).

During the past few years, the range of people interested in leafing-out phenology has grown, as have the methods employed to study it, largely as a result of its relevance to global climate change (Forrest & Miller-Rushing, 2010; Polgar & Primack, 2011). In fact, in papers associated with the ISI Web of Science, the proportion of papers that mention 'phenolog' along with 'climate' has been rising steadily since 1990 (Sparks *et al.*, 2009). In this technologically focused age, we are developing new methods with which to continue this centuries-old trend of monitoring natural events, such as using satellites and digital cameras, that can greatly expand the ability of researchers to study the trends in current timing of leaf-out and to model those of the future (Zhang *et al.*, 2004; Delbart *et al.*, 2008).

In order to quantify long-term variation in leaf-out timing, it is necessary to have historical records of these events. Fortunately, there is a long history of interest in phenological monitoring from around the world, particularly in Asia and Europe, where historical phenological records, some over 1000 yr old, have been discovered (Wolfe *et al.*, 2005; Aono & Kazui, 2008). Although most records are more recent than these, sufficient historical data exist to offer a clear picture of leaf-out history in many parts of the world (Sparks *et al.*, 2009). These records vary widely in their scope and length, but they have made possible much of the contemporary research into the phenological effects of climate change and have led to some important discoveries.

Several recent papers have applied an ecological perspective in reviewing studies detailing changes in plant phenology as a result of climate change (Parmesan, 2006; Cleland *et al.*, 2007; Rutishauser *et al.*, 2009). Cleland *et al.* (2007) give a particularly noteworthy examination of the literature, approaching the subject of changing plant phenology from different angles, including modeling, observational and experimental studies, and remote sensing work. In this present review, we look exclusively at leaf-out phenology, focusing on the factors that control leaf-out and the changes over time, at both the level of particular species and that of ecosystem processes. We also examine the physiological differences among species in order to explain the large differences in leaf-out times within a single plant community. We discuss specific leaf-out phenology monitoring programs and techniques, and the effect that warming has had on the leaf-out dates of different species. We also explore the possibility of changing species composition and phenology in temperate forests as a result of

shifting ranges caused by the ongoing warming of our climate.

II. What triggers a plant to leaf-out?

Within any temperate plant community, trees and shrubs vary widely in leaf-out times, both among and within species (Lechowicz, 1984). Variation is seen year-to-year, but can also be observed in one growing season among individuals in different microhabitats within one population. Sugar maple (*Acer saccharum*) seedlings growing in the understory will often leaf-out earlier than adults in the canopy, thus taking advantage of the light availability that will be sharply decreased once the forest canopy fills in (Kwit *et al.*, 2010). Individuals of the same species often have different requirements for leaf-out based on geographic location. In Norway, Scots elm (*Ulmus glabra*) individuals in different locations leaf-out at different times, even when growing under similar conditions; individuals from inland populations generally leaf-out before those from coastal regions (Myking & Skroppa, 2007). The high sensitivity of bud and leaf development to temperature makes variation in leaf-out a normal occurrence, and an adaptive trait that ensures maximization of growing season length while minimizing the danger of frost damage (Kramer *et al.*, 2010). The exact combination of factors and the genes involved in triggering leaf-out are still largely unknown for most species (Howe *et al.*, 2003). At the simplest level, most experts agree that a combination of temperature and photoperiodic cues is responsible for the timing of budburst in most temperate woody plants.

1. Temperature

Air temperature is the most important factor in regulating budburst and leaf-out in temperate and boreal woody plants (Linkosalo *et al.*, 2006). The aspects of temperature that most influence leaf-out timing can be broken down into two components: sufficient chilling in the winter, and warm temperatures in the spring that allow for the subsequent development of buds to the point of bursting (Hunter & Lechowicz, 1992). The term 'chilling requirement' refers to the obligate exposure of plants to cold temperatures for a period of time before they break dormancy. The specific amount of exposure to cold temperatures required to meet this chilling requirement differs among species (Morin *et al.*, 2009). Freezing temperatures are not required to fulfill the chilling requirements of most species; for many species of temperate trees and shrubs, 12°C seems to be a temperature threshold below which both the induction of dormancy in late fall and the breaking of dormancy in the late winter occur (Heide & Prestrud, 2005). Although 12°C is a threshold, the optimal temperature at which chilling occurs for most species is *c.* 6°C, with temperatures

< 0°C and > 10°C, generally not contributing to the chilling requirement (Perry, 1971; Heide & Prestrud, 2005). In addition to the differences among species, there is evidence that the position of the bud on the branch also dictates the importance of chilling. For example, in European beech (*Fagus sylvatica*), chilling has a stronger effect on apical buds than on lateral buds (Falusi & Calamassi, 1990). The role of chilling requirements in breaking dormancy in woody plants is still debated by experts, but is generally agreed to differ among species (Vitasse *et al.*, 2009). The period of dormancy is reduced throughout the winter as the individual is exposed to chilling temperatures (Cannell & Smith, 1986). Sufficient chilling is a signal to the plant that it is safe to begin leaf development within the bud (Perry, 1971).

After chilling requirements are met, a certain amount of thermal time (degree days; time above a given temperature threshold; often somewhere between 0 and 5°C) is required for budburst and the unfolding of leaves or flushing of needles (Cannell & Smith, 1986; Heide, 1993). The temperature threshold from which accumulated thermal time begins differs among species, and there is a strong genetic control over requirements (Rousi & Pusenius, 2005; Sanz-Perez *et al.*, 2009). Thermal time required for leaf-out decreases as individuals experience increased duration of chilling, although the exact relationship varies among species (Fig. 1) (Heide, 1993). The rate of development of many species is linearly correlated with temperature and the growing season begins earlier in warmer years (Snyder *et al.*, 1999). In northern Europe, an increase of 1°C can advance the start of the growing season anywhere from 3 to 8 d (Karlsen *et al.*, 2007). While much of the preparation for
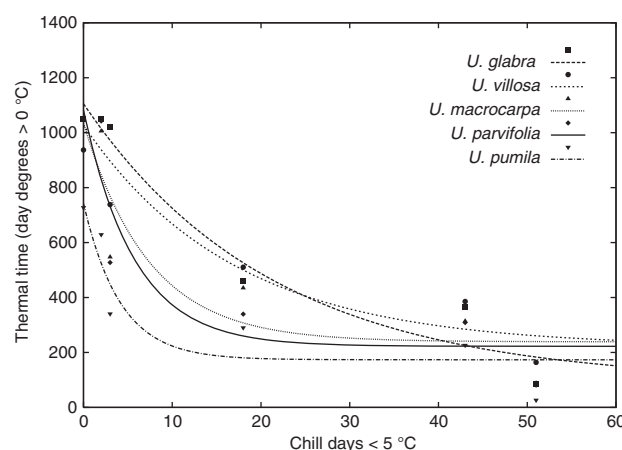
Fig. 1 The thermal time to budburst decreases for five elm species (*Ulmus* spp.) as they are exposed to more days with mean temperatures below 5°C. All species required less thermal time before budburst with increased chilling, but despite the fact that they are members of the same genus, the exact relationships among thermal time, chill days, and budburst are quite varied (figure reprinted from Ghelardini *et al.*, 2010, with the permission of Oxford University Press).

