

Leaf out phenology in temperate forests

Caroline A. Polgar, Richard B. Primack*

Department of Biology, Boston University, Boston, MA 02215

Abstract: Monitoring phenology, the study of the timing of natural events, is an ancient practice that has experienced renewed interest in the wake of awareness of climate change. Spring onset has been occurring significantly earlier in temperate regions worldwide. Leaf out phenology is of particular interest because the emergence of leaves in the spring is extremely sensitive to temperature, and leaf out timing controls many essential ecosystem processes. This article reviews the current literature concerning the different methods used to study leaf out phenology, the controls on leaf out in temperate woody plants, and the effects of climate change on leaf out phenology. In addition to the traditional method of on-the-ground leaf out monitoring, new methods using remote sensing and dedicated cameras have been developed which allow scientists to track spring onset at a much larger scale than had previously been possible. Further work is needed on how leaf phenology will respond to future climate change, and the implications of this for interactions among trophic levels.

Key words: phenology, climate change, leaf out, temperate forest, dormancy release

Introduction

Interest in the timing of spring, and particularly in when leaves come out in temperate regions, has exploded over the past few decades (Cleland *et al.*, 2007; Forrest & Miller-Rushing, 2010). The study of the timing of leafing out, and other natural annual phenomena, is known as phenology. This resurgence of interest in the centuries-old practice of monitoring phenological events is directly related to the concern over anthropogenic climate change (Polgar & Primack, 2011). Because leaf out timing is closely linked to temperature, it is a reliable way to monitor the effects of global warming (Perry, 1971; Linkosalo *et al.*, 2006). Around the world researchers have begun closely monitoring the timing of the onset of the growing season, marked by the leaf out of trees and shrubs. These studies often rely on the same methods that have been used by naturalists for centuries, but as interest in phenology has increased, so have the methods employed to study it. New technology, including satellites, is now being used to monitor the timing of leafing out over wider areas than was possible in the past (Delbart *et al.*, 2008; Gonsamo *et al.*, 2012). Forest and ecosystem ecologists are connecting these observations of leaf-out dates to larger issues of global climate change, with implications for carbon sequestration, the availability of fresh water, and wood and tree crop production. Despite all of the research that has been done on the effects of climate change on leaf out, many questions still remain in the field. The

specific physiological controls on leaf out in temperate plants are still not well understood. There has also been a lot of interest in the possibility that as a result of differing responses to climate change, there may be temporal mismatches between important trophic level interactions.

Methods used in monitoring leaf out phenology

Monitoring phenology is an ancient tradition; the oldest known records of phenological observations are thought to date back to China from around 1,000 BCE. In Japan there are records of cherry blossoming dates for over 1,200 years and in the United States, well known figures such as Thomas Jefferson (the third president of the United States), Henry David Thoreau (famous philosopher and early environmentalist), and Aldo Leopold (famous conservationist) all kept detailed phenology records (Bradley *et al.*, 1999; Primack & Miller-Rushing, 2012). As technology continually advances, new methods are being developed to monitor leaf out phenology. Currently, there are three common ways to study leaf out: on-the-ground observations, remote sensing using aerial sensors, and near-surface remote sensing using digital cameras. These different methods capture phenological data at different spatial and temporal scales.

The recent resurgence of interest in phenology has led to leaf out monitoring projects around the world. For example, the Japanese Meteorological Agency has been recording leaf out, flowering time, autumn leaf

color, and other phenological data of individual marked plants in phenological gardens at over 100 weather stations since 1953 (Ibáñez *et al.*, 2010). In China the Chinese Phenological Observation Network has been monitoring various phenological events for several decades (Wang *et al.*, 2012). The International Phenological Gardens (IPG) project, a network of botanical gardens across Europe, has been collecting similar data on leaf-out dates of individual plants since 1951 (Menzel, 2000). In the United States there are several relatively new phenology monitoring projects including Project BudBurst (<http://neoninc.org/budburst/>), and Nature's Notebook (<http://www.usanpn.org/how-observe>), which is run through the relatively recently formed National Phenology Network (<http://www.usanpn.org/>).

