RESEARCH PAPER

Shifting and extension of phenological periods with increasing temperature along elevational transects in southern Bavaria

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ABSTRACT

The impact of global warming on phenology has been widely studied, and almost consistently advancing spring events have been reported. Especially in alpine regions, an extraordinary rapid warming has been observed in the last decades. However, little is known about phenological phases over the whole vegetation period at high elevations. We observed 12 phenological phases of seven tree species and measured air temperature at 42 sites along four transects of about 1000 m elevational range in the years 2010 and 2011 near Garmisch-Partenkirchen, Germany. Site- and species-specific onset dates for the phenological phases were determined and related to elevation, temperature lapse rates and site-specific temperature sums. Increasing temperatures induced advanced spring and delayed autumn phases, in which both yielded similar magnitudes. Delayed leaf senescence could therefore have been underestimated until now in extending the vegetation period. Not only the vegetation period, but also phenological periods extended with increasing temperature. Moreover, sensitivity to elevation and temperature strongly depends on the specific phenological phase. Differences between species and groups of species (deciduous, evergreen, high elevation) were found in onset dates, phenological response rates and also in the effect of chilling and forcing temperatures. Increased chilling days highly reduced forcing temperature requirements for deciduous trees, but less for evergreen trees. The problem of shifted species associations and phenological mismatches due to species-specific responses to increasing temperature is a recent topic in ecological research. Therefore, we consider our findings from this novel, dense observation network in an alpine area of particular importance to deepen knowledge on phenological responses to climate change.

INTRODUCTION

Phenology has proved to be a good indicator of the impacts of climate change on vegetation (Murray *et al.* 1989; Hänninen 1991; Kramer 1994; Menzel *et al.* 2001). The growing period of trees has extended in recent decades due to global warming (Menzel & Fabian 1999; Linderholm 2006). This trend is mainly due to advanced spring events (bud burst; Ahas *et al.* 2002; Cleland *et al.* 2007), which are predominantly triggered by spring warming (Hickin & Vittum 1976; Castonguay *et al.* 1984) and a sufficient dormancy chilling period (Chuine & Cour 1999). Additionally, but less frequently, delayed leaf senescence is reported (Menzel *et al.* 2006; Vitasse *et al.* 2009a). In mountainous regions such as the Alps, a high impact of global warming has been detected in recent decades, since these areas have warmed by almost double (1.5 °C) the global average (0.7 °C; Theurillat & Guisan 2001; Schröter *et al.* 2005; Nogués-Bravo *et al.* 2007) temperature. Animals and plants often experience harsh or inhospitable living conditions here due to extreme climate conditions, combined with a high variation in topography and habitat. Therefore they react with a high degree of specialisation and adaption (Körner 2003). Faced with an increasing speed of warming ('left behind') and the lack of areas to retreat ('nowhere-to-go'), alpine species are considered as highly threatened by climate change (Beniston

et al. 1997; Schröter *et al.* 2005). Moreover, climate warming will lead to an upward shift in species distribution, which initially increases species richness but enforces species competition at higher elevations and will thus result in a loss of biodiversity at longer time scales (Klanderud & Birks 2003; Parmesan 2006; Lenoir *et al.* 2008; Erschbamer *et al.* 2009).

Phenological observations along elevational transects allow the study of phenological responses to a wide range of temperatures in relatively short time (Dittmar & Elling 2006; Vitasse *et al.* 2009b). However, since observations in alpine surroundings require extensive effort, detailed phenological data as recorded in our study are still rare. Only a few studies have observed both spring flushing and leaf senescence (Vitasse *et al.* 2009b), and most studies have only focused on a few phenological phases (such as bud burst and leaf colouration) and the length of the vegetation period. However, knowledge on the relations of phenology, temperature and elevation based on field observations helps to predict phenological changes under future global warming and improve phenological model fitting. Many efforts have been undertaken to develop complex phenological models (Hänninen 1990; Hunter & Lechowicz 1992; Chuine & Cour 1999; Migliavacca *et al.* 2008), but also simple models provide convincing results (Rötzer *et al.* 2004).

On the forest-covered slopes in the Bavarian Alps, we find optimal conditions for tree phenological studies on

elevational transects. Along four transects, we installed 42 observation sites including temperature and relative humidity measurements, and observed seven tree species according to a species-modified BBCH Code (Meier 1997) in the years 2010 and 2011. We determined responses of single phenological phases based on phenological elevational rates and temperature lapse rates, as well as based on temperature sums. Finally, we compared phenological temperature response rates from both approaches.

The objectives of this study were (i) to identify species-specific response rates to elevation and temperature as we expected them to be highly variable. We wanted to quantify differences between (ii) responses from a high number of phenological phases and (iii) between species groups (MD, montane deciduous; ME, montane evergreen; and HE, high-elevation species). Since Davi *et al.* (2006) found, in temperate trees, that 55% of the increase of the vegetation period is attributable to advanced spring and 45% to delayed autumn events, another aim was (iv) to compare phenological periods in terms of their role in lengthening the total vegetation period. Additionally, we wanted (v) to determine the behaviour of our seven tree species regarding chilling and forcing temperatures, since spring forcing (Hickin & Vittum 1976; Hunter & Lechowicz 1992) and winter chilling (Perry 1971) are known to be the main drivers of temperate spring phenology.

