

Increased heat requirement for leaf flushing in temperate woody species over 1980–2012: effects of chilling, precipitation and insolation

YONGSHUO H. FU^{1,2}, SHILONG PIAO^{1,3,9}, YANN VITASSE^{4,5,6}, HONGFANG ZHAO¹, HANS J. DE BOECK², QIANG LIU¹, HUI YANG¹, ULRICH WEBER⁷, HEIKKI HÄNNINEN⁸ and IVAN A. JANSSENS²

¹College of Urban and Environmental Sciences, Peking University, Yiheyuan Road 5, 100871 Beijing, China, ²Department of Biology, Centre of Excellence PLECO (Plant and Vegetation Ecology), University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium, ³Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Center for Excellence in Tibetan Earth Science, Chinese Academy of Sciences, Beijing, 100085, China, ⁴Institute of Geography, University of Neuchâtel, Neuchâtel, Switzerland, ⁵Snow and Landscape Research, WSL Swiss Federal Institute for Forest, Neuchâtel, Switzerland, ⁶Group Mountain Ecosystems, WSL Institute for Snow and Avalanche Research SLF, Davos, Switzerland, ⁷Max Planck Institute for Biogeochemistry, Hans Knöll Strasse 10, 07745 Jena, Germany, ⁸Department of Biosciences, University of Helsinki, Biocenter 3, FIN-00014 Helsinki, Finland

Abstract

Recent studies have revealed large unexplained variation in heat requirement-based phenology models, resulting in large uncertainty when predicting ecosystem carbon and water balance responses to climate variability. Improving our understanding of the heat requirement for spring phenology is thus urgently needed. In this study, we estimated the species-specific heat requirement for leaf flushing of 13 temperate woody species using long-term phenological observations from Europe and North America. The species were defined as early and late flushing species according to the mean date of leaf flushing across all sites. Partial correlation analyses were applied to determine the temporal correlations between heat requirement and chilling accumulation, precipitation and insolation sum during dormancy. We found that the heat requirement for leaf flushing increased by almost 50% over the study period 1980–2012, with an average of 30 heat units per decade. This temporal increase in heat requirement was observed in all species, but was much larger for late than for early flushing species. Consistent with previous studies, we found that the heat requirement negatively correlates with chilling accumulation. Interestingly, after removing the variation induced by chilling accumulation, a predominantly positive partial correlation exists between heat requirement and precipitation sum, and a predominantly negative correlation between heat requirement and insolation sum. This suggests that besides the well-known effect of chilling, the heat requirement for leaf flushing is also influenced by precipitation and insolation sum during dormancy. However, we hypothesize that the observed precipitation and insolation effects might be artefacts attributable to the inappropriate use of air temperature in the heat requirement quantification. Rather than air temperature, meristem temperature is probably the prominent driver of the leaf flushing process, but these data are not available. Further experimental research is thus needed to verify whether insolation and precipitation sums directly affect the heat requirement for leaf flushing.

Keywords: chilling requirement, climate change, heat requirement, insolation, leaf flushing phenology, precipitation

Received 30 October 2014 and accepted 30 December 2014

Introduction

In plants, the timing of spring phenological events, such as leaf flushing or fruit ripening, is related to the temperature sum of the preceding period (Réaumur, 1735). This temperature sum, also called the heat

requirement, is often calculated using the classical growing degree day concept (Wang, 1960; Baskerville & Emin, 1969; Sarvas, 1972; Chuine *et al.*, 1998). Growing degree day-based phenology models are widely used to simulate plant phenology and their response to climate change (Chuine, 2000; Schwartz, 2003; Hänninen & Kramer, 2007; Richardson *et al.*, 2013). However, recent studies have revealed that this approach can lead to large unexplained variation, resulting in considerable uncertainty when predicting ecosystem carbon and water balance responses to cli-

⁹Present address: Department of Ecology, Peking University, Beijing 100871, China

Correspondence: Shilong Piao, tel. 86 10 6276 5578, fax 86 10 6275 6560, e-mail: slpiao@pku.edu.cn

mate variability (Levis & Bonan, 2004; Kucharik *et al.*, 2006; Piao *et al.*, 2007; Randerson *et al.*, 2009; Jeong *et al.*, 2012; Keenan *et al.*, 2012; Migliavacca *et al.*, 2012; Richardson *et al.*, 2012). To decrease such uncertainties, we need to improve our understanding of how heat requirements may interact with other environmental cues to affect spring phenology. By exploring these potential correlations, predictions of spring phenology could be improved and hence increase our understanding of the global carbon balance in the context of climate warming (Richardson *et al.*, 2012).

The concept of heat requirement for spring leaf flushing implies that temperate woody species require a certain amount of heat to initiate leaf flushing after winter dormancy. The concept of accumulated heat is most often used as a measure for the physiological time or heat requirement (Baskerville & Emin, 1969; Wilson & Barnett, 1983). Theoretically, the heat requirement for leaf flushing remains (relatively) constant, even if temperatures during dormancy vary from year to year (Baskerville & Emin, 1969; Wilson & Barnett, 1983). As such, several studies that compare phenology models have reported that models with constant heat requirement performed similarly or even better than more sophisticated models that account for other environmental drivers (Linkosalo *et al.*, 2008; Vitasse *et al.*, 2011). However, there are also numerous studies suggesting that the amount of heat required to initiate leaf flushing after winter is inversely correlated with the duration of cold temperatures during dormancy (hereafter called chilling requirement) (Murray *et al.*, 1989; Botta *et al.*, 2000; Zhang *et al.*, 2004; Harrington *et al.*, 2010; Jeong *et al.*, 2012; Fu *et al.*, 2013). Considering the rapid rise of winter temperatures in the Northern Hemisphere (IPCC, 2014; Fu *et al.*, 2014b), chilling accumulation may have decreased below the required chilling threshold in many regions during the past decades, which subsequently may have resulted in increased heat requirement for spring leaf flushing. In this study, we therefore test the hypothesis that heat requirement for leaf flushing has increased in recent decades in the Northern Hemisphere due to warming winters that have provided lower duration/amount of chilling accumulations (Fu *et al.*, 2014b).

Among temperate woody species, different chilling and heat requirements for leaf flushing have been documented. For example, Murray *et al.* (1989) reported larger chilling requirement for late flushing species (such as *Fagus sylvatica* L.) than for early flushing species. Analysis of the Belgian phenology network dataset indicated larger chilling requirement for *Fagus sylvatica* L. than for *Quercus robur* L. and *Betula pendula* L. (Fu *et al.*, 2012a). This species-specific chilling requirement suggests differentiated heat requirement responses to

climate warming. Unlike late flushing species, changes in the heat requirement of some early flushing species are more likely to be subtle or even absent, because their low chilling requirement may be still fulfilled in warmer winters. Therefore, we expect a more pronounced increase in heat requirement over the last decades in late than in early flushing species. How the temporal changes of chilling accumulation are affecting the heat requirement for spring leaf flushing among different woody species has not yet been thoroughly investigated at large scales and over large areas.