dormancy, such as the growth of new buds, occurs during the summer, temperatures during the summer are reported to have no measurable effect on the timing of leaf-out the following spring (Chuine & Cour, 1999).

2. Photoperiod

Photoperiod is understood to play a role in regulating the leaf-out of some temperate woody plants. Not all species respond to photoperiod cues, and not all populations of a species have the same requirements (Farmer, 1968; Ghelardini *et al.*, 2010). The exact role of photoperiod in timing of leaf-out and its interaction with temperature requirements is not fully understood, but it is better documented for some species than others. For example, studies dating back to the 1960s of Norway spruce (*Picea abies*) confirm the importance of photoperiod to needle flush (Heide, 1974). Sensitivity to photoperiod may be an important defense for plants against the variability of temperature; by taking cues from the amount of night-time darkness experienced, plants can avoid breaking dormancy too early in the event of an abnormally early warm spell (Vihera-Aarnio *et al.*, 2006; Korner & Basler, 2010). Populations of a given species often have differing photoperiodic requirements across a latitudinal gradient, which are known as photoperiodic ecotypes (Partanen, 2004; Vihera-Aarnio *et al.*, 2006). Some species must experience a certain photoperiod for leaf-out to occur, regardless of how high the temperature gets (Caffarra & Donnelly, 2010). In particular, long-lived trees of mature forests, such as American beech (*Fagus grandifolia*), some oak species (*Quercus* spp.), and hackberry (*Celtis occidentalis*), rely on a combination of photoperiod and temperature cues to break dormancy (Caffarra & Donnelly, 2010).

Many early successional opportunistic species such as birches (*Betula* spp.), hazelnuts (*Corylus* spp.), and poplars (*Populus* spp.) do not have a photoperiod requirement to break winter dormancy, but do have chilling requirements (Korner & Basler, 2010). This allows trees to respond more quickly to episodes of warm temperature in early spring, but also creates more susceptibility to late frosts (Korner & Basler, 2010; Caffarra & Donnelly, 2010). Although these species have no photoperiod requirement as such (they can break dormancy given the correct temperature regardless of day length), they are nonetheless able to respond to day-length cues. In many cases, exposure to longer days and shorter nights allows them to break dormancy even if the chilling requirement has not been met (Farmer, 1968). A third group of species, which includes mostly ornamental plants from warmer climates such as domestic cherries (*Prunus* spp.), has a leafing strategy linked almost exclusively to spring temperature, with minimal chilling and no photoperiod requirement (Korner & Basler, 2010).

III. Variation in leaf-out among species

There are large interspecific differences in leaf-out timing, even when individuals are exposed to the same conditions (Lechowicz, 1984; Murray *et al.*, 1989). In terms of opportunity for carbon fixation, it should benefit a tree to leaf-out as early as possible in the spring. The cost for early-leafing trees is the danger of a late frost that could damage its leaves and conducting tissues (Bennie *et al.*, 2010). The tradeoff between greater productivity and higher frost risk may play a role in the variation in leafing strategies of different species.

Differences in stem anatomy may partly explain why certain coexisting species tend to consistently leaf-out at different times (Lechowicz, 1984; Sanz-Perez *et al.*, 2009). Diffuse porous species, those that produce uniformly small vessel elements throughout the growing season, tend to leaf-out earlier in the spring, including maples (*Acer* spp.), birches, alders (*Alnus* spp.), and poplars (Lechowicz, 1984). Their smaller vessel elements are less susceptible to embolism during the winter, which allows them to begin to meet demands of transpiration earlier in the growing season (Wang *et al.*, 1992; Barbaroux & Breda, 2002). Ring porous species, such as oaks, ashes (*Fraxinus* spp.), and hickories (*Carya* spp.), have less uniform vessel elements, producing larger vessels in the spring and smaller ones later in the growing season. Their large vessels suffer more damage from winter freezing, requiring them to produce new vessels in the spring to transport water and often leading them to leaf-out later than coexisting diffuse porous species. Although the presence of fewer embolisms in conductive tissue has been found to be linked to earlier leafing, there are many exceptions to this trend, and stem anatomy does not explain all of the variation in foliar phenology (Lechowicz, 1984; Wang *et al.*, 1992).

There are several other factors that likely contribute to the differences in leaf-out time among species. The amount of genetic diversity of a species impacts its ability to respond phenologically to changing temperatures; species with low genetic diversity have far more limited variation in budburst dates across a region than those species with high diversity (Doi *et al.*, 2010). Another theory for explaining differences in leaf-out timing among species is evolutionary response to herbivory pressures (Wang *et al.*, 1992). In two co-occurring varieties of the English oak (*Quercus robur*), one variety leafs-out as much as 5 wk earlier than the other but suffers significantly more herbivore damage, suggesting that the opportunity cost of losing > 1 month of photosynthesis is offset by the decrease in foliar damage (Wesolowski & Rowinski, 2008).

Detecting differences in leaf-out both within and among species – whether during a single growing season across a variable regional landscape or during a time-frame of years,

decades, or centuries – requires a system of phenological monitoring to compare springtime events with those of the past in order to observe temporal trends.