Obtaining annual observations of leaf-out dates can be time and labor intensive, often limiting studies to a small area and/or a small number of study species (Fig. 1). To measure leafing out (or green up) on a larger scale, remote sensing is emerging as a valuable new tool. Remote sensing is the use of aerial sensors, such as those mounted on satellites or aircrafts, to obtain information about the earth. There are two distinct types of remote sensing used for phenology research. Traditional 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; Ahl *et al.*, 2006; Schwartz & Hanes 2010). These sensors identify the presence of green vegetation by the ratio of red to far-infrared wavelengths of sunlight being reflected from Earth's surface. Because the chlorophyll in leaves preferentially absorbs red light as trees leaf out and canopies close in the spring, the ratio of red to far-red radiation being reflected off of the earth's surface gradually decreases. From this ratio, the Normalized Difference Vegetation Index (NDVI) can be derived (Pettorelli *et al.*, 2005). NDVI is increasingly being used in remote sensing phenology studies. Several recent research papers have shown that regional leaf-out data from satellites accurately match ground observations. This is particularly important because there is a concern that different topographic features, such as mountains, fields, cities, and lakes, might create errors in the detection of green-up dates (Fig. 2, Fisher *et al.*, 2006). Remote sensing allows us to monitor trends in the onset of spring at a much broader scale than would be feasible through on-the-ground monitoring alone (Hufkens *et al.*, 2012a).

The other type of remote sensing that is increasingly being used to study leaf out timing is near-surface remote sensing. With this method scien-



Fig. 1 Leaf out pictures taken at the Arnold Arboretum in Boston, Massachusetts USA by scientists monitoring leafing in a traditional on-the-ground study (taken by Dr. Richard B. Primack)

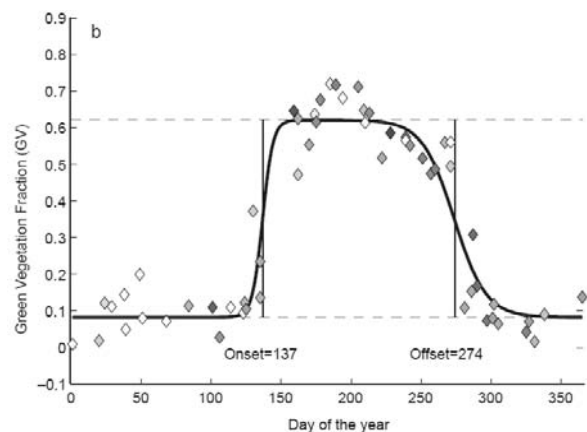


Fig. 2 A graph showing the growth of the leaf canopy over a growing season using satellite data from a location in New England, in the northeastern United States. The vegetation data is fit to logistic growth sigmoid functions and the onset and offset of greenness are calculated at the half-maxima of the curve. The quality of the data points is indicated by the symbol shading, with black diamonds having the least error and white diamonds having the most error (Figure from Fisher *et al.*, 2006).

tists are using digital or web cameras to obtain photographs of a plant canopy at regular intervals (Crimmins & Crimmins, 2008; Ide & Oguma, 2010) (Fig. 3). These images are analyzed in a similar way to satellite data and can be used in conjunction with data obtained by satellites (Hufkens *et al.*, 2012a). Networks of these phenology cameras can fill in the spatial and temporal gaps between plant monitoring by human observers and regional remote sensing images. There has been one such network set up in 12 forests across the northern United States that have been successfully used to monitor leafing phenology of the plant canopy (Richardson *et al.*, 2009). Seven of these sites in the United States also have eddy covariance towers that monitor the exchange of carbon dioxide and water between the atmosphere and the forest, determining how much CO₂ the forest is taking up; this combination of data from webcams, satellites, and gas sensors is providing crucial information on the relationship between phenology and ecosystem processes, especially carbon uptake (Richardson *et al.*, 2009).

What factors control when leaf out will occur?