Besides winter chilling, the heat requirement for initiating leaf flushing may also be influenced by other environmental factors, such as day length (Wareing, 1953; Heide, 1993; Basler & Körner, 2012, 2014), light intensity (Partanen *et al.*, 1998, 2001; Fitter & Fitter, 2002; Caffarra & Donnelly, 2011) and precipitation (Yuan *et al.*, 2007; Piao *et al.*, 2011; Shen, 2011; Fu *et al.*, 2014c). The mechanism of light control on plant phenology is still unclear because of the difficulty to disentangle the effects of day length and light intensity (Calle *et al.*, 2010), especially given their correlation with temperature. Total daily insolation could be used as an integrated measure of solar intensity at a particular site and day of the year (Calle *et al.*, 2010). In this study, we therefore investigate the correlation between heat requirement and light using the sum of daily absorbed downward short wave radiation over the time period preceding leaf flushing (hereafter referred to as insolation sum). Other studies have suggested an important role for precipitation (Yuan *et al.*, 2007; Piao *et al.*, 2011; Shen, 2011). A positive spatial correlation between heat requirement and precipitation sum was found over the northern middle and high latitudes using remote sensing-based NDVI data (Fu *et al.*, 2014c). In contrast, in areas with dry winters (e.g. Central Asia), negative spatial correlations were found between precipitation and heat requirement (Yu *et al.*, 2003). Moreover, the above-mentioned spatial correlations do not necessarily hold interannually (Dunne *et al.*, 2004; Jochner *et al.*, 2013). Therefore, a temporal analysis of the correlations between heat requirement, chilling, precipitation and insolation sum, using long term *in situ* data, may provide insights into the relative importance of these three environmental factors in determining spring leaf flushing dates and how these are affected by global warming.

In this study, we estimated the species-specific heat requirement for leaf flushing of 13 temperate woody species by combining long term, *in situ* series of phenological observations from Europe and North America and gridded climate data. The species were defined as early and late flushing species according to the mean date of leaf flushing across all observation sites. We applied a partial correlation analysis to determine the

temporal correlations between heat requirement and chilling accumulation, sum of precipitation and insolation during the dormancy period. The objectives of our analysis were (1) to determine the temporal changes of heat requirement for spring leaf flushing over the period 1980–2012, specifically we test the hypothesis that a more pronounced increase in heat requirement in late than in early flushing species; and (2) to relate changes in the heat requirement for leaf flushing to differences in chilling, precipitation and insolation.

Materials and methods

In situ phenology dataset and climate data

An extensive dataset of *in situ* phenology observations across northern temperate regions was obtained from the Pan European Phenology network (<http://www.pep725.eu/>), which provides an open European phenological database comprising multiple plant phenological records. Additionally, a phenology dataset for *Syringa chinensis* (lilac) was obtained from a network of sites distributed across the US (USA National Phenology Network, USA-NPN, <https://www.usanpn.org/results/data>). For this study, we selected the records of leaf flushing date of 13 woody species for the period 1980–2012. Data were excluded from the analysis when the study species were reported to flush later than the end of June. The details of the selected species are shown in Table 1. The leaf

flushing dates extracted from the PEP dataset were defined according to the BBCH code (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie) (Meier *et al.*, 2007), whereas leaf flushing dates from USA-NPN lilac dataset were defined as the first observation when leaf flushing occurs. For each species, leaf flushing dates were recorded at least in 10 phenological sites reporting minimum 15 year data records over the period 1980–2012. In total, 2594 phenological sites and 315 142 phenological records were used. The location of the selected phenological sites is shown in Fig. 1.

We used a gridded climate dataset, including daily mean air temperature, precipitation and insolation (absorbed downward short wave radiation), with a spatial resolution of 0.5°. The climate data were obtained from a bias-corrected reanalysis climate dataset covering the study period, that is 1980–2012 (Beer *et al.*, 2014). To investigate the correlation between heat requirement and precipitation and insolation sum, we calculated the cumulative precipitation and insolation as the sum of the precipitation and insolation during the dormancy period that was defined as the time period from the day when the land surface first froze in the previous autumn to the day of leaf flushing. The soil freeze status was derived from the land surface dielectric status, obtained by passive microwave remote sensing. Specifically, we used combined datasets obtained by SMMR and SSM/I, providing daily land surface freeze status from 1979 to 2011 with a spatial resolution of 25 km (Kim *et al.*, 2012). In the year 2012 and for the years when the land surface did not freeze, the onset date of the

Table 1 Species-specific heat requirement for leaf flushing and its temporal changes calculated using simple linear regression over the period 1980–2012

Species		N	LU (DOY)	LU changes (days)	Heat requirement (HU)		Heat requirement changes (HU)		Ratio (%)
Scientific name	Common name				Mean	SD	Mean	SD	
<i>Syringa chinensis</i>	Lilac	29	105	−3.2	98.3	70.6	25.7	30.2	26
<i>Alnus glutinosa</i>	European alder	1529	107	−13.7	166.4	44.8	70.7	46.9	42
<i>Pyrus communis</i>	European Pear	18	107	−13.1	191.9	59	88.1	49	46
<i>Sorbus aucuparia</i>	Rowan	1115	107	−5.5	169.9	44.9	59.3	42.5	35
<i>Aesculus hippocastanum</i>	Chestnut	2348	109	−12	166.3	45.9	77.2	45.3	46
<i>Betula pendula</i>	Silver birch	2355	109	−10.6	165.4	48.2	71.7	45.5	43
<i>Corylus avellana</i>	European filbert	128	112	−7.8	115.8	91.9	33.8	30.9	29
<i>Fagus sylvatica</i>	European beech	1965	117	−13.5	203.4	56.3	102.3	48.7	50
<i>Tilia cordata</i>	Littleleaf linden	115	118	−10.9	177.7	90.5	70.3	37.2	40
<i>Acer platanoides</i>	Norway maple	69	119	−8.6	146.7	111.9	55.9	42.6	38
<i>Quercus robur</i>	European oak	2045	123	−16.3	246.4	48.8	127.3	56.6	52
<i>Robinia pseudoacacia</i>	Black locust	21	124	−17.1	248.3	131.3	80.9	40.1	33
<i>Fraxinus excelsior</i>	Ash	1569	127	−16.6	271.6	53.2	131	57.2	48
All species		2596	115	−12.7	196.8	66.0	91.0	55.5	46

N indicates the number of observation sites, LU is the mean date of leaf flushing across all sites for each species; DOY is day of the year; HU is the heat unit, Ratio is the relative changes in heat requirement (%).