1. Monitoring leaf-out

Phenological changes in response to a changing climate, unlike changes in population size or distribution, can be relatively easy to detect, which is one reason for the popularity of phenological studies for climate change research (Forrest & Miller-Rushing, 2010). Quantifying what constitutes leaf-out or budburst, however, is not straightforward, and definitions vary from study to study. For example, Project Budburst, an American citizen-science phenology network, considers the first-leaf date to be the day on which there are completely opened leaves, in which the leaf stem or base is visible, on at least three places on the tree or shrub. A similar, but slightly different, definition is used by the International Phenological Gardens (IPG) in Europe, where a plant is considered to have leafed when the first regular surfaces of the leaf are visible in three to four places on the plant (Chmielewski & Rotzer, 2001). In Germany, a comprehensive phenological scale has been developed for a wide variety of crop plants. The scale, which also describes plant phenophases in general, is called the **B**iologische **B**undesanstalt, Bundessortenamt and **Ch**emical Industry (BBCH) scale. A cooperative effort between several governmental agencies, the scale gives each plant phenological stage a number and defines it. Leaf development is plant principal growth stage 1. Originally intended for use in the agricultural and forestry fields, this scale has been used to define leaf-out in many phenology studies (Nordli *et al.*, 2008; Kalvane *et al.*, 2009). The Spanish government has a similar standardized protocol for phenological studies (Gordo & Sanz, 2010). While a more universal protocol for monitoring leaf-out would be helpful to make more precise comparisons between studies possible, quantification of changes in leaf-out timing have been found to be quite robust across studies despite methodological differences (Parmesan, 2007).

Scientists and others interested in nature have been monitoring the leafing and flowering times of plants for hundreds of years. In Japan, records of the flowering dates of cherry trees date back to 705 BCE; in Europe, flowering records date back to 371 BCE (Aono & Kazui, 2008; Sparks *et al.*, 2009). Although, to our knowledge, there are no American records of equivalent age, there is an extensive dataset of leaf-out dates compiled by Henry David Thoreau for the plant community of Concord, Massachusetts, in the 1850s. The existence of historical records, particularly for flowering dates but also for leaf-out, has proven extremely valuable for determining the effect of climate change on plants (Bradley *et al.*, 1999; Miller-Rushing & Primack, 2008; Ibanez *et al.*, 2010).

Traditional phenological monitoring consists of walking around an area and recording which plants have reached a given phenophase. While that method is still practiced today, the development of new technology has led to a variety of new techniques, such as remote sensing, which are now widely used (Reed *et al.*, 1994; Fisher *et al.*, 2006; Ide & Oguma, 2010). As with definitions of leaf-out, the many methodologies that exist to monitor leaf-out present a challenge for comparing results across different studies (Morisette *et al.*, 2009; Schwartz & Hanes, 2010b).

2. Phenological monitoring by direct observation

Interest in phenology has led to the implementation of leaf-out monitoring projects around the world. For example, the dates of leaf emergence of individual trees and shrubs of several common species have been monitored at Harvard Forest in Massachusetts each spring for over 20 yr (Harvard Forest, http://harvardforest.fas.harvard.edu/). The Japanese Meteorological Agency has been recording leaf-out and other phenological data of marked individual plants in phenological gardens at over 100 weather stations since 1953 (Ibanez *et al.*, 2010). Europe, which also has a rich history of phenological observation, has the IPG, a network of botanical gardens that has planted clones of several species across 89 sites in 19 countries in a concerted effort to establish a large standardized phenology project. The IPG project has been collecting data on leaf-out dates and other phenophases of individual plants since 1951 (Menzel, 2000; Defila & Clot, 2001).

The USA historically has had fewer continental-scale ecological monitoring programs than Europe or Japan (Richardson *et al.*, 2007). One of the few long-term, planned phenology projects in the USA was the planting of lilacs (*Syringia vulgaris* and *Syringia chinensis*) and honeysuckles (*Lonicera tatarica* and *Lonicera korolkowii*) in the 1950s and 1960s (Schwartz, 1994). This project was initiated to monitor phenology with the ultimate goal of improving farming practices. In addition to information generated for farming, it provides a long-term North American dataset that may be used to look at the effect of climate change on important ornamental species (Wolfe *et al.*, 2005). While the USA lags behind Europe in phenological networks, recent efforts have been made to close this gap, and the establishment of the National Phenology Network has created an umbrella organization where new and historical phenological datasets can be gathered in one place (Mayer, 2010).

Although the phenology monitoring schemes that are best represented in the scientific literature are those run by scientists, citizen science projects that include leafing-out times can also be a valuable tool for phenological monitoring, particularly in residential areas (Cooper *et al.*, 2007). The combination of the relative ease with which phenological

observations can be carried out, the abundance of plants in most urban, suburban, and rural areas, and the recent surge of interest in climate change and all things 'green', makes monitoring flowering and leafing-out times a perfect focus for citizen science projects. Although there is much debate as to just how much scientific value these projects provide, with proper oversight and quality control they can potentially generate detailed observations over a wide area (Mayer, 2010). In the USA, Project Budburst and the National Phenology Network's Nature's Notebook program are just two examples of nationwide projects using volunteers to collect phenological data, including the date of first leaf-out for a number of common and easily identifiable species, that participants submit through a website (USA-NPN, http://www.usanpn.org/participate/observe; Project Budburst, http://www.neoninc.org/budburst) (Morisette *et al.*, 2009).

3. Phenological monitoring through remote sensing

Obtaining annual observations of leaf-out dates can be time- and labor-intensive, constraints that often limit studies to a small area around a field station and/or to a small number of focal species. Remote sensing has emerged as a valuable new tool that can effectively monitor leaf-out phenology at a larger scale, such as an entire forest, ecosystem, or region. Remote sensing studies typically use data obtained by sensors aboard orbiting satellites, such as the Advanced Very High Resolution Radiometer (AVHRR) and the Moderate-resolution Imaging Spectroradiometer (MODIS), or equipment aboard Landsat satellites (Reed *et al.*, 1994; Kathuroju *et al.*, 2007; Schwartz & Hanes, 2010b). Data obtained from satellites are used to calculate changes in greenness over a growing season, which offers several options to create data values that will be used to correlate with leaf-out on the ground. Some common methods used for remote sensing data are the point of inflection of the greenness curve and the date at which half of the total leaf cover has developed (Reed *et al.*, 1994).