Leaf out in temperate species is predominantly controlled by temperature, with plants generally leafing out earlier in warmer conditions, although warm temperature is not the only factor controlling the timing of leaf out. For many species it is a combination of warm and cold temperatures that dictates when the leaves will emerge from the bud, and for other species, photoperiod is also important (Körner & Basler, 2010). There are three broad combinations of factors that control leaf out of most temperate woody plant species: (1) chilling + warming degree-days + photoperiod; (2) chilling + warming degree-days; and (3) extremely limited chilling + warming degree-days. Chilling requirements refer to a requirement that a plant experiences a certain number of cold days in winter, generally somewhere between 0 and 10°C, before the buds are able to break dormancy. The exact number of chilling units required depends both on species and on the weather of the preceding growing season (Perry, 1971; Hunter & Lechowicz, 1992).

The first category, trees requiring a combination of chilling, warming, and photoperiod for leaf out, is largely seen in long-lived trees of mature forests, such as American beech (*Fagus grandifolia*), the exact requirements of each factor are largely unknown, but vary by species and geographically within a species (Farmer, 1968; Partanen, 2004; Ghelardini *et al.*, 2010). Other temperate species fall into the second category, with chilling and warming as dominant controls on leaf out, although many still have the ability

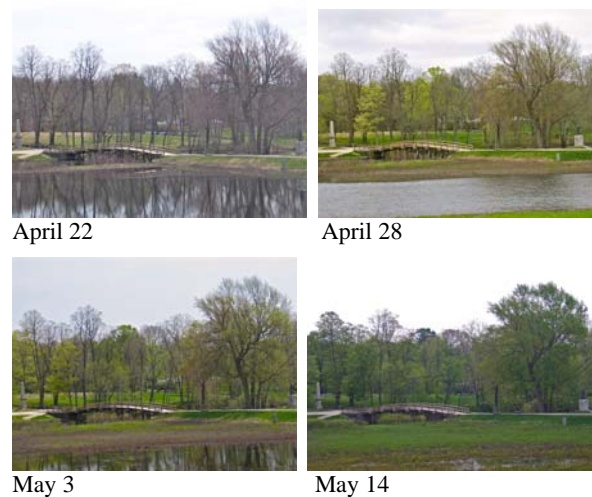


Fig. 3 A sequence of photos taken over a three week period in the spring of 2011 showing the development of the leaf canopy at Minute Man National Historical Site, a park in Concord, Massachusetts, with a bridge, a monument, and statue as points of reference. The leaf out times of individual trees can be seen in these photos. Photos by Richard B. Primack.

to respond to photoperiod (Caffarra & Donnelly, 2010). This strategy is favored by early successional species, such as hazelnuts (*Corylus* spp.). This somewhat risky strategy allows trees to respond more quickly to episodes of warm temperature in the early spring, but also creates more susceptibility to late frosts. Yet a third group of species, which includes mostly ornamental plants, such as the winged euonymus (*Euonymus alatus*) and Japanese barberry (*Berberis thunbergii*), has a leafing strategy linked to spring temperature with minimal chilling requirements and no photoperiod requirement (Körner & Basler, 2010).

The vulnerability of trees and other plants to frost damage was recently demonstrated when two weeks of abnormally warm weather in March 2007 led to early leafing out all across eastern and central North America. A return of freezing weather in early April killed the young leaves and flowers, and caused the die back of tree canopies across the region (Gu *et al.*, 2008). A similar situation occurred in 2010 (Fig. 4, Hufkens *et al.*, 2012b). Plants with more conservative growth strategies, those that do not respond as quickly to warm temperatures were less affected by the frost than those species that respond more strongly (Fig. 4 Hufkens *et al.*, 2012b). This type of incident with frost damage after a spell of warm weather is predicted to become increasingly common as climate change continues.