MATERIAL AND METHODS

Study area

The study area is located in southern Bavaria near the city of Garmisch-Partenkirchen (708 m a.s.l., 47°30′ N, 11°5′ E) and the Zugspitze (2962 m a.s.l., 47°25′16″ N, 10°59′11″ E), the highest mountain in Germany. In this alpine region, annual precipitation varies from 1363 mm in Garmisch to 2003 mm at Zugspitze, and annual mean temperature ranges from 6.5 °C (Garmisch) to −4.8 °C (Zugspitze; 1961–1990). Mixed mountainous deciduous–coniferous forest covers most of the slopes from 700 m a.s.l. in the valley up to the tree line at 1700–1900 m a.s.l. For the present study, four transects within the montane forest zone were installed (Fig. 1): Garmisch-Partenkirchen–Kramer Pass (700–1700 m a.s.l., S aspect, KRA), Garmisch-Partenkirchen–Kreuzeck/Längenfelder (800–1800 m a.s.l., N aspect, KRE), Reintal/Brandwiese–Kreuzeck (900–1600 m a.s.l., S aspect, BRA) and Reintal–Schachen (800–1800 m a.s.l., N aspect, SCH).

Meteorological measurements

Four meteorological stations were installed in autumn 2009 and early spring 2010: one at each transect, but at different elevations, to provide data from these different elevations (900 m a.s.l. at BRA, 1250 m a.s.l. at KRA, 1600 m a.s.l. at KRE and 1830 m a.s.l. at SCH). Air, surface and soil temperature, air humidity, precipitation, solar radiation, wind speed and wind direction were recorded every 10 min. Along the four transects, 42 observation sites in the forest were chosen every 100 m in elevation (Fig. 1). At each forest site, air temperature and relative humidity were measured using onset HOBO® PRO V2 loggers fixed in a solar radiation shield at 2-m height on a stake. Logger measurements were recorded every 30 min from April 2010 onwards.

Phenological observations

At each of the 42 sites, six individuals (three mature and three juvenile tees) from each species present were selected for phenological observations, resulting in 571 individual trees: *Abies alba* (45), *Acer pseudoplatanus* (95), *Fagus sylvatica* (133), *Larix decidua* (17), *Picea abies* (220), *Pinus mugo* (41), *Pinus sylvestris* (20). While *P. abies* is one of the dominant species everywhere, *A. alba* is only found in smaller numbers and not at all sites. Elevational limits for *A. pseudoplatanus* and *F. sylvatica* are around 1600 and 1500 m a.s.l., respectively. *P. sylvestris* is present only at the KRA transect. *L. decidua* and *P. mugo* are mostly distributed at higher elevations above 1100 m a.s.l.

For each species, an observation guide was set up according to the general BBCH Code (Meier 1997) and the general growth stage key for trees and woody plants (Finn *et al.* 2007). The observation guide included eight phases for leaf development (BBCH phases 1, 7, 9, 10, 10.5, 11, 15, 17; Table 1) and four phases for leaf senescence (93, 95, 96, 97; Table 1). In this study,
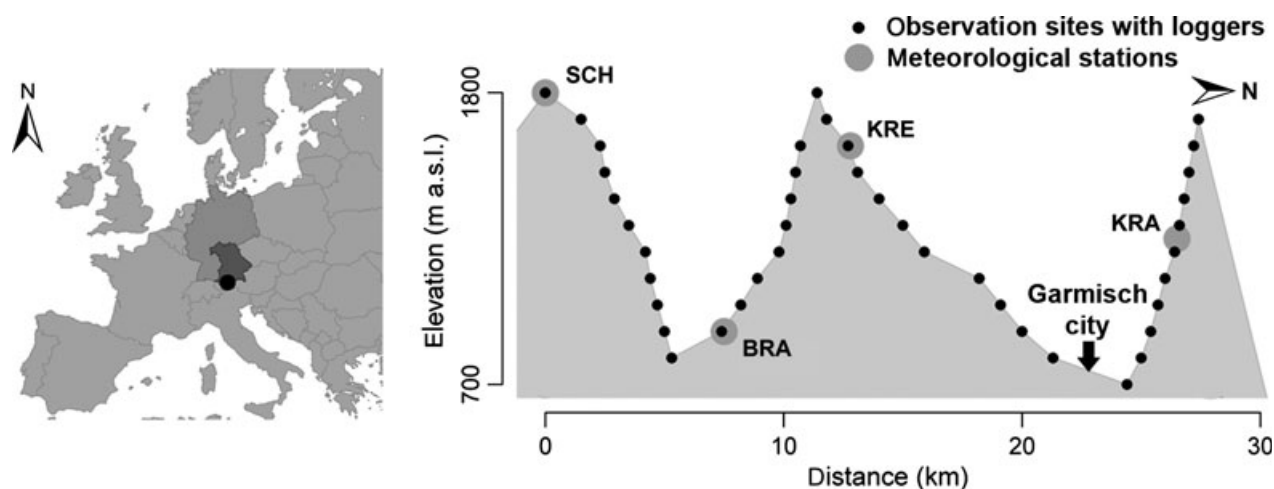