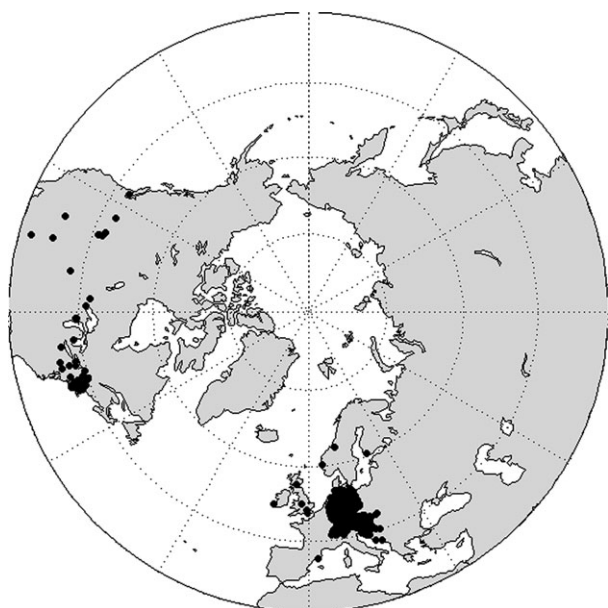


Fig. 1 Distributions of the *in situ* phenological sites.

dormancy period was fixed on the mean date of land freeze over the study period 1980–2012. At those sites where the soil never froze during the study period, the starting date of heat accumulation was fixed on 1st January.

Heat requirement for spring leaf flushing

Many studies have shown that measuring the heat accumulation in late winter/early spring can provide a physiological estimation of spring leaf flushing dates in temperate woody species (Cannell & Smith, 1983; Hänninen, 1990; Kramer, 1994b; Chuine, 2000; Vitasse *et al.*, 2011). The heat requirement for leaf flushing is typically calculated using a linear regression (Murray *et al.*, 1989) (equation 1) or a sigmoid function of the average daily air temperature (Hänninen, 1990; Kramer, 1994b) (equation 2), following these equations:

$$HU_{\text{req}} = \sum_{t_0}^{t_{\text{LF}}} (T_t - T_{\text{th}}) \quad \text{if } T_t > T_{\text{th}} \quad (1)$$

$$HU_{\text{req}} = \sum_{t_0}^{t_{\text{LF}}} D_{\text{HU}} \quad \text{if } T_t > T_{\text{th}} \quad \text{where } D_{\text{HU}} = \frac{28.4}{1 + e^{-0.185 \cdot (T_t - 18.4)}} \quad (2)$$

where HU_{req} is the heat unit (HU) requirement for leaf flushing, D_{HU} is the daily heat unit, t_{LF} is the day of leaf flushing, t_0 is the starting date for heat accumulation, T_{th} is the threshold temperature for heat accumulation, and T_t is the mean daily air temperature. The parameter values of the function (2) were fitted by Hänninen (Hänninen, 1990) based on Sarvas' experimental results on *Betula pendula* *Betula pubescens* and *Populus tremula* in Finland (Sarvas, 1972). Temperatures above 5 °C normally contribute to heat accumulation in temperate regions (Smith & Kefford, 1964; Perry, 1971; Hänninen,

1990; Kramer, 1994a) (but 0 °C in Sarvas' study) and is therefore used as a threshold for T_{th} . Physiologically, t_0 is the date when endodormancy is released (Lang *et al.*, 1987; Hänninen, 1990), here assumed to be the day when the land surface freezes or otherwise January 1st (see earlier). The heat requirement for leaf flushing was calculated using both equations (1) and (2), but the results were very similar (1), as shown in Figs S1 and S2. Hereafter, we therefore only report results obtained with the sigmoid function.

To investigate the correlation between heat requirement and chilling requirement, we calculated the species-specific chilling requirement at each site. The chilling requirement is normally defined as the time period (days or hours) during which temperatures were within a specific range. Most previous studies have reported that temperatures slightly above freezing are most effective in satisfying the chilling requirement (Coville, 1920; Kramer, 1994b) and suggested that the temperature range between 0 and 5 °C is the most effective across species. To calculate the chilling requirement, we therefore summed the days when daily temperature was comprised within this range:

$$CD_{\text{req}}(t) = \sum_{t_0}^{t_{\text{LF}}} 1 \quad \text{if } 0 \leq T_t \leq 5. \quad (3)$$

where CD_{req} is chilling requirement, t_{LF} is the day of leaf flushing and t_0 is the starting date for chilling accumulation. As for heat accumulation, t_0 was fixed on the onset date of the dormancy period, approximated as the date when the land surface froze or as January 1st. We also used 1st September in the previous year as the start day of chilling accumulation (following Chuine, 2000), and similar results were found. We therefore only report the results obtained with the onset date of the dormancy period as the starting date for chilling accumulation.

Data analysis

For each phenological site, linear regression analyses of the dates of leaf flushing and heat requirement for leaf flushing, as well as chilling accumulation, precipitation sum and insolation sum during dormancy, against year, were performed for each species during the study period 1980–2012. Histograms were made to show the frequency distribution of the regression coefficients for each of these variables, that is leaf flushing dates, heat requirement, chilling accumulation, and precipitation and insolation sum, across all species. The mean values of the regression coefficients were defined as the temporal trends of leaf flushing and heat requirement for each species as well as across all species. The difference in heat requirement and temporal trends of heat requirement among species were tested using independent *t*-test and were quantified using linear regression.

We applied a partial correlation analysis between heat requirements and chilling accumulation, precipitation and insolation sum. The heat requirement and the other climate variables were detrended before the partial correlation analysis was conducted. This method has been successfully applied to remove covariate effects between multiple influential

factors (Beer *et al.*, 2010; Peng *et al.*, 2013; Fu *et al.*, 2014a), that is chilling, precipitation and insolation in this study.

Results

Temporal changes of heat requirement for leaf flushing

During the study period 1980–2012, the date of leaf flushing advanced at almost 90% of the study sites (significantly at almost 50%). On average, the date of leaf flushing advanced by 13 days across all observation sites (Fig. 2, grey histogram). An advancing trend was observed in all species, but this phenological shift was more pronounced in late than in early flushing species (Table 1).

The heat requirement for leaf flushing was significantly different among the study species ($df = 1, 12$, $F = 740.0$ $P < 0.001$), with late flushing species exhibiting as expected the highest heat requirement. Assuming a linear relationship, the heat requirement for leaf flushing increased significantly ($P = 0.002$), at a rate of 5 heat units per day delay in leaf flushing across the 13 study species (Fig. 3a).

The heat requirement for leaf flushing increased during the study period 1980–2012 at almost all observation sites (97%; significantly at ~30%; Fig. 2, black histogram). With an average increment of 30 HU decade⁻¹, the heat requirement increased by almost 50% (averaged across all species, Table 1). The temporal increase in heat requirement for leaf flushing was

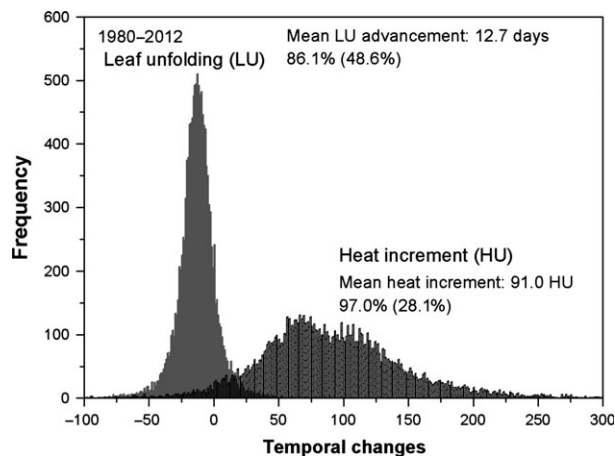


Fig. 2 Histogram of the number of observed temporal trends (in days, slope of linear regression * years) for *in situ* based leaf flushing (grey histogram) and heat requirement for leaf flushing (HU, black histogram) across all species and sites during the study period 1980–2012. The percentages of the total number of positive (temperature and insolation) or negative (precipitation and chilling) correlations, as well as the percentages of statistically significant correlations (in parentheses), are also provided.