Fig. 4 A hillside in the northeastern United States showing the effects of a late frost following a period of warming. Trees that responded more quickly to warm temperatures, such as sugar maples, suffered damage to early leaves, while more conservative leafing species, such as American beech, fared better and are developing normally. Figure from (Hufkens *et al.*, 2012b)

Results from leaf out phenology studies around the world

Climate change is already affecting many ecological processes, including leafing out (Menzel, 2000; Richardson *et al.*, 2006; Ibáñez *et al.*, 2010). By analyzing long-term records of leaf out dates, much can be learned about how the onset of spring has changed over time as temperatures have increased. From long-term data collected at the International Phenological Gardens researchers determined that trees in northern Europe have advanced their leaf out by an average of one week over the past 50 years (Menzel, 2000). In Northern China, the Chinese Ash (*Fraxinus chinensis*) is leafing out earlier across the country, at an average rate of 1.1 days/decade, but as much as 2 days/decade in northern regions (Wang *et al.*, 2012). In Japan, woody plants such as forsythia (*Forsythia koreana*), mulberry (*Morus bombycis*), and various cherry species (*Prunus* spp.) have advanced their leaf out timing at a rate ranging from 2–7 days/°C since 1953. In the northeastern United States the onset of leafing of three native species, American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), has advanced an average of 5–10 days over the past five decades (Richardson *et al.*, 2006).

Projections for the future

Using information about phenological responses to temperature combined with predictions of future climate scenarios, scientists can develop models to project future phenological changes at the species and ecosystem levels. These models are also useful for agricultural systems, particularly those dependent on

tree crops. One modeling study found that the advance in leaf out time for most species and places is most likely going to continue in coming decades as the climate continues to warm (Morin *et al.*, 2009). Over the next century, advancement in leaf out date is expected to greater with increasing latitude for many species across Canada, the northern United States, and northern China (Morin *et al.*, 2009; Wang *et al.*, 2012). Delays in leaf out, or abnormal leaf out events, are likely to occur at the southern end of species ranges if those species fail to meet their winter chilling requirement (Morin *et al.*, 2009). Species with photoperiod requirements are also unlikely to continue to show linear advancements in leaf out dates with increasing temperatures since photoperiod will not change (Körner & Basler, 2010).

Another method used to inform leaf out phenology models in response to climate change is the use of results from experimental warming studies. While these experimental setups can provide interesting data, there is evidence that results from these experiments tend to underpredict the response of leaf out to warming temperatures (Wolkovich *et al.*, 2012).

As a consequence of the complicated host of factors involved in leafing phenology, it is hard to predict whether leaf out at the forest level will continue to advance linearly with changes in temperature (Morin *et al.*, 2009). The possibility of shifts in species composition resulting from climate change, as some species expand their range and others contract theirs, adds yet another layer of uncertainty. If certain early successional species with minimal photoperiod and chilling requirements continue to leaf earlier in the spring, they may outcompete native plants, leading to an increase in their abundance and distribution, leading to these species becoming more dominant, thus shifting the leafing out time of the whole forest (Harrington *et al.*, 1989; Willis *et al.*, 2010). Additionally, there is evidence that in the northeastern United States, non-native understory vegetation is also maintaining photosynthetically active vegetation later in the autumn than native vegetation, which may also contribute to shifting species composition (Fridley, 2012). The unmet chilling and photoperiod requirements of other species may significantly slow the advance of leaf out at the whole forest level. These two scenarios have consequences for many ecosystem processes, including the uptake of carbon dioxide, tree growth, forest temperature, and water movement.

Leaf out and the possibility of trophic mismatches

The onset of spring affects not only plants and eco-

system processes, but also organisms that depend on those plants. The time during which trees begin leafing out determines the availability of food and shelter for many species, particularly insects. The timing of early spring is particularly important for the many species that have gone through a long winter with little available food, or those bird species completing a migration north (Visser & Holleman, 2001). While plants are extremely responsive to changes in temperature; other organisms that interact with plants may not be quite so quick to respond. For instance, while 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 *et al.*, 2008). Similar work is being done with insects as well. Select species of butterflies and bees have been reported to advance their spring phenology at a rate similar to that of plants (Roy & Sparks, 2000; Bartomeus *et al.*, 2011). Despite these general results there is still the possibility that there may be mismatches between specific organisms, if certain insects feed only on the young leaves of a particular plant species that are present for a limited time in the spring, those insect species may decline in abundance if they emerge too early or late in the spring relative to their food resource (Egusa *et al.*, 2006; Coyle *et al.*, 2010). This could have cascading effects through ecosystems, affecting not only the insects, but also the birds or other animals that rely on those insects as their primary food source (Both *et al.*, 2009).