Fig. 1. Study site in southern Bavaria, Germany (left), and transects around the city of Garmisch-Partenkirchen with logger and tree phenological observation sites (black points) as well as meteorological stations (grey points).

the most advanced phase found at an individual defined its actual development stage (status monitoring). In autumn, the percentage of green, coloured and fallen leaves was estimated in 5% intervals. Onset dates for the BBCH codes were calculated by logistic regression on the observations (see Analysis methods). The annual observation period started with visible spring events (bud swelling) and ended when leaves were fully unfolded (end of April to end of July 2010, beginning of April to mid July 2011). The leaf senescence phases were observed weekly for *A. pseudoplatanus* and *F. sylvatica* in September and October 2010 and 2011. Observations took place regularly once a week using binoculars with 10-fold magnification.

In addition to classical onset dates, we defined phenological periods between BBCH phases (onset$_{BBCH\ b}$ − onset$_{BBCH\ a}$ with BBCH a < BBCH b), *e.g.* leaf development period (onset$_{BBCH\ 17}$ − onset$_{BBCH\ 7}$), full leaf period (onset$_{BBCH\ 93}$ − onset$_{BBCH\ 17}$), leaf senescence period (onset$_{BBCH\ 97}$ − onset$_{BBCH\ 93}$) and vegetation period (onset$_{BBCH\ 97}$ − onset$_{BBCH\ 7}$).

Analysis methods

Temperature lapse rates (°C 100 m^{-1}) were calculated by linear regression of mean air temperatures at the logger sites against elevation, separately for each month (monthly mean temperature), the spring (April–July) and autumn period (September–October, mean of monthly mean temperature lapse rates) and for annual mean temperatures.

In order to model spring leaf development and to derive site- and species-specific onset dates of each phase, logistic regressions (equation 1) were fitted for each species at each site to the BBCH observations. For the regressions, the classes of BBCH phases were first converted to percentages of total leaf development (Table 1) and a binominal GLM model was used in R (R Development Core Team 2009). Based on the respec-

tive parameters (*a*, *b*) of the regression, single onset dates for each phenological phase of each species at each site were calculated separately for 2010 and 2011.

$$y = \frac{e^{a+bx}}{1 + e^{a+bx}} \qquad (1)$$

y is the percentage of spring development derived from BBCH observations; *x* is the time (day of year); and *a*, *b* is the coefficients fitted individually for each regression.

Onset dates for the autumn phases were also calculated by logistic regressions (equation 1) on the observed percentages of green (BBCH 93 and 95) and fallen leaves (BBCH 96 and 97). This logistic regression method is suitable to fill gaps in observations in order to ensure a complete set of consistent onset dates. In the literature, the most common phenological phases are BBCH 7 (bud burst), BBCH 10.5 (leaf unfolding for deciduous trees) in spring and BBCH 95 (50% leaves coloured or fallen, 50% still green) in autumn. Thus, response rates of all phases determined are presented, but not all of them are discussed.

Phenological elevational rates were calculated for all species and BBCH phases by linear regression of determined onset dates against elevation (per, days 100 m^{-1}). Combining per (days 100 m^{-1}) with the temperature lapse rates measured by the logger network (tlr, °C 100 m^{-1}) using formula (equation 2), phenological response rates (prr, days °C^{-1}) were determined for 2010, 2011 and 2010/2011.

$$\text{prr} \left[\frac{\text{days}}{°\text{C}}\right] = \text{per} \left[\frac{\text{days}}{100\,\text{m}}\right] * \frac{1}{\text{tlr} \left[\frac{°\text{C}}{100\,\text{m}}\right]} \qquad (2)$$

prr is the phenological response rate; per is the phenological elevational rate; and tlr is the temperature lapse rate.

Table 1. Observed phenological phases, modified after Meier (1997) and Finn *et al.* (2007), phenological periods and development percentages for logistic regressions.

BBCH	leaf unfolding (deciduous species)	needle elongation	percentage
0	buds closed	buds closed	0
1	start of bud swelling		5
7	start of bud burst (first green visible)	start of bud burst (first green visible)	10
9	green leaf tips <10 mm out of bud scale	green needles bunched, <10 mm	20
10	green leaf tips >10 mm out of bud scale (mouse ear phase)		30
10.5	first leaves start unfolding		40
11	leaf blade unfolded, leaf base not visible	needles loose (not bunched), >10 mm, shoot growth starts	50
15	first leaves completely unfolded; light green and weak	shoot and needles approx. ½ size; light green and weak	70
17	>50% of leaves unfolded; approx. end size and colour	>50 % of shoots and needles approx. end size and colour	90
BBCH	senescence (deciduous species)		
91	leaves still green		
93	start of leaf colouring (5% coloured)		
95	50% leaves still green, 50% coloured or fallen		
96	50% leaves fallen		
97	end of leaf fall (95% fallen)		

periods
spring leaf development period (onset$_{BBCH\ 17}$ − onset$_{BBCH\ 7}$, days)
summer full leaf period (onset$_{BBCH\ 93}$ − onset$_{BBCH\ 17}$, days)
autumn leaf senescence period (onset$_{BBCH\ 97}$ − onset$_{BBCH\ 93}$, days)
vegetation period (onset$_{BBCH\ 97}$ − onset$_{BBCH\ 7}$, days)