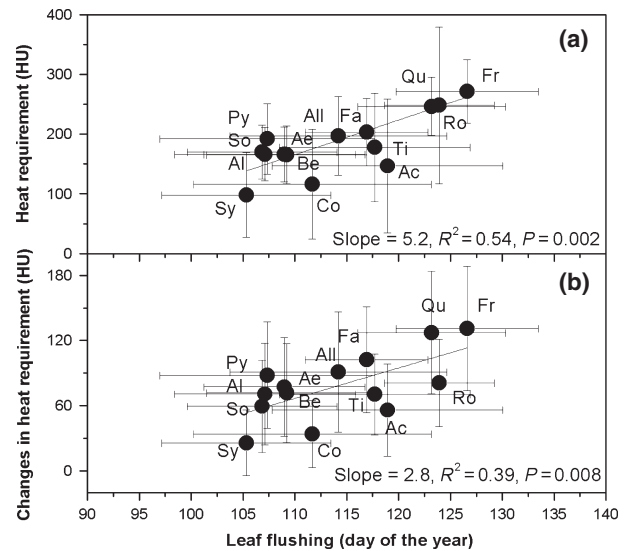


Fig. 3 Species-specific linear regression between heat requirement of leaf flushing and date of leaf flushing (a); and temporal change in the heat requirement and date of leaf flushing (b) over the study period 1980–2012. The symbols indicate mean values and the error bars one standard deviation. The solid lines indicate the simple linear regression. Ac indicates *Acer platanoides*; Ae: *Aesculus hippocastanum*; Al: *Alnus glutinosa*; Be: *Betula pendula*; Co: *Corylus avellana*; Fa: *Fagus sylvatica*; Fr: *Fraxinus excelsior*; Py: *Pyrus communis*; Qu: *Quercus robur*; Ro: *Robinia pseudoacacia*; So: *Sorbus aucuparia*; Sy: *Syringa chinensis*; Ti: *Tilia cordata*; All: all species.

observed in all species, but was much larger for late than for early flushing species (Fig. 3b). For example, compared to 1980, more than 120 extra heat units are now required for flushing of late species, such as *Q. robur* and *Fraxinus excelsior*, whereas only ~30 extra heat units are required for the early species *S. chinensis* and *Corylus avellana* (Fig. 3b and Table 1). On average, across the 13 study species, each day delay in leaf flushing corresponds to an increase in the heat requirement of almost 3 heat units (Fig. 3b).

Changes in climate and chilling requirement over 1980–2012

Averaged across all our observation sites, the mean temperature during the dormancy period increased by 1.4 °C over the period 1980–2012. While temperature increased at almost 90% of the study sites, this increase was significant at only 5% of the sites (at $P < 0.05$; Fig. 4a), which was likely due to the nonlinear warming pattern over the study period. In parallel with the warming trend, the sum of insolation substantially increased at more than 80% of the sites (Fig. 4b), suggesting more occurrences of clear-sky conditions, with a mean increment of 516 W m⁻² over

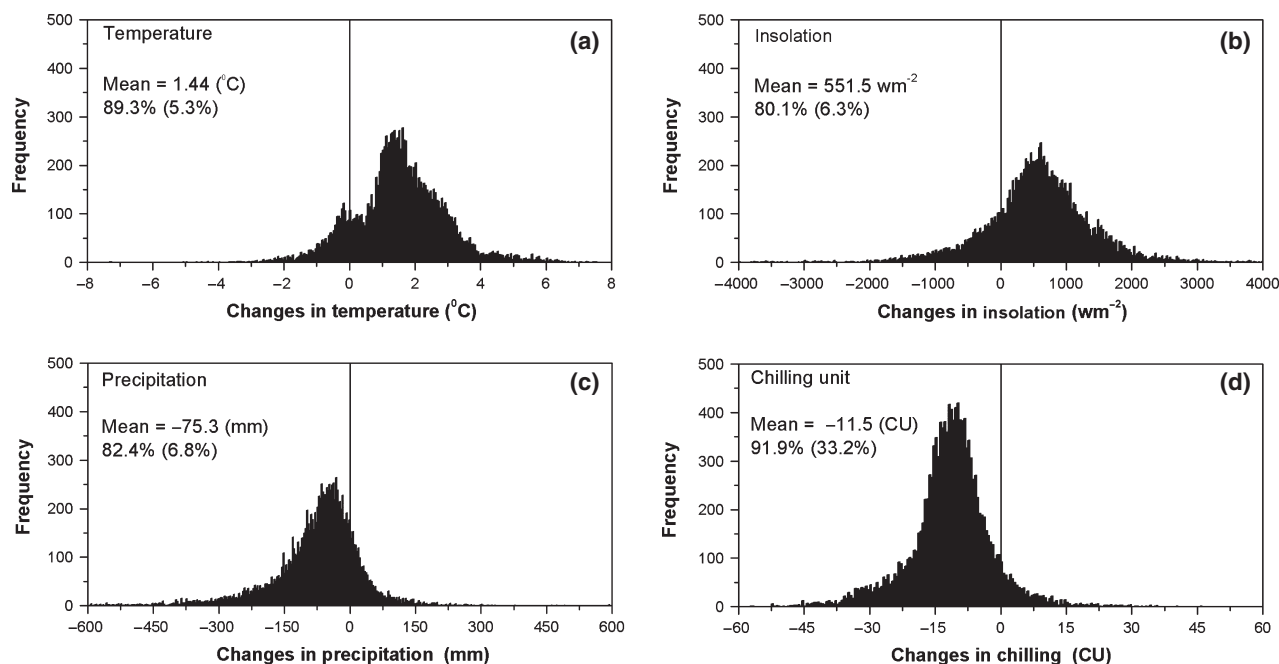


Fig. 4 Histograms of temporal changes of temperature (a), insolation sum (b), precipitation sum (c) and chilling accumulation (d) during the dormancy period across all species and sites during the study period 1980–2012. The mean temporal changes and percentages of the total number of positive (temperature and insolation) or negative (precipitation and chilling) correlations, as well as the percentages of statistically significant correlations (in parentheses), are also provided.