Conclusions

Earlier leaf-out dates are expected to continue in coming decades across much of the temperate regions across the world as a result of continued global climate change. This is likely to have large-scale implications species composition of forests, species ranges, and ecosystem processes such as carbon sequestration and water cycling. Through continued monitoring of phenology, both observations from on-the-ground and remote sensing measurements, ecologists will make further progress in understanding the dynamics that govern these processes. More work must also be done to understand the physiological requirements of leaf out, including untangling the chilling, warming and day length requirements of individual species, and the genetic variation that exists with an individual species across its range. Botanical gardens, national phenology networks, field stations, and keepers of long term phenological records can contribute to these efforts by quantifying the differences among species and among years in leafing dates for trees, shrubs and vines.

References

- Ahl DE, Gower ST, Burrows SN, Shabanov NV, Myneni RB, Knyazikhin Y (2006) Monitoring spring canopy phenology of a deciduous broadleaf forest using MODIS. *Remote Sensing of Environment*, **104**, 88–95.
- Bartomeus I, Ascher JS, Wagner D, Danforth BN, Colla S, Kornbluth S, Winfree R (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences, USA*, **108**, 20645–20649.
- Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, **78**, 73–83.
- Bradley NL, Leopold AC, Ross J, Huffaker W (1999) Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences, USA*, **96**, 9701–9704.
- Caffarra A, Donnelly A (2010) The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *International Journal of Biometeorology*, DOI:10.1007/s00484-00010-00386-00481.
- Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution*, **22**, 357–365.
- Coyle DR, Jordan MS, Raffa KF (2010) Host plant phenology affects performance of an invasive weevil, *Phyllobius oblongus* (Coleoptera: Curculionidae), in a northern hardwood forest. *Environmental Entomology*, **39**, 1539–1544.
- Crimmins MA, Crimmins TM (2008) Monitoring plant phenology using digital repeat photography. *Environmental Management*, **41**, 949–958.
- Delbart N, Picard G, Le Toans T, Kergoat L, Quegan S, Woodward I, Dye D, Fedotova V (2008) Spring phenology in boreal Eurasia over a nearly century time scale. *Global Change Biology*, **14**, 603–614.
- Egusa S, Nishida T, Fujisaki K, Sawada H (2006) Spatio-temporal abundance of flushing leaves shapes host selection in the willow leaf beetle, *Plagioderma versicolora*. *Entomologia Experimentalis et Applicata*, **120**, 229–237.
- Farmer RE (1968) Sweetgum dormancy release: effects of chilling photoperiod and genotype. *Physiologia Plantarum*, **21**, 1241–1248.
- Fisher JJ, Mustard JF, Vadeboncoeur MA (2006) Green leaf phenology at Landsat resolution: scaling from the field to the satellite. *Remote Sensing of Environment*, **100**, 265–279.
- Forrest J, Miller-Rushing AJ (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B—Biological Sciences*, **365**, 3101–3112.
- Fridley JD (2012) Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature*, **485**, 359–362.
- Ghelardini L, Santini A, Black-Samuelsson S, Myking T,