Mean phenological response rates were determined for the groups: montane deciduous species (MD: *A. pseudoplatanus*, *F. sylvatica*), montane evergreen species (ME, *A. alba*, *P. abies*, *P. sylvestris*) and species at high elevation (HE: *L. decidua*, *P. mugo*).

The response of phenology to temperature was tested using a second method: First, we calculated respective temperature sums (equation 3) for each of the phenological periods defined.

$$T_{sum} = \sum_{onsetBBCH\,a}^{onsetBBCH\,b} T \qquad (3)$$

Onset dates of all BBCH phases with BBCH a < BBCH b.

Then, the lengths of the phenological periods were correlated with the temperature sums using Pearson correlations. The resulting regression slope indicates the extension of the respective periods with increasing temperature sum (days $\sum °C^{-1}$) and can be interpreted as the sensitivity of the phenological periods to temperature. Again, mean phenological response rates were determined for the groups MD, ME and HE, in order to compare them with the lapse rate method.

For all bud burst onset dates in 2011 we calculated the number of chilling days (daily mean temperature ≤5 °C) in the period from BBCH 97 to BBCH 7 for deciduous and from 1 November to BBCH 7 for evergreen species. Equally, the number of forcing days, as well as the forcing temperature sum (daily mean temperature >5 °C, 1 January to BBCH 7) was determined. The threshold of 5 °C is commonly used in the literature (Murray *et al.* 1989; Hunter & Lechowicz 1992; Heide 2003). Since there was a huge variation in winter days due to the elevational difference of around 1000 m of each transect,

we also calculated the relative number of chilling days (equation 4a), forcing days (equation 4b), and the relative forcing temperature sum (equation 4c). We then correlated the number of chilling days with forcing days/temperature sums for all species.

Relative chilling days

$$= \frac{\sum_{BBCH\,97\,or\,1st\,November}^{BBCH\,7} \text{chilling days} \, (\leq 5°C)}{\sum_{BBCH\,97\,or\,1st\,November}^{BBCH\,7} \text{all days}}, \qquad (4a)$$

$$\text{Relative forcing days} = \frac{\sum_{1st\,January}^{BBCH\,7} \text{forcing days} \, (>5°C)}{\sum_{1st\,January}^{BBCH\,7} \text{all days}}, \qquad (4b)$$

Relative forcing sum

$$= \frac{\sum_{1st\,January}^{BBCH\,7} \text{forcing temperature} \, (>5°C)}{\sum_{1st\,January}^{BBCH\,7} \text{all temperature} \, (\geq 0°C)}. \qquad (4c)$$

RESULTS

Meteorological data

Mean air temperatures at the four meteorological stations in 2011 were generally warmer than in 2010 (Fig. 2). In detail, the spring period (April–July) was 0.63 °C warmer in 2011 (BRA +0.53 °C, KRA +0.51 °C, KRE +0.74 °C, SCH +0.72 °C), especially at higher elevations (KRE, SCH). Mean autumn temperature (September–October) in 2011 was even 2.78 °C warmer than in 2010 (BRA +2.01 °C, KRA +3.08 °C, KRE
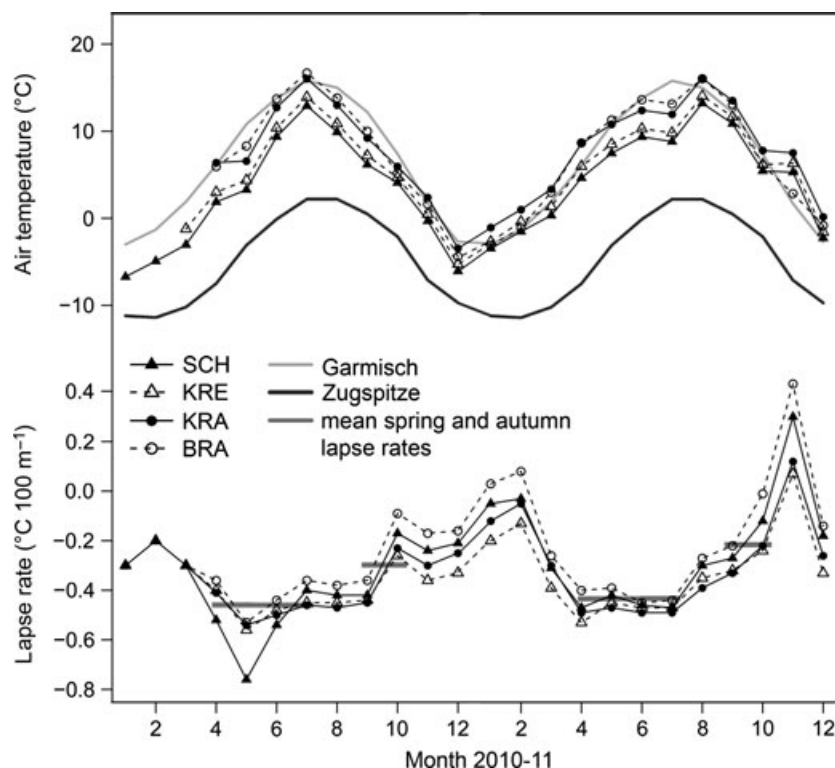