Several recent papers have shown that regional leaf-out data from satellites can accurately match ground observations, although the method is not without complications (Delbart *et al.*, 2005; Fisher & Mustard, 2007; Liang *et al.*, 2011; Pouliot *et al.*, 2011). For example, difficulties arise from a variety of factors relative to the scale at which the study is being done, the particular source of the data, and the cloud, shadow and other signal noise that can interfere with the collection of data using satellites (Pouliot *et al.*, 2011). In studies examining small areas, there is concern that different topographic features, such as mountains, fields, cities, and lakes, might create errors in the detection of green-up dates. Mixtures of deciduous and evergreen trees can also lead to problems of interpretation. In one study, Fisher *et al.* (2006) used Landsat and MODIS data

and incorporated landscape features into their analysis. Adding landscape feature data into the analysis enabled the research team to detect a delay in leafing-out at the base of hills as a result of cold air drainage, a delay in coastal areas as a result of the cooling effects of the ocean, and a 1 wk delay in leaf-out for deciduous forests in rural areas compared with nearby urban areas (Fig. 2). While such variations in leaf-out dates are sometimes already known from ground observations, the ability to detect such effects using remote sensing greatly extends our ability to map leafing-out over large areas and to detect regional patterns.

While remote sensing techniques capture data at larger scales than on-the-ground monitoring, they are not practical for monitoring individual plants or species. Remote sensing also generally captures only images from the canopy, and overlooks understory vegetation.

Remote sensing is not confined to the use of satellite data; the term can also be applied to 'near-surface' remote sensing approaches for monitoring leaf-out, such as the use of digital cameras mounted in forest canopies. This can be carried out using commercially available cameras, including webcams, point-and-shoot cameras, and digital SLR cameras, making it relatively inexpensive (Crimmins & Crimmins, 2008; Richardson *et al.*, 2009a). Cameras are generally placed in fixed locations that are used to record images of the leaf canopy or individual trees at regular intervals throughout the growing season. Networks of these cameras can fill in the spatial and temporal gaps between localized, labor-intensive monitoring by human observers and regional remote-sensing images; they continuously cover an entire canopy, yet they can still be used with higher resolution, for individual tree, species or community-scale studies, than would be possible with satellite imagery (Richardson *et al.*, 2007; Ide & Oguma, 2010). The use of digital cameras for phenological monitoring is particularly helpful in areas that experience frequent cloud cover and therefore have gaps in satellite data. Cameras mounted in forest canopies are below clouds and are therefore unaffected.

Images from digital cameras can be analyzed to determine the seasonal trajectory of budburst, green-up, and senescence, similar to the analysis done on satellite data. For example, at 12 forests in the northern USA, researchers have set up a network of phenology-monitoring cameras. Seven of the sites in this network also have eddy flux towers that monitor the exchange of CO_2 and water between the atmosphere and the forest. This combination of data from cameras, satellites, and gas sensors is providing crucial information on the relationship between phenology and ecosystem processes, especially carbon uptake and loss (Richardson *et al.*, 2009a). Results of this study and other, similar studies from Japan and elsewhere show that analysis of images from digital cameras can be accurately used to detect the green-up dates of various plant types (Ahrends *et al.*, 2009; Ide & Oguma, 2010). A nationwide phenology
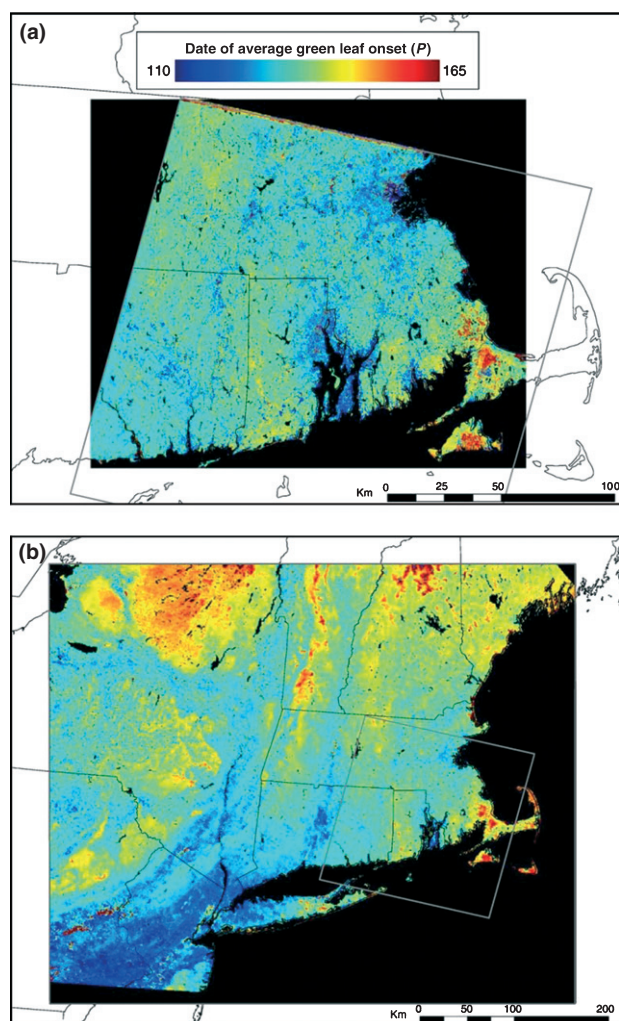
Fig. 2 The average onset of leaf-out in (a) southeastern New England (USA) from Landsat (1984–2002); and (b) a portion of the northeastern USA using MODIS (2000–2005). These images demonstrate that leaf-out occurs later at higher elevations, such as the Adirondacks and White Mountains, at higher latitudes. On Cape Cod, Martha's Vineyard, and Nantucket (islands off the coast of Cape Cod), late leafing-out is generally the result of the moderating influence of the ocean, with particularly late patches occurring as a result of scrub-oak frost pockets. Trees in Boston, New York, and other metropolitan areas leaf-out earlier because of the higher temperatures associated with the urban heat island effect; earlier leaf-out is also seen in warm river valleys. Colors indicate the date on which half of the tree canopy has leafed-out (from day 110 (April 20) to day 165 (June 15)), with earlier onset shown by blue and later onset by orange and red (figure reprinted from Fisher & Mustard, 2007, with the permission of Elsevier).

monitoring project using internet-connected cameras across the USA has been set up by accessing free data from cameras originally set up for nonscientific purposes, such as cameras on highways or at airports (Graham *et al.*, 2010). Searching for these cameras online, the researchers were able to obtain enough high-quality data that they could reliably calculate the date of spring onset across the USA.

IV. Leaf-out and climate change

There is overwhelming evidence that anthropogenic climate change is already affecting phenology (Walther *et al.*, 2002; Root *et al.*, 2003; Parmesan, 2006). In a meta-analysis of the effect of climate change on 677 species of plants and animals, 62% showed advancement of spring events, including bud-burst, flowering, and arrival of migratory birds (Parmesan & Yohe, 2003). The high degrees of phenotypic plasticity in plants and the close relationship between timing of leaf-out and temperature makes spring plant phenology particularly responsive to temperature changes, and therefore one of the best systems in which to observe the effects of climate change (Menzel, 2000; Richardson *et al.*, 2006; Ibanez *et al.*, 2010; Vitasse *et al.*, 2010).