- Falusi M (2010) Bud dormancy release in elm (*Ulmus* spp.) clones: a case study of photoperiod and temperature responses. *Tree Physiology*, **30**, 264–274.
- Gonsamo A, Chen JM, Wu CY, Dragoni D (2012) Predicting deciduous forest carbon uptake phenology by upscaling FLUXNET measurements using remote sensing data. *Agricultural and Forest Meteorology*, **165**, 127–135.
- Gu LH, Hanson PJ, Mac Post W, Kaiser DP, Yang B, Nemani R, Pallardy SG, Meyers T (2008) The 2007 eastern US spring freeze: increased cold damage in a warming world? *BioScience*, **58**, 253–262.
- Harrington RA, Brown BJ, Reich PB (1989) Ecophysiology of exotic and native shrubs in southern Wisconsin I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. *Oecologia*, **80**, 356–367.
- Hufkens K, Friedl M, Sonnentag O, Braswell BH, Milliman T, Richardson AD (2012a) Linking near-surface and satellite remote sensing measurements of deciduous broadleaf forest phenology. *Remote Sensing of Environment*, **117**, 307–321.
- Hufkens K, Friedl MA, Keenan TF, Sonnentag O, Bailey A, O'Keefe J, Richardson AD (2012b) Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change Biology*, **18**, 2365–2377.
- Hunter AF, Lechowicz MJ (1992) Predicting the timing of budburst in temperate trees. *Journal of Applied Ecology*, **29**, 597–604.
- Ibáñez I, Primack RB, Miller-Rushing AJ, Ellwood E, Higuchi H, Lee SD, Kobori H, Silander JA (2010) Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society B—Biological Sciences*, **365**, 3247–3260.
- Ide R, Oguma H (2010) Use of digital cameras for phenological observations. *Ecological Informatics*, **5**, 339–347.
- Körner C, Basler D (2010) Phenology under global warming. *Science*, **327**, 1461–1462.
- Linkosalo T, Häkkinen R, Hänninen H (2006) Models of the spring phenology of boreal and temperate trees: Is there something missing? *Tree Physiology*, **26**, 1165–1172.
- Menzel A (2000) Trends in phenological phases in Europe between 1951 and 1996. *International Journal of Biometeorology*, **44**, 76–81.
- Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Satzing P (2008) Bird migration times, climate change, and changing population sizes. *Global Change Biology*, **14**, 1959–1972.
- Morin X, Lechowicz MJ, Augspurger C, O'Keefe J, Viner D, Chuine I (2009) Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology*, **15**, 961–975.
- Partanen J (2004) Dependence of photoperiodic response of growth cessation on the stage of development in *Picea abies* and *Betula pendula* seedlings. *Forest Ecology and Management*, **188**, 137–148.
- Perry TO (1971) Dormancy of trees in winter. *Science*, **171**, 29–36.
- Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, **20**, 503–510.
- Polgar CA, Primack RB (2011) Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist*, **191**, 926–941.
- Primack RB, Miller-Rushing AJ (2012) Uncovering, collecting, and analyzing records to investigate the ecological impacts of climate change: a template from Thoreau's Concord. *BioScience*, **62**, 170–181.
- Reed BC, Brown JF, Vanderzee D, Loveland TR, Merchant JW, Ohlen DO (1994) Measuring phenological variability from satellite imagery. *Journal of Vegetation Science*, **5**, 703–714.
- Richardson AD, Bailey AS, Denny EG, Martin CW, O'Keefe J (2006) Phenology of a northern hardwood forest canopy. *Global Change Biology*, **12**, 1174–1188.
- Richardson AD, Braswell BH, Hollinger DY, Jenkins JP, Ollinger SV (2009) Near-surface remote sensing of spatial and temporal variation in canopy phenology. *Ecological Applications*, **19**, 1417–1428.
- Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.
- Schwartz MD, Hanes JM (2010) Intercomparing multiple measures of the onset of spring in eastern North America. *International Journal of Climatology*, **30**, 1614–1626.
- Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B—Biological Sciences*, **268**, 289–294.
- Wang HJ, Dai JH, Ge QS (2012) The spatiotemporal characteristics of spring phenophase changes of *Fraxinus chinensis* in China from 1952 to 2007. *Science China-Earth Sciences*, **55**, 991–1000.
- Willis CG, Ruhfel BR, Primack RB, Miller-Rushing AJ, Losos JB, Davis CC (2010) Favorable climate change response explains non-native species' success in Thoreau's woods. *PLOS ONE*, **5**, e8878.
- Wolkovich EM, Cook BI, Allen JM, Crimmins TM, Betancourt JL, Travers SE, Pau S, Regetz J, Davies TJ, Kraft NJB, Ault TR, Bolmgren K, Mazer SJ, McCabe GJ, McGill BJ, Parmesan C, Salamin N, Schwartz MD, Cleland EE (2012) Warming experiments underpredict plant phenological responses to climate change. *Nature*, **485**, 494–497.

(Handling editor: Yurong Zhou)