Fig. 2. Course of the 2010 and 2011 monthly mean temperature at the four meteorological stations compared to the long-term mean of Garmisch and Zugspitze (1961–1990) and the monthly mean temperature lapse rates at the four transect in 2010 and 2011.

+3.00 °C, SCH +3.04 °C). Consequently, relative humidity was lower in 2011 than in 2010 at all stations (−3.9% in spring and −6% in autumn). A special situation was recorded in November 2011 (Fig. 2): while for the whole of Germany, mean air temperature was only 0.5 °C above the long-term mean, in mountainous regions, new temperature and sunshine records were measured (DWD 2011). Moreover it was the driest month since the start of meteorological observations in 1881 (DWD 2011).

Predominantly, negative monthly mean temperature lapse rates at the transects indicate the expected decrease in temperature with elevation (Fig. 2). Lapse rates were pronounced in spring (April–July) and moderate in winter (October–January). Maximum and minimum were +0.43 °C 100 m^{-1} (November 2011, BRA) and −0.76 °C 100 m^{-1} (May 2010, SCH). Here too, in November 2011 there were extraordinarily high (positive) lapse rates at all transects due to frequent inversion situations. The spring and autumn means of monthly lapse rates are also indicated in Fig. 2: for spring leaf development period (April–July), mean of monthly mean temperature lapse rate was −0.48 °C 100 m^{-1} in 2010 and −0.46 °C 100 m^{-1} in 2011 (−0.47 °C 100 m^{-1} for 2010/2011). In the leaf senescence period (September–November), lapse rates were less strong due to frequent inversion situations: −0.3 °C 100 m^{-1} in 2010 and −0.22 °C 100 m^{-1} in 2011 (−0.26 °C 100 m^{-1} for 2010/2011). These lapse rates were used to determine phenological response rates from the phenological elevational rates.

Phenological elevational and response rates

A total of 134 logistic regressions was calculated to determine the site and species-specific onset dates for 2010, 139 for 2011. The numbers of significant regressions were: 80 ($P < 0.001$), 36 ($P < 0.01$), 7 ($P < 0.05$), 16 (not significant) in 2010 and 114 ($P < 0.001$), 16 ($P < 0.01$), 5 ($P < 0.05$), 4 (not significant) in 2011. Here, it can be seen that results of onsets dates in 2011 are based on slightly better fittings than the onset dates of 2010. Significance parameter P varied from 3.5E−7 to 0.32 (2010) and from and from 4.9E−8 to 0.39 (2011).

Phenological onset dates in spring were generally delayed; onset dates in autumn advanced with elevation (Fig. 3, Table 2). For early spring phases, *L. decidua*, *A. pseudoplatanus* and *P. abies* showed the highest response rates, followed by *F. sylvatica*. *A. alba* and the *Pinus* spp. revealed lower response rates. We found a strong effect of elevation on early-spring phases and late-autumn phases compared to late-spring and early-autumn phases. In fact, phenological elevational rates decreased from early- to late-spring phases and increased again from early- to late-autumn phases (Table 2). This effect is more pronounced for deciduous species and less for evergreen species. *A. alba* and *P. sylvestris* even showed approximately constant phenological elevational rates for all spring BBCH phases. Based on the phenological elevational rates, we calculated phenological response rates using the mean lapse rates of the respective phenological period (see Meteorological data results). Due to the constant factor (lapse rate), the pattern of decreasing response rates in spring and increasing response rates in autumn persists.

The difference in rates between the 2 years (2010 and 2011) is small relative to their standard error, except for *L. decidua* and *P. sylvestris*, the two species with the lowest number of

individuals in the study. Rates of *L. decidua* were not significant in 2010; rates of *P. sylvestris* were not significant in 2011. Here, the variance between individuals might strongly influence the rate and lead to higher differences between the years. In the following, mean data of both years (2010/2011) are presented, since the higher number of observations leads to more significant results.