Long-term data sets are invaluable in quantifying the changes occurring over time in leafing onset. Analysis of data collected at the IPG allowed researchers to determine that trees in northern Europe have advanced their leaf-out by an average of 1 wk over the past 50 yr (Fig. 3) (Menzel, 2000). Data gathered by the Japanese Meteorological Agency showed that woody plants such as forsythia (*Forsythia koreana*), ginkgo (*Ginkgo biloba*), and various cherry species leafed-out 2–7 d earlier for every 1°C of warming between 1953 and 2005; it is also true that at a few sites ginkgo trees were actually leafing-out later than they did in the past (Ibanez *et al.*, 2010). In North America, at the Hubbard Brook Experimental Forest in New Hampshire, the onset of leaf-out of American beech, sugar maple (*A. saccharum*), and yellow birch (*Betula alleghaniensis*) has advanced an average of 5–10 d over the past five decades (Richardson *et al.*, 2006).

To help predict how ecosystems, populations, and particular species will respond to climate change, models are being developed in association with climate projections to give us some insight into the future of temperate forests and their associated species. Models range in scope from specific to quite broad. Experimental studies where plants are subjected to simulated future conditions are often used to provide additional insight into future plant phenological changes and to test, or inform, leaf-out models (Hanninen *et al.*, 2007). By examining the future of leaf-out phenology under future climate change, we can more accurately predict the changes to ecosystem processes and species distributions that may result.

1. Ecological interactions at risk from earlier leaf-out?

The possibility of ecological mismatches between different groups of interdependent organisms as a result of rapid climatic changes is a concern across aquatic and terrestrial ecosystems worldwide (Sagarin *et al.*, 1999; Both *et al.*, 2009). While many groups of organisms are responsive to changes in temperature, the response rates across trophic
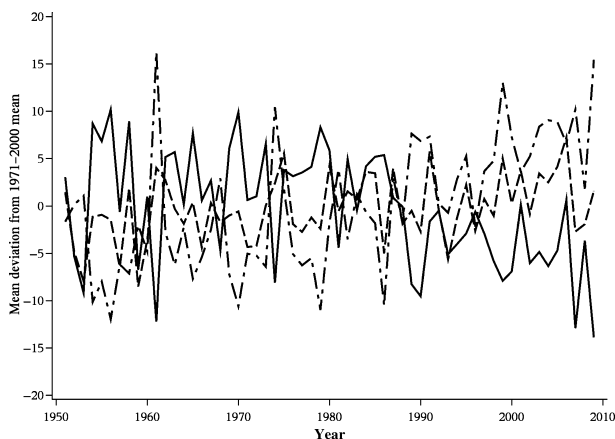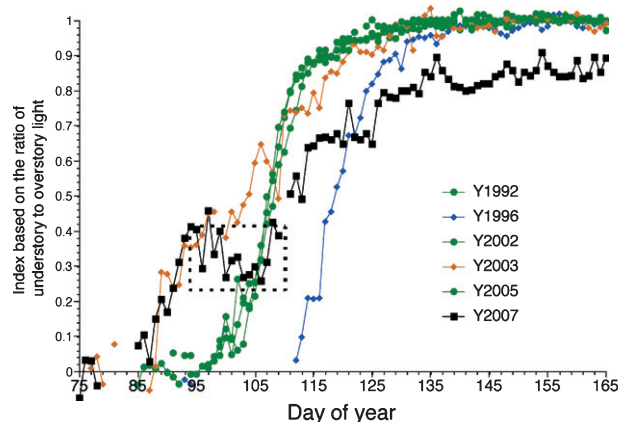
Fig. 3 The yearly anomalies from the 1971–2000 mean for the onset of leaf unfolding (solid line) and leaf coloration (dashed line) and the overall length of the growing season (dashed and dotted line) for *Fagus sylvatica*, *Quercus robur* and *Betula pendula* in central Europe. The anomalies in the length of the growing season were calculated by taking the differences in the spring and autumn anomalies. The onset of autumn is generally less variable than that of spring, and thus spring phenology is the main driver of the changes in growing season length for the time period shown. Spring was quite late in 1970, while other large deviations from the mean were generally toward an earlier spring (updated figure reproduced from Menzel, 2003, with the permission of Springer).

Fig. 4 Canopy development of a temperate deciduous forest in Oak Ridge, Tennessee (USA), in 2007 started out earlier than in previous years, but after suffering foliar damage from a late frost (which occurred during the time outlined by the dashed line box), the forest canopy never developed to the normal degree seen in typical years, such as 1992, 2002, and 2005. Comparing 2007 with a cold year, such as 1996, when canopy development started late but eventually achieved normal levels, it can be seen that fluctuations in spring temperature can be more dangerous to trees than a uniformly cold spring. Spring started early in 2003 as well, although it did not suffer from frost and gives an indication of how the trajectory of canopy development might have looked in 2007 without the late frost. Canopy development was quantified by measuring the amount of light penetrating the canopy, with a fuller canopy intercepting a greater percentage of the light (figure reprinted from Gu *et al.*, 2008, with the permission of the American Institute for Biological Sciences).

levels can be different (Both *et al.*, 2009). For instance, while the flowering dates of almost all plant species in Concord, Massachusetts, are advancing, only certain species of birds arrive earlier in warmer years, other birds do not change their arrival dates, and some species are even arriving later (Miller-Rushing & Primack, 2008; Miller-Rushing *et al.*, 2008). The time at which trees begin to leaf-out determines the availability of food and shelter for many species, particularly insects. It is common for insects to feed only on the young leaves of a particular plant species; as leaves age, they often become tougher and contain compounds that make them unpalatable or poisonous for herbivores (Feeny, 1970; Egusa *et al.*, 2006; Coyle *et al.*, 2010). If these insects emerge too early or late in the spring relative to their food resource, their abundance is likely to decline, as has been reported in populations of winter moths (Visser & Holleman, 2001) and red admiral butterflies (Visser & Both, 2005). Animals such as birds, mammals, and spiders that depend on those insects for food may similarly decline in abundance, creating cascading effects through multiple trophic levels (Philippart *et al.*, 2003; Both *et al.*, 2009).