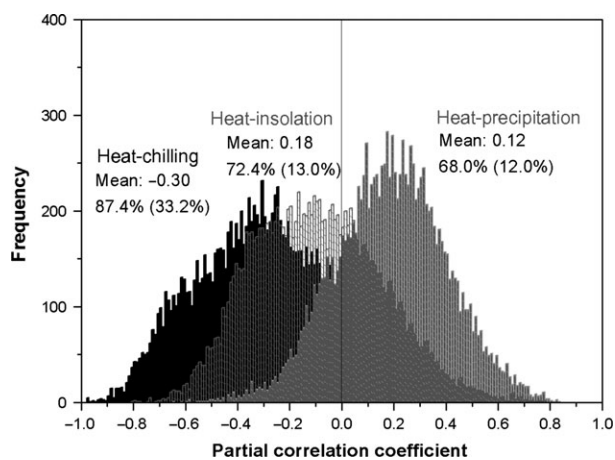


Fig. 5 Frequency distribution of partial correlation coefficients between heat requirement for leaf flushing and chilling (black), after controlling for precipitation and insolation sum, and between heat requirement and insolation sum (light grey), after controlling for chilling and precipitation sum, and between heat requirement and precipitation sum (dark grey), after controlling for chilling and insolation sum. Mean values of the partial correlation coefficients across all species and phenological sites, and percentages of the total number of positive (precipitation) or negative (chilling and insolation) correlations, as well as the percentages of statistically significant correlations (in parentheses), are also provided.

the period 1980–2012. In agreement with the increase of clear-sky conditions, precipitation sum declined during this period at 80% of the sites, with a mean reduction of 75 mm (Fig. 4c). As expected in relation to the warming trend, chilling accumulation was reduced at almost all sites (90% of sites showed a trend, which was significant at $p < 0.05$ in more than 30% of the sites, Fig. 4d), with the average reduction amounting to chilling days.

Correlations between heat requirement and other environmental factors

The heat requirement for leaf flushing was negatively correlated with the chilling requirement at almost 90% of the study sites (mean partial correlation coefficient $r = -0.30$), and this correlation was significant at more than 30% of the sites (Fig. 5, black histogram). This negative correlation was found in all study species, but was much less pronounced in *Acer platanoides* and *S. chinensis* (Fig 6, left panels).

Interestingly, the partial correlation analysis also revealed the predominance of a negative partial correlation between heat requirement and insolation sum during dormancy at more than 70% of the observation sites, with an average partial correlation coefficient of -0.18 (Fig 5, light grey histogram). This means that

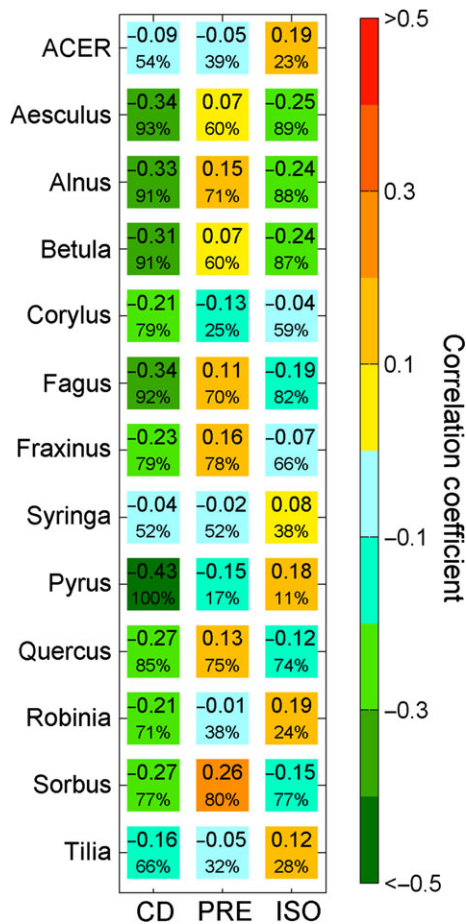


Fig. 6 Species-specific mean partial correlation coefficient between heat requirement for leaf flushing and chilling (CD), precipitation sum (PRE) and insolation sum (ISO). Percentages of the total number of positive (precipitation) or negative (chilling and insolation) correlations are also provided.

under similar chilling conditions and precipitation, years with more insolation tend to lead to earlier leaf flushing (in response to the reduced heat requirement). This negative correlation was found in 8 of the 13 species (Fig. 6, right panels), while the opposite pattern was found in *Acer platanoides* ($r = 0.19$), *Pyrus communis* ($r = 0.18$), *Robinia pseudoacacia* ($r = 0.19$), *S. chinensis* ($r = 0.08$) and *Tilia cordata* ($r = 0.12$). This result suggests that the amount of insolation during dormancy may influence the heat requirement for leaf flushing, but that the impact is species specific.

In contrast to chilling and insolation sum, a predominantly positive partial correlation was found between heat requirement and precipitation sum during dormancy at around 70% of the observation sites (Fig. 5, dark grey histogram, average partial correlation coefficient, $r = 0.12$). This partial correlation was, however, species specific and the positive correlation was only

found in seven species (Fig. 6, middle panels). Two species even showed a rather strong negative correlation between heat requirement and precipitation sum, that is *C. avellana* ($r = -0.13$) and *Pyrus communis* ($r = -0.15$). This predominantly positive correlation implies that under wetter conditions (= more cloudy), more heat is needed to trigger leaf flush under similar chilling accumulation.

Discussion

Heat requirement for leaf flushing increased over 1980–2012

In the Northern Hemisphere, the last three decades were likely the warmest 30-year period during the previous millennia (IPCC, 2014). Averaged across all our study sites, the mean temperature during dormancy increased by 1.4 °C throughout the 1980–2012 period, which is twice the global warming rate over the same time period (i.e. 0.74 °C, IPCC, 2014). Numerous studies have revealed that climate warming has substantially advanced the spring phenology of temperate plants (Chmielewski & Rotzer, 2001; Fitter & Fitter, 2002; Parmesan & Yohe, 2003; Menzel *et al.*, 2006; Piao *et al.*, 2008; Friedl *et al.*, 2014; Fu *et al.*, 2014b). In line with these results, we found that the timing of leaf flushing across our 13 study species was advanced by 13 days over the 1980–2012 period. Interestingly, we found that the heat requirement for leaf flushing (across the study species) also increased by 50%, which substantially moderated the advancing trend of leaf flushing in response to warming and demonstrates that phenological responses to temperature increase are not necessarily linear (Morin *et al.*, 2010; Fu *et al.*, 2012b).

The increasing heat requirement for leaf flushing was negatively correlated with chilling accumulation and with insolation sum, and positively correlated with precipitation sum. During the study period 1980–2012, we found decreased chilling accumulation and precipitation sum, but increased insolation sum. The combination of these factors finally resulted in an increment of heat requirement for leaf flushing. Furthermore, as expected, we found species-specific differences in the heat requirement shifts with the ongoing warming trend, that is much larger heat requirement shifts in late- than in early flushing species, which is consistent with previous studies (Murray *et al.*, 1989; Vitasse *et al.*, 2009; Fu *et al.*, 2013). The larger increment of heat requirement for late flushing species may mainly relate to the larger chilling requirement deficit (chilling requirement minus chilling accumulation) due to climate warming (reducing the chilling accumulation), as

these later flushing species usually require more chilling to fully break bud dormancy, especially *Fagus sylvatica* (Vitasse *et al.*, 2009; Harrington *et al.*, 2010; Vitasse & Basler, 2013).