Species groups

Comparing different groups of species (MD, ME and HE), mean onset dates (day of year, 2010/2011 data) were 111 ± 12, 133 ± 14 and 138 ± 27 for bud burst (BBCH 7) and 170 ± 6, 200 ± 8 and 204 ± 23 for the end of leaf development (BBCH 17). For MD, mean onset dates for BBCH 93 and BBCH 97 were 257 ± 4 and 304 ± 9. Therefore, the mean length of the leaf development period was 59, 67 and 66 days (MD, ME and HE). For MD in the study area, mean length of full leaf, leaf senescence and vegetation period were 87, 47, 193 days, respectively. Mean phenological response rates for bud burst (BBCH 7) were −8.5 ± 0.4, −5.7 ± 1.1 and −7.7 ± 1.2 days °C^{-1} for MD, ME and HE, respectively. End of leaf unfolding (BBCH 17) advanced by −2.6 ± 0.3, −4.8 ± 0.2 and −1.9 ± 0.1 days °C^{-1}, respectively. Mean delay of autumn phases for MD was 1.5 ± 0.6 and 7.9 ± 0.1 days °C^{-1} (BBCH 93 and BBCH 97). Combining these phenological response rates (prr) of deciduous trees for specific periods, the vegetation period was extended by 16.4 days °C^{-1} ($|$prr $_{BBCH\ 7}| + |$prr $_{BBCH\ 97}|$), leaf development by 5.9 days °C^{-1} ($|$prr $_{BBCH\ 7}| - |$prr $_{BBCH\ 17}|$) full leaf period by 4.1 days °C^{-1} ($|$prr $_{BBCH\ 17}| + |$prr $_{BBCH\ 93}|$), and leaf senescence period by 6.4 days °C^{-1} ($|$prr $_{BBCH\ 97}| - |$prr $_{BBCH\ 93}|$) for MD. For ME and HE, leaf development extended by 0.9 and 5.8 days °C^{-1} ($|$prr $_{BBCH\ 7}| - |$prr $_{BBCH\ 17}|$).

Extension of phenological periods

For all species, the length of leaf development, leaf senescence, full leaf and vegetation period was highly correlated with the respective temperature sum (Fig. 4, Table 3). Even the lengths between two phases were extended (not shown). Since temperature sums are calculated with daily means, with a general warming of 1 °C, the temperature sum within a period will increase by the number of days of this period. The increased length of the period is the previous length of the period multiplied by the slope. Therefore, the regression slope can be interpreted as percentage increase of the period length per °C (*i.e.* a slope of 0.05 would lengthen a period by 5%). Regarding the groups (MD, ME and HE), mean values were 9.1%, 3.7%, 10.5% and 7.1% for MD (leaf development, full leaf, leaf senescence, vegetation period) and 7.7% and 7.9% for ME and HE, respectively (leaf development, correlation coefficients ranged from 0.87 to 0.95). Applying this percentage increase to the mean length of the respective period (2010/2011 data), we calculated lengthening of 5.1, 3.5, 4.5 and 13.7 days per degree for MD (leaf development, full leaf, leaf senescence and vegetation period; Table 3 2010/2011 data). Leaf development period for ME and HE extended by 5.1 and 4.8 days per °C, respectively.

Comparing the lengthening of phenological periods based on temperature sums at the specific sites with the lengthening of the periods resulting from the lapse rate method (combina-
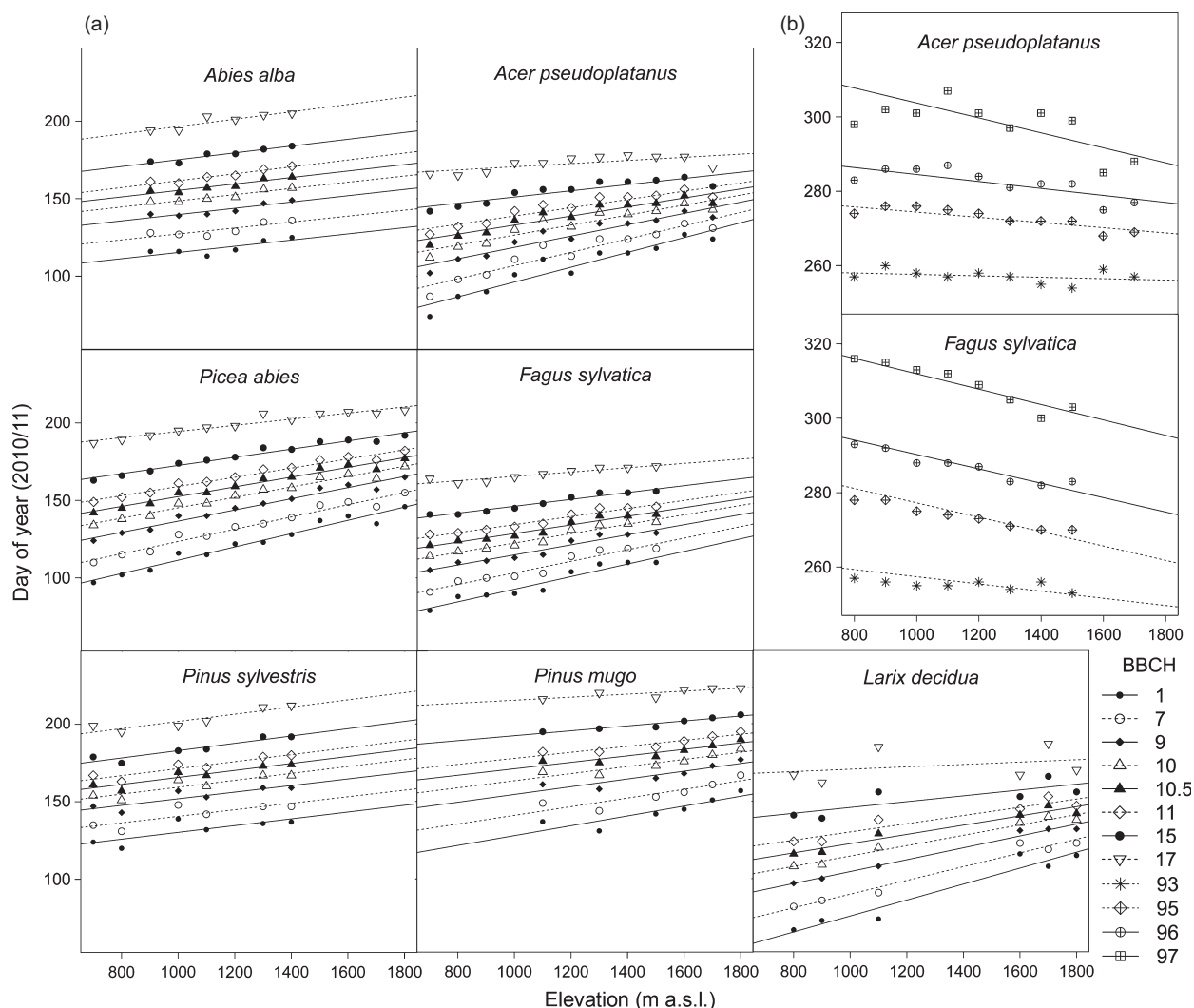
Fig. 3. Linear regression of BBCH onset dates (mean 2010/2011 data) for the seven species in spring (a) and the two deciduous species in autumn (b) on elevation. Slopes of the regression lines (phenological elevational rates) are given in Table 2.