2. Increased likelihood of frost damage with early spring warming

The increased risk of frost damage to trees and other plants with increased springtime warming was suggested as a possi-

ble threat from global warming as early as the 1980s (Cannell & Smith, 1986). This prediction has been realized in recent years. In 2007 eastern and central North America experienced abnormally warm weather in March, which triggered early leafing-out. Subsequent freezing temperatures in early April caused the young leaves and flowers of woody plants to suffer from serious frost damage. The immediate result was a dieback of young growth. While many trees produced new growth, the canopy never reached the stage of development seen in other years (Fig. 4) (Gu *et al.*, 2008).

In the Trelease Woods of Illinois (USA), the damage from this extreme warming/cooling event varied among species, depending on the individual stage of development. Plants undergoing leaf elongation suffered much more than those that were just bursting their buds (Augspurger, 2009). Because species develop at different rates, the date of leaf-out did not perfectly correlate with amount of damage suffered from frost. Species that burst their leaf buds early but developed slowly were less vulnerable to the late frost than plants that had early budburst and relatively quick leaf development. Species with late budburst and quick development of leaves also suffered high damage (Augspurger, 2009).

Experimental work has shown that in boreal trees, the developmental response to air temperature during dormancy is a good predictor of the likelihood of frost damage; those species that are more responsive to temperature are also most likely to suffer frost damage (Hanninen, 2006). Unfortunately, we are still unable to predict accurately whether frost damage will occur in most phenological models, but it is widely believed that these late frost events causing heavy damage may become more common as climate warming continues (Linkosalo *et al.*, 2000).

3. Predicting the future of leaf-out phenology through models and experimental warming and changes in CO_2 concentrations

Analysis of historical phenological records offers many insights, but these data alone cannot provide clarity about the future responses to climate change needed to understand the ecosystem dynamics related to the timing and length of the growing season (Ibanez *et al.*, 2010; Lebourgeois *et al.*, 2010). To predict how climate change will affect woody plants in coming decades, ecologists, land managers, and horticulturalists rely on results from modeling studies or experimental data, or a combination of the two (Chuine, 2000; Morin *et al.*, 2010). Results from warming experiments can be studied on their own, can be used to validate model predictions, and can also serve as crucial information in constructing models (Hanninen *et al.*, 2007). Despite the advances in modeling, the increasing abundance of historical data and the numerous warming experiments being developed, there are still large uncertainties associated with predicting changing leaf-out dates and resulting ecological consequences under future climate change (Kramer, 1994; Chuine, 2000).

Modeling of phenology has been commonly practiced since the 1970s, with most studies focusing on temperate and boreal ecosystems. Models are created through the integration of information about individual species, communities, or ecosystems, and future climate scenarios. Models range from simple to extremely complex, but are ultimately limited by the information available. As more data on phenological response to climate change emerge, and a better understanding of physiological mechanisms controlling leaf-out develops, more accurate representations of ecosystem dynamics will be possible (Clark *et al.*, 2001; Lebourgeois *et al.*, 2010). The data on individual species come from analysis of historical records or experimental studies (Murray *et al.*, 1989; Ibanez *et al.*, 2010). Depending on the complexity of the model, different factors are included or omitted. For example, some models predicting budburst take into account only the warm forcing temperatures, others also account for the need for a chilling requirement to be met, and still others take into account the increased need for warm temperature with decreased exposure to chilling (Murray *et al.*, 1989; Chuine, 2000; Morin *et al.*, 2009; Lebourgeois *et al.*, 2010). Model outputs can help to predict how species and ecosystems will respond to future climates, and give insight into shifts in species abundance and distribution. Phenological models can be linked to general climate change models, making the models more dynamic and reducing some uncertainty in model outputs (Fig. 5) (Rotzer *et al.*, 2004, 2010).

The two most dramatic impacts of global change that have already affected, and will continue to influence, temperate plant communities are increasing temperatures and CO_2 concentrations, both of which have been the focus of experimental studies on leaf-out phenology. Experimental studies replicating future climate scenarios are an important tool for investigating the future of leaf-out phenology because they increase the information available for building models and making management decisions (Clark
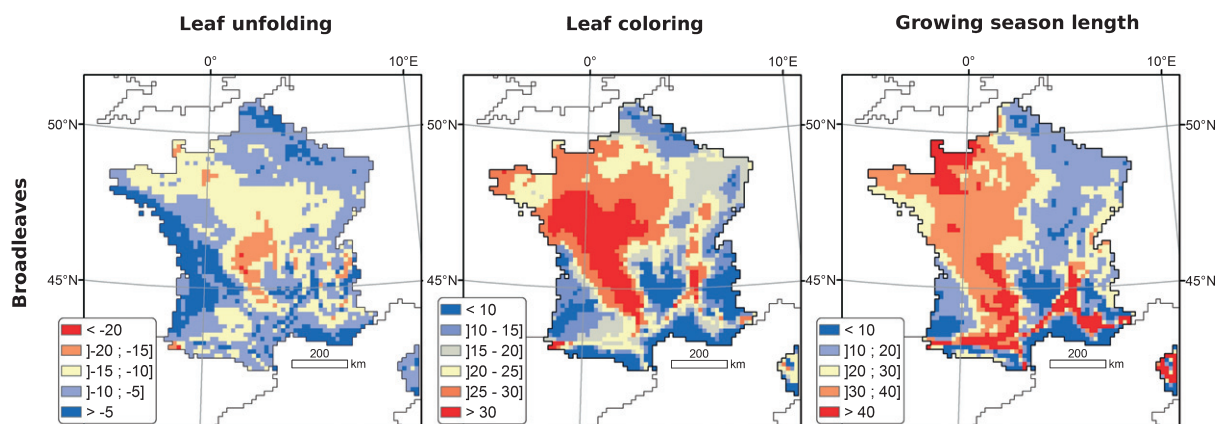
Fig. 5 The predicted change (in d), for date of leaf unfolding, onset of leaf color, and length of the growing season for broadleaved trees in temperate forests of France for the period 2071–2100 from the mean values of the period 1991–2000 under the climate scenario A2-HadCM3 (figure reprinted from Lebourgeois *et al.*, 2010, with the permission of Springer).