Partial correlations between heat requirement and chilling, precipitation and insolation

The heat requirement has been widely identified as the primary driver for leaf flushing in temperate woody species (Cannell & Smith, 1983; Hänninen, 1990; Chuine, 2000; Fu *et al.*, 2013; Friedl *et al.*, 2014). However, the causal mechanisms that determine the interannual variation in the heat requirement for leaf flushing remain poorly understood. Consistent with previous studies, we found that the heat requirement negatively correlates with chilling accumulation (Murray *et al.*, 1989; Zhang *et al.*, 2004; Harrington *et al.*, 2010; Vitasse & Basler, 2013). However, after removing the variation induced by chilling accumulation in the partial correlation analysis, we also observed a predominantly positive partial correlation between heat requirement and precipitation, and a predominantly negative correlation with insolation, both summed during dormancy period. A similar correlation between heat requirement and precipitation was found in a remote sensing-based study focusing on the spatial correlations across the Northern Hemisphere (Fu *et al.*, 2014c). That spatial analysis also suggested a substantial role for winter precipitation in controlling spring phenological responses to global warming, but these spatial patterns need to hold temporally because space-for-time substitutions may be inappropriate (Jochner *et al.*, 2013; Mäkelä, 2013). Nonetheless, using an *in situ* dataset and temporal correlation analysis, this study supports the idea of a winter precipitation impact on phenology of deciduous woody species. Previous studies have reported that precipitation influences spring phenology in grassland ecosystems (Stewart & Dwyer, 1994; Yuan *et al.*, 2007), but not noticeably in temperate tree species (Dose & Menzel, 2004; Sherry *et al.*, 2007; Morin *et al.*, 2010). The latter was attributed to the deeper root system, which allows them to reach available water at depth (Sarmiento & Monasterio, 1983). In contrast to these earlier studies, we do find that wetter years result in delayed spring phenology (associated with larger GDD requirement), although we could only detect it in the partial correlation analysis which removes the over-riding temperature effects.

The influence of precipitation on spring phenology is apparent, while it remains unclear how precipitation sum could directly affect spring phenology of deciduous woody species, but indirect effects can be proposed. We propose two mutually nonexclusive

hypotheses to explain the positive correlation between heat requirement and precipitation sum during dormancy.

First, less precipitation during plant dormancy may imply more clear days and nights, and thereby increase the daytime temperature but reduce the night time temperature (De Boeck *et al.*, 2010). The combination of increased day and reduced night temperatures may result in a stable mean daily temperature. However, chilling accumulation may be more associated with the cooler night temperature than with mean daily temperature. Thus, the lower precipitation may actually indicate increased chilling accumulation that remained undetected in this analysis that used daily mean temperature. Increased chilling could explain the observed reduction of heat requirement at lower rainfall. Second, more clear days could increase both air and meristem temperatures, but the increment of meristem temperature could be much higher than air temperature as measured in standard weather stations, that is 2 m air-temperature recorded in shade conditions (Savvides *et al.*, 2014). These two temperatures are substantially different because under clear-sky conditions buds are heating up at the canopy level, and the leaf flushing process may be more related to the meristem temperature within buds (Grace *et al.*, 1989). Therefore, clear-sky conditions may fulfil the meristem temperature-based heat requirement earlier than the air temperature-based heat requirement as calculated in this study.

This would also explain the negative correlation between heat requirement and the insolation sum (Fig. 2b). However, how exactly the insolation sum may affect leaf flushing process remains poorly understood, although it has been widely reported as an important factor, at least in its day length component (Murray *et al.*, 1989; Körner & Basler, 2010; Caffarra & Donnelly, 2011; Basler & Körner, 2012, 2014). Some studies have claimed that insolation sum could directly modulate the heat requirement, independent of chilling (Wareing, 1953). Most studies, however, have suggested that the insolation sum effect is greater when there is a deficit in the amount of accumulated chilling (Falusi & Calamassi, 1996; Caffarra & Donnelly, 2011; Basler & Körner, 2014) and may not play a significant role in case of sufficient chilling (Kramer, 1994b; Fu *et al.*, 2012a; Laube *et al.*, 2014). In addition, species-specific differences in the insolation sum of spring leaf flushing phenology should be considered (Basler & Körner, 2012, 2014). In our study, we used insolation sum as an integrating value of day length and light intensity over the dormancy period and found a predominantly negative, but species-specific, correlation between insolation sum and heat requirement. Thus, all else being equal, more insolation advances leaf flushing

in most species. However, the underlying mechanism through which insolation sum affects spring leaf flushing remains poorly understood in temperate woody species and requires additional, well-designed manipulation experiments.

Limitations and implications

In this study, we estimated the heat requirement for leaf flushing using an *in situ* phenology dataset for Northern Hemispheric temperate woody species and investigated the role of environmental factors in the heat requirement by applying a partial correlation analysis to exclude the covariate effects between these factors. This approach helped us to better understand how different environmental factors influence the heat requirement for leaf flushing of different species. Nonetheless, caution should be taken. First, the parameter values of the sigmoid function for heat requirement were calculated following Hänninen (1990), based on Sarvas' (Sarvas, 1972) experimental results on Finnish birch and poplar saplings. Similarly, accumulated chilling was calculated using arbitrary thresholds, albeit this too was based on empirical observations. These parameter values likely differ among species, climatic conditions and even life stages (Luedeling, 2012; Vitasse, 2013). Evaluating the species-specific parameter values is beyond the scope of this study, but would likely reduce the uncertainty of both heat and chilling requirement estimates. A second limitation of this study is that we calculated the heat accumulation from the average daily temperatures. However, within-day temperature variations have been found to influence heat accumulation (Chung *et al.*, 2009). Furthermore, a recent study reported that the period preceding leaf flushing exerts a disproportional influence on leaf flushing (Friedl *et al.*, 2014). Therefore, a detailed study of which periods and times of day contribute most to heat accumulation could fine tune the interpretation of the phenology observations and reduce the uncertainty of our results.

Nonetheless, the results of this study do have important implications for improving the understanding of spring leaf flushing. The present study suggests that besides the well-known effect of chilling, the heat requirement for leaf flushing is also influenced by precipitation and insolation sum during dormancy, either directly or indirectly. We speculate that the observed precipitation and insolation effects might be due to the inappropriate use of standard air temperature record in the heat requirement estimation, instead, meristem temperature is likely more directly related to the leaf flushing process. To date, the mechanisms through which chill-

ing, precipitation and insolation affect the leaf flushing process remain unclear. Experimental efforts are needed to improve our understanding of the interactions between heat requirement and other environmental factors, as well as to improve our understanding of the different effects of air and meristem temperature on leaf flushing, and ultimately result in more accurate simulation of spring phenology and better understanding of the ecosystems response to future climate warming.