tion of phenological response rates for the start and end of each period), both methods yielded similar results (Fig. 5, example for *A. pseudoplatanus* and *F. sylvatica*, 2010/2011 data, see also Tables 2 and 3). In our observation years, the contribution of delayed leaf senescence to lengthening of the total vegetation period was as high as or even higher than the advance of leaf development. Only for *A. pseudoplatanus* in the lapse rate method (Fig. 5 black arrows) was there an approximately 55% contribution of advanced spring (BBCH 7) and 45% of delayed autumn (BBCH 97) to the lengthening of the vegetation period, as found by Davi *et al.* (2006).

Chilling and forcing

All linear regressions between chilling and forcing days (or temperature sums) had negative slopes, except for *L. decidua*. This indicates that the more chilling days were experienced, the less forcing days or temperature sums were required for bud burst. The regressions between relative chilling days and relative forcing days revealed similar slopes for all species: -1.26 ± 0.04 (*F. sylvatica*), -1.27 ± 0.07 (*A. pseudoplatanus*),

-1.24 ± 0.03 (*A. alba*), -1.23 ± 0.01 (*P. abies*), -1.10 ± 0.06 (*P. sylvestris*), -1.25 ± 0.02 (*P. mugo*) and -1.11 ± 0.13 (*L. decidua*). However, slopes of the regressions between relative chilling days and relative forcing sums were similar for deciduous trees (-1.28 ± 0.15 *F. sylvatica*, -1.33 ± 0.23 *A. pseudoplatanus*), but lower for evergreen species (Fig. 6). Mean absolute chilling days ranged from 115.8 days (700 m a.s.l.) to 160.3 days (1800 m a.s.l.). With regard to the suggested natural required chilling of 145 days (Murray *et al.* 1989), this amount was only achieved at higher elevations ($\geq$1300 m *F. sylvatica* and *A. pseudoplatanus*, $\geq$1400 m *A. alba*, $\geq$1500 m *P. abies*, $\geq$1700 m *P. mugo*, not achieved on south-facing sites for *L. decidua* and *P. sylvestris*).

DISCUSSION

Referring to our initial questions, we could (i) prove that phenological responses to elevation and temperature varied highly between species, and we were able to determine species-specific rates. A surprising result was the relatively high temperature response of *F. sylvatica*, which is known to be less sensitive to

Table 2. Phenological response to elevation and temperature for leaf unfolding and senescence BBCH phases (2010, 2011 and 2010/2011 data).