et al., 2001). Setups vary among environmental manipulation studies. Some common methods include the use of open- or closed-top field chambers where air temperature is manipulated (Norby *et al.*, 2003; Kilpelainen *et al.*, 2006; Walker *et al.*, 2006), heating plots with radiant heaters, or taking advantage of a naturally occurring temperature gradient that exists along an altitudinal or latitudinal gradient (Vitasse *et al.*, 2010). Other studies have used electric heating cables to warm canopy-level branches of mature trees (Nakamura *et al.*, 2010). Another approach is to install heating cables in the ground to warm the soil and root system. Warming has been found to induce earlier leaf-out in many studies (Repo *et al.*, 1996; Norby *et al.*, 2003; Morin *et al.*, 2010). Other studies have enriched the air around plants with additional CO_2, but have found that the concentration of CO_2 does not have a consistent effect on leaf-out timing (Asshoff *et al.*, 2006; Kilpelainen *et al.*, 2006; Morin *et al.*, 2010). Although less research has been undertaken to examine the effects of precipitation on spring vegetative phenology in temperate ecosystems, published research suggests that the relationship is not very strong, unlike the relationship between vegetative phenology and precipitation in dryland habitats such as deserts and tropical deciduous forests (Ogle & Reynolds, 2004; Sherry *et al.*, 2007; Morin *et al.*, 2010).

With the abundance of phenology modeling and experimental warming studies in the literature, there are also myriad predictions for the future timing of leaf-out. Results from most studies suggest that the advance in leaf-out for most species, in most locations, will likely continue in coming decades as average temperatures continue to rise (Morin *et al.*, 2009, 2010; Lebourgeois *et al.*, 2010). For a given climate scenario, the magnitude of these advances depends on several factors, including the location of a population within the species range, the phenotypic plasticity of a species, and the specific physiological factors that control leaf-out (Rotzer *et al.*, 2004; Vitasse *et al.*, 2010). Many temperate tree species will show particularly large advances in leaf-out at higher latitudes (Morin *et al.*, 2009). Increases in temperature to the point where some species are not able to fulfill their chilling requirement changes the rate of budburst advancement for populations of certain species, particularly those populations at the southern end of species' ranges (Morin *et al.*, 2009; Schwartz & Hanes, 2010a). Examples of species for which chilling requirements may be unmet by the end of the century include black ash (*Fraxinus nigra*) and sugar maple in the southern USA (Morin *et al.*, 2009) and European beech (*Fagus sylvatica*) in Europe (Kramer *et al.*, 2010; Vitasse *et al.*, 2010). In fact, in some high-latitude locations, warmer winters have already led to a delay in spring as a result of chilling requirements not being fulfilled (Yu *et al.*, 2010).

4. Changes in abundance and distribution

How will the distribution and abundance of species be affected by changes in the timing of leaf-out? If species with minimal photoperiod and chilling requirements continue to leaf earlier in the spring, they may increase their abundance and distribution to become the dominant species, and shift the leafing-out time of the whole forest. On the other hand, the unmet chilling and photoperiod requirements of other species may significantly slow the advance of leaf-out at the whole forest level (Morin *et al.*, 2009). These divergent possibilities emphasize the importance of phenological observations at several scales.

Another consideration is the degree to which plants will be able to advance leaf-out in response to warming with a purely phenotypic response, and at what point genetic adaptations of the physiological mechanisms regulating budburst need to occur if species are to remain competitive in new climatic conditions (Billington & Pelham, 1991; Kramer *et al.*, 2010; Vitasse *et al.*, 2010). Phenology is known to be a heritable trait with high variability within species and populations, suggesting that plants may be able to undergo genetic changes in response to new conditions over the course of several generations (Chuine, 2010). Leafing phenology in temperate plants is also highly plastic, allowing them to survive variability in weather conditions. Despite this plasticity and suggestion of ability for rapid genetic changes, evidence of plant distribution shifts, often involving contractions of their ranges, indicates that some populations may have already passed the point at which they can respond with plasticity and populations have not evolved to new conditions quickly enough to maintain their previous range (Jump & Penuelas, 2005).

While species with low plasticity and adaptability may suffer under warming conditions, other species will likely thrive. The earlier leafing-out times of many exotic shrubs, such as buckthorn (*Rhamnus cathartica*) and several honey-suckle (*Lonicera* spp.) species, may help to explain why these species are increasing in abundance in northern American forests to such a large degree (Harrington *et al.*, 1989). Their earlier leafing-out times may give them a competitive advantage over native species with more restrictive requirements for leafing-out (Willis *et al.*, 2010). The increase in abundance of invasive exotics, many of which have early leaf-out times, is likely to become an increasing ecological threat to native species.

5. Economic considerations

The impact of unmet chilling requirements and risk of frost damage from global change on agricultural orchards, and the resulting possibility of a severe economic impact and reduction in food production, should not be overlooked. Crops including, but not limited to, walnuts, peaches, and

plums have been found to be susceptible to frost damage. Apples, cherries, and pears are likely to be even more at risk, with the area of suitable chilling requirements virtually disappearing in many current fruit-growing areas by the end of the 21st century according to one study (Luedeling *et al.*, 2009). Some of these same crops and others are also at risk of frost damage to their flowers and young fruits should they experience warming followed by a severe cold snap (Cannell & Smith, 1986; Eccel *et al.*, 2009). Timber and paper pulp production can also be negatively impacted when young leaves and twigs are damaged by a frost after leaf-out (Fady *et al.*, 2003). Given the long time period needed to establish productive, mature orchards, production forests, and woodlots, accurate climate change predictions and phenological models are essential to diverse tree-based industries.
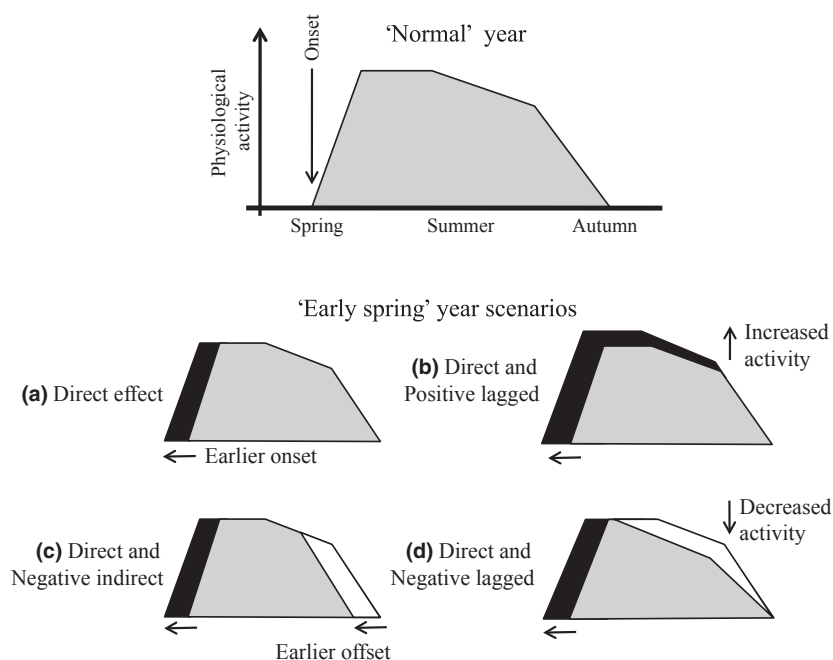
6. Vegetative phenological changes affect ecosystem processes