Acknowledgements

This study was supported by the National Natural Science Foundation of China (41125004), National Basic Research Program of China (2013CB956303), and National Youth Top-notch Talent Support Program in China. Ivan A. Janssens acknowledges support from the European Research Council through Synergy grant 610028 'P-IMBALANCE' and from the University of Antwerp Centre of Excellence 'Eco'.

References

- Baskerville GL, Emin PE (1969) Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology*, **50**, 514–517.
- Basler D, Körner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology*, **165**, 73–81.
- Basler D, Körner C (2014) Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree physiology*, **34**, 377–388.
- Beer C, Reichstein M, Tomelleri E *et al.* (2010) Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science*, **329**, 834–838.
- Beer C, Weber U, Tomelleri E, Carvalhais N, Mahecha MD, Reichstein M (2014) Harmonized European long-term climate data for assessing the effect of changing temporal variability on land-atmosphere CO₂ fluxes. *Journal of Climate*, **27**, 4815–4834.
- Botta A, Viovy N, Ciais P, Friedlingstein P, Monfray P (2000) A global prognostic scheme of leaf onset using satellite data. *Global Change Biology*, **6**, 709–725.
- Caffarra A, Donnelly A (2011) The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *International journal of Biometeorology*, **55**, 711–721.
- Calle Z, Schlumpberger BO, Piedrahita L, Leftin A, Hammer SA, Tye A, Borchert R (2010) Seasonal variation in daily insolation induces synchronous bud break and flowering in the tropics. *Trees-Structure and Function*, **24**, 865–877.
- Cannell MGR, Smith RI (1983) Thermal time, chill days and prediction of budburst in *Picea-sitchensis*. *Journal of Applied Ecology*, **20**, 951–963.
- Chmielewski F, Rotzer T (2001) Response of tree phenology to climate change across Europe. *Agricultural and Forest Meteorology*, **108**, 101–112.
- Chuine I (2000) A unified model for budburst of trees. *Journal of Theoretical Biology*, **207**, 337–347.
- Chuine I, Cour P, Rousseau DD (1998) Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant Cell and Environment*, **21**, 455–466.
- Chung U, Jung JE, Seo HC, Yun JI (2009) Using urban effect corrected temperature data and a tree phenology model to project geographical shift of cherry flowering date in South Korea. *Climatic Change*, **93**, 447–463.
- Coville FV (1920) The Influence of cold in stimulating the growth of plants. *Proceedings of the National Academy of Sciences of the United States of America*, **6**, 434–435.
- De Boeck HJ, Dreesen FE, Janssens IA, Nijs I (2010) Climatic characteristics of heat waves and their simulation in plant experiments. *Global Change Biology*, **16**, 1992–2000.
- Dose V, Menzel A (2004) Bayesian analysis of climate change impacts in phenology. *Global Change Biology*, **10**, 259–272.
- Dunne JA, Saleska SR, Fischer ML, Harte J (2004) Integrating experimental and gradient methods in ecological climate change research. *Ecology*, **85**, 904–916.
- Falusi M, Calamassi R (1996) Geographic variation and bud dormancy in beech seedlings (*Fagus sylvatica* L.). *Annales Des Sciences Forestieres*, **53**, 967–979.

- Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689–1691.
- Friedl MA, Gray JM, Melaas EK *et al.* (2014) A tale of two springs: using recent climate anomalies to characterize the sensitivity of temperate forest phenology to climate change. *Environmental Research Letters*, **9**, 054006.
- Fu YSH, Campioli M, Deckmyn G, Janssens IA (2012a) Bayesian comparison of six different temperature-based budburst models for four temperate tree species. *Ecological Modelling*, **230**, 92–100.
- Fu YSH, Campioli M, Deckmyn G, Janssens IA (2012b) The impact of winter and spring temperatures on temperate tree budburst dates: results from an experimental climate manipulation. *PLoS ONE*, **7**. DOI: 10.1371/journal.pone.0047324.
- Fu YSH, Campioli M, Deckmyn G, Janssens IA (2013) Sensitivity of leaf unfolding to experimental warming in three temperate tree species. *Agricultural and Forest Meteorology*, **181**, 125–132.
- Fu YSH, Campioli M, Vitasse Y *et al.* (2014a) Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 7355–7360.
- Fu YSH, Piao S, Op De Beek M *et al.* (2014b) Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology and Biogeography*, **23**, 1255–1263.
- Fu YSH, Piao S, Zhao H *et al.* (2014c) Unexpected role of winter precipitation in determining heat requirement for spring vegetation green-up at northern middle and high latitudes. *Global Change Biology*, **20**, 3743–3755.
- Grace J, Allen SJ, Wilson C (1989) Climate and the meristem temperatures of plant communities near the tree-line. *Oecologia*, **79**, 198–204.
- Hänninen H (1990) Modelling bud dormancy release in trees from cool and temperate regions. *Acta Zoologica Fennica*, **213**, 1–47.
- Hänninen H, Kramer K (2007) A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva Fennica*, **41**, 167–205.
- Harrington CA, Gould PJ, St Clair JB (2010) Modeling the effects of winter environment on dormancy release of Douglas-fir. *Forest Ecology and Management*, **259**, 798–808.
- Heide OM (1993) Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum*, **88**, 531–540.
- IPCC (2014) Climate Change 2014: Impacts, Adaptation, and Vulnerability. *Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL), Cambridge University Press, Cambridge.
- Jeong SJ, Medvigy D, Shevliakova E, Malyshev S (2012) Uncertainties in terrestrial carbon budgets related to spring phenology. *Journal of Geophysical Research: Biogeosciences*, **117**, G01030.
- Jochner S, Caffarra A, Menzel A (2013) Can spatial data substitute temporal data in phenological modelling? A survey using birch flowering. *Tree physiology*, **33**, 1256–1268.
- Keenan TF, Baker I, Barr A *et al.* (2012) Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO₂ exchange. *Global Change Biology*, **18**, 1971–1987.
- Kim Y, Kimball JS, Zhang K, McDonald KC (2012) Satellite detection of increasing Northern Hemisphere non-frozen seasons from 1979 to 2008: Implications for regional vegetation growth. *Remote Sensing of Environment*, **121**, 472–487.
- Körner C, Basler D (2010) Phenology under global warming. *Science*, **327**, 1461–1462.
- Kramer K (1994a) A modeling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in the Netherlands and Germany. *Plant Cell and Environment*, **17**, 367–377.
- Kramer K (1994b) Selecting a model to predict the onset of growth of *Fagus-sylvatica*. *Journal of Applied Ecology*, **31**, 172–181.
- Kucharik CJ, Barford CC, El Maayar M, Wofsy SC, Monson RK, Baldocchi DD (2006) A multiyear evaluation of a Dynamic Global Vegetation Model at three AmeriFlux forest sites: vegetation structure, phenology, soil temperature, and CO₂ and H₂O vapor exchange. *Ecological Modelling*, **196**, 1–31.
- Lang GA, Early JD, Martin GC, Darnell RL (1987) Endo-, para- and eco-dormancy, physiological terminology and classification for dormancy research. *HortScience*, **22**, 371–377.
- Laube J, Sparks TH, Estrella N, Höfler J, Ankerst DP, Menzel A (2014) Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology*, **20**, 170–182.
- Levis S, Bonan GB (2004) Simulating springtime temperature patterns in the community atmosphere model coupled to the community land model using prognostic leaf area. *Journal of Climate*, **17**, 4531–4540.
- Linkosalo T, Lappalainen HK, Hari P (2008) A comparison of phenological models of leaf bud burst and flowering of boreal trees using independent observations. *Tree physiology*, **28**, 1873–1882.
- Luedeling E (2012) Climate change impacts on winter chill for temperate fruit and nut production: a review. *Scientia Horticulturae*, **144**, 218–229.
- Makela A (2013) En route to improved phenological models: can space-for-time substitution give guidance? *Tree physiology*, **33**, 1253–1255.
- Meier N, Rutishauser T, Pfister C, Wanner H, Luterbacher J (2007) Grape harvest dates as a proxy for Swiss April to August temperature reconstructions back to AD 1480. *Geophysical Research Letters*, **34**. doi: 10.1029/2007GL031381.
- Menzel A, Sparks TH, Estrella N *et al.* (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976.
- Migliavacca M, Sonntag O, Keenan TF, Cescaati A, O'keefe J, Richardson AD (2012) On the uncertainty of phenological responses to climate change, and implications for a terrestrial biosphere model. *Biogeosciences*, **9**, 2063–2083.
- Morin X, Roy J, Sonie L, Chuine I (2010) Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist*, **186**, 900–910.
- Murray MB, Cannell MGR, Smith RI (1989) Date of budburst of 15 tree species in Britain following climatic warming. *Journal of Applied Ecology*, **26**, 693–700.
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Partanen J, Koski V, Hänninen H (1998) Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*). *Tree physiology*, **18**, 811–816.
- Partanen J, Leinonen I, Repo T (2001) Effect of accumulated duration of the light period on bud burst in Norway spruce (*Picea abies*) of varying ages. *Silva Fennica*, **35**, 111–117.
- Peng SS, Piao SL, Ciais P *et al.* (2013) Asymmetric effects of daytime and night-time warming on Northern Hemisphere vegetation. *Nature*, **501**, 88–92.
- Perry TO (1971) Dormancy of trees in winter. *Science*, **171**, 29–36.
- Piao SL, Friedlingstein P, Ciais P, Viovy N, Demarty J (2007) Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Global Biogeochemical Cycles*, **21**. doi: 10.1029/2006GB002888.
- Piao SL, Ciais P, Friedlingstein P *et al.* (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, **451**, U49–U43.
- Piao SL, Cui MD, Chen AP, Wang XH, Ciais P, Liu J, Tang YH (2011) Altitude and temperature dependence of change in the spring vegetation green-up date from 1982 to 2006 in the Qinghai-Xizang Plateau. *Agricultural and Forest Meteorology*, **151**, 1599–1608.
- Randerson JT, Hoffman FM, Thornton PE *et al.* (2009) Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models. *Global Change Biology*, **15**, 2462–2484.
- Réaumur RAFD (1735) Observation du thermomètre, faites à Paris pendant l'année 1735, comparées avec celles qui ont été faites sous la ligne, à l'Isle de France, à Alger et quelques-unes de nos isles de l'Amerique. In *Mémoires de l'Académie Royal des Sciences*. pp. 545–579.
- Richardson AD, Anderson RS, Arain MA *et al.* (2012) Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program Site Synthesis. *Global Change Biology*, **18**, 566–584.
- Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonntag O, Toomey M (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, **169**, 156–173.
- Sarmiento G, Monasterio M (1983) Life forms and phenology. In: *Tropical Savannas* (ed. Bourlière F), pp. 79–104. Elsevier, Amsterdam.
- Sarvas R (1972) Investigations on the annual cycle of development of forest trees active period. *Communicationes Instituti Forestalis Fenniae*, **76**, 1–110.
- Savvides A, Ntagkas N, Van Ieperen W, Dieleman JA, Marcelis LFM (2014) Impact of light on leaf initiation: a matter of photosynthate availability in the apical bud? *Functional Plant Biology*, **41**, 547–556.
- Schwartz MD (2003) *Phenology: An Integrative Environmental Science*. Kluwer Academic Publishers, Dordrecht.
- Shen MG (2011) Spring phenology was not consistently related to winter warming on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 91–92.
- Sherry RA, Zhou XH, Gu SL *et al.* (2007) Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 198–202.

- Smith H, Kefford HP (1964) The chemical regulation of the dormancy phases of bud development. *American Journal of Botany*, **51**, 1002–1012.
- Stewart DW, Dwyer LM (1994) Appearance time, expansion rate and expansion duration for leaves of field-grown maize (*Zea-mays* L.). *Canadian Journal of Plant Science*, **74**, 31–36.
- Vitasse Y (2013) Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist*, **198**, 149–155.
- Vitasse Y, Basler D (2013) What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research*, **132**, 1–8.
- Vitasse Y, Dufrene E, Pontailier JY, Louvet JM, Kremer A, Michalet R, Delzon S (2009) Leaf phenology sensitivity to temperature in European trees: do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology*, **149**, 735–744.
- Vitasse Y, Francois C, Delpierre N, Dufrene E, Kremer A, Chuine I, Delzon S (2011) Assessing the effects of climate change on the phenology of European temperate trees. *Agricultural and Forest Meteorology*, **151**, 969–980.
- Wang JY (1960) A critique of the heat unit approach to plant response studies. *Ecology*, **41**, 785–790.
- Wareing P (1953) Growth studies in woody species. V. Photoperiodism in dormant buds of *Fagus sylvatica* L. *Physiologia Plantarum*, **6**, 692–706.
- Wilson LT, Barnett WW (1983) Degree-days: an aid in crop and pest management. *California Agriculture*, **37**, 4–7.
- Yu FF, Price KP, Ellis J, Shi PJ (2003) Response of seasonal vegetation development to climatic variations in eastern central Asia. *Remote Sensing of Environment*, **87**, 42–54.
- Yuan WP, Zhou GS, Wang YH, Han X, Wang YS (2007) Simulating phenological characteristics of two dominant grass species in a semi-arid steppe ecosystem. *Ecological Research*, **22**, 784–791.
- Zhang XY, Friedl MA, Schaaf CB, Strahler AH (2004) Climate controls on vegetation phenological patterns in northern mid- and high latitudes inferred from MODIS data. *Global Change Biology*, **10**, 1133–1145.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Histogram of the number of observed temporal trends for *in situ* based heat requirement for leaf flushing.
Figure S2. Frequency distribution of partial correlation coefficients between heat requirement (calculated using equation 1) and chilling (dark green), insolation sum (red) and precipitation sum (green).