The timing of the leaf flushing, and the corresponding growing season length, can have important impacts on ecosystem processes, including the uptake of CO_2, tree growth, microclimate, and water movement (White *et al.*, 1999; Morisette *et al.*, 2009). When they leaf-out, canopy trees alter the water and light environments of coexisting organisms. Earlier leaf-out leads to the canopy intercepting more of the incoming solar radiation and precipitation, leading to reduced throughfall, soil water, and soil evaporation (White *et al.*, 1999). Timing of leaf-out has also has strong controls over rates of water uptake by trees (Tabacchi *et al.*, 2000).

The reduced light and water availability on the forest floor could have negative consequences for herbaceous understory plants, which generally need high intensities of light early in the growing season to complete their life cycle (Graves, 1990).

In many higher-latitude forests across the globe, the growing season is not just expanding at the front end, but is also ending later, leading to a longer overall growing season (Menzel & Fabian, 1999; Piao *et al.*, 2008). A simplistic and commonly held view of the relationship between the length of the growing season and carbon sequestration is that if leaf-out occurs earlier in the spring and senescence occurs later in the autumn, there will be an increase in the net amount of carbon sequestered in the forest (Richardson *et al.*, 2010). The exact effect of phenological shifts on ecosystem processes is not always straightforward and it could affect productivity in several ways (Fig. 6). This has been supported by several studies, including a study by Richardson *et al.* (2010) in which the earlier onset of spring did result in an increase of carbon sequestered in deciduous forests and, to a lesser degree, in coniferous forests (Chen *et al.*, 1999; Barr *et al.*, 2002; Richardson *et al.*, 2009b).

Ecosystem respiration rate, however, is also increased by temperature, which can reduce the net carbon gained by an ecosystem. In some temperate systems, there is evidence that respiration has more control over net ecosystem carbon exchange than gross primary productivity (Valentini *et al.*, 2000). Dunn *et al.* (2007) found that the carbon losses from increased rates of respiration canceled out gains in sequestration obtained through a longer growing season.

Fig. 6 A representation of different possibilities for the way that vegetative phenology can affect ecosystem processes or physiological activity. Four possibilities resulting from an early spring are presented and contrasted to the productivity of a 'normal' year through direct and indirect as well as positive and negative lagged effects on productivity. Black shading indicates an increase in productivity and white space indicates productivity decreases (figure reprinted from Richardson *et al.*, 2010, with the permission of Royal Society Publishing). MODIS, Moderate-resolution Imaging Spectroradiometer.

Other research has shown that with a longer growing season, increases in carbon losses through respiration can outpace gains made through photosynthesis, thereby reducing the strength of the carbon sink in forest ecosystems (Milyukova *et al.*, 2002; Piao *et al.*, 2008). Currently there is no consensus over which process will end up dominating, and more data, as well as a better understanding of the role of increased CO_2 concentration, are needed to elucidate these relationships. The direction and extent to which changes in climate and subsequent changes in growing season length will affect rates of carbon sequestration in temperate and boreal forests remain uncertain (Grace & Rayment, 2000; Barr *et al.*, 2002).

V. Conclusions

Throughout the world, forests are being altered in many ways by the rising temperatures associated with global climate change, and the earlier leafing dates of trees and shrubs represent one such example. Earlier leaf-out dates are expected to continue in coming decades across much of the world's temperate regions (Morin *et al.*, 2009; Lebourgeois *et al.*, 2010). Over a longer period of time, some trees species may be extirpated on a local scale and shift their ranges in response to the changing climate (Morin *et al.*, 2009). Because there is a wide variation among species in leafing-out times, changes in the species composition of a forest will also mean changes in leaf-out dates at the level of the whole forest. Remote sensing is being increasingly used to disentangle the effects of changing species composition and changing climate on leaf-out trends. Long-term field studies can contribute to these efforts by quantifying the differences among species in leafing dates for trees and other woody plants all growing at one location, both within and outside their native ranges. Such information can then aid in calibrating leaf-out dates over a large area using remote sensing (Fisher & Mustard, 2007).

This review has shown that species do not all respond to changing temperature in the same way, and species show wide variation in leaf-out timing as a result of differing control mechanisms. Most temperate woody plant species use a combination of winter temperature, spring temperature, and photoperiod cues to control when to leaf-out in the spring, balancing the advantages of additional time for photosynthesis with the risk of damage to fragile young tissue from a late frost. At some point, certain tree species of mature forests may no longer be able to respond to warming temperatures with continued earlier onset of leaf-out as a result of unmet winter chilling and photoperiod requirements. In others, their leafing-out times may be delayed. There is some suggestion that this phenomenon is already beginning to occur in some places (Yu *et al.*, 2010). However, the number of tree species that have been investigated for their leaf-out requirements is still relatively small,

adding to the uncertainty of predictions for the impacts of future climate change on leaf-out times.

At this point, probably the most urgent need is for research on the effect that changes in leaf-out timing will have on trophic-level interactions and ecosystem processes. We need to understand how warming conditions and earlier leaf-out will affect plant and animal species on the forest floor, carbon sequestration, nutrient flow, and water movement. Changes in climate and leaf-out will also have major effects on tree products directly used by society such as fruits, nuts and timber. Many of these effects may be positive in the short term, but could become negative in the long term at the local level and require shifts in the locations in which economically important trees are grown.

Finally, this review has focused mainly on the effects of temperature on temperate woody plants. The focus is due largely to the relative abundance of information from these regions and the dominant role of temperature in controlling leaf-out times. Further work is needed in other parts of the world where the timing and amount of precipitation are important drivers of leaf-out times, such as grasslands, deserts, boreal regions, and tropical deciduous forests.

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