species	BBCH	2010				2011				2010/2011			
		per ± SE	R^2	onset 1000 m	prr	per ± SE	R^2	onset 1000 m	prr	per ± SE	R^2	onset 1000 m	prr
Abies alba	7	1.6 ± 0.3**	0.90	138	−3.3	1.9 ± 0.7*	0.67	124	−4.2	1.9 ± 0.6*	0.71	127	−4.1
	9	1.9 ± 0.3**	0.93	148	−3.9	2.0 ± 0.6*	0.71	135	−4.3	2.0 ± 0.5*	0.83	139	−4.3
	11	2.1 ± 0.6*	0.75	167	−4.4	1.9 ± 0.6*	0.76	155	−4.2	2.2 ± 0.3**	0.92	160	−4.7
	15	2.3 ± 0.8	0.65	178	−4.7	1.9 ± 0.6*	0.74	167	−4.2	2.2 ± 0.4**	0.91	173	−4.7
	17	2.6 ± 1.2	0.53	195	−5.5	1.9 ± 0.8	0.61	186	−4.2	2.4 ± 0.6*	0.80	194	−5.0
Acer pseudoplatanus	1	4.6 ± 0.6***	0.88	125	−9.5	4.1 ± 1.0**	0.64	94	−8.9	4.8 ± 0.5***	0.91	101	−10.2
	7	4.1 ± 0.5***	0.90	132	−8.4	3.7 ± 0.9**	0.65	104	−8.1	4.3 ± 0.5***	0.91	111	−9.1
	9	3.5 ± 0.4***	0.91	139	−7.3	3.4 ± 0.7**	0.70	115	−7.4	3.7 ± 0.4***	0.90	122	−7.8
	10	3.1 ± 0.3***	0.92	144	−6.5	3.1 ± 0.6***	0.72	123	−6.6	3.2 ± 0.4***	0.89	130	−6.9
	10.5	2.9 ± 0.3***	0.93	147	−6.0	2.8 ± 0.5***	0.75	129	−6.2	2.9 ± 0.4***	0.88	136	−6.2
	11	2.6 ± 0.3***	0.93	151	−5.4	2.6 ± 0.5***	0.76	135	−5.7	2.7 ± 0.3***	0.87	142	−5.7
	15	2.1 ± 0.3***	0.89	158	−4.3	2.3 ± 0.3***	0.83	146	−4.9	2.0 ± 0.3***	0.80	154	−4.3
	17	1.2 ± 0.3**	0.60	170	−2.4	1.5 ± 0.2***	0.82	165	−3.3	1.0 ± 0.4*	0.48	173	−2.2
Fagus sylvatica	1	5.8 ± 0.5***	0.95	107	−12.1	4.2 ± 0.5***	0.92	82	−9.1	4.1 ± 0.4***	0.92	90	−8.7
	7	5.0 ± 0.4***	0.96	115	−10.4	3.8 ± 0.4***	0.93	94	−8.3	3.7 ± 0.4***	0.93	101	−7.9
	9	4.2 ± 0.3***	0.96	124	−8.7	3.4 ± 0.3***	0.94	106	−7.3	3.3 ± 0.3***	0.94	113	−6.9
	10	3.6 ± 0.3***	0.97	130	−7.4	3.1 ± 0.2***	0.96	115	−6.7	3.0 ± 0.2***	0.96	121	−6.4
	10.5	3.1 ± 0.2***	0.97	135	−6.5	2.9 ± 0.2***	0.95	121	−6.3	2.8 ± 0.3***	0.95	127	−5.9
	11	2.7 ± 0.3***	0.94	139	−5.7	2.6 ± 0.2***	0.96	128	−5.6	2.6 ± 0.2***	0.95	133	−5.5
	15	1.8 ± 0.3***	0.81	148	−3.8	2.2 ± 0.1***	0.99	141	−4.7	2.2 ± 0.2***	0.96	145	−4.7
	17	0.4 ± 0.5	0.07	163	−0.7	1.5 ± 0.1***	0.99	161	−3.3	1.4 ± 0.2***	0.87	165	−3.0
Larix decidua	7	1.8 ± 0.8	0.71	114	−3.8	4.7 ± 0.9**	0.87	82	−10.1	4.4 ± 0.4***	0.97	99	−9.4
	9	2.1 ± 0.3*	0.95	125	−4.3	4.0 ± 0.7**	0.89	96	−8.7	3.8 ± 0.3***	0.98	115	−8.1
	11	2.4 ± 0.5*	0.93	147	−5.0	2.9 ± 0.5**	0.91	121	−6.3	2.7 ± 0.5**	0.89	140	−5.6
	15	2.7 ± 1.0	0.81	156	−5.7	2.3 ± 0.3***	0.95	138	−4.9	1.9 ± 0.7	0.65	155	−4.0
	17	3.2 ± 1.6	0.65	173	−6.6	1.2 ± 0.1***	0.98	161	−2.7	0.8 ± 1.1	0.10	180	−1.6
Picea abies	7	4.1 ± 0.2***	0.97	143	−8.5	4.0 ± 0.2***	0.97	122	−8.6	4.0 ± 0.2***	0.97	128	−8.4
	9	3.6 ± 0.2***	0.97	153	−7.6	3.5 ± 0.2***	0.97	134	−7.6	3.6 ± 0.2***	0.97	140	−7.7
	11	2.9 ± 0.2***	0.97	169	−6.1	2.6 ± 0.2***	0.94	154	−5.7	3.0 ± 0.2***	0.97	161	−6.3
	15	2.4 ± 0.2***	0.96	179	−5.0	2.1 ± 0.2***	0.90	165	−4.7	2.6 ± 0.2***	0.96	174	−5.6
	17	1.7 ± 0.2***	0.87	195	−3.4	1.4 ± 0.2***	0.77	185	−2.9	2.0 ± 0.2***	0.92	195	−4.2
Pinus mugo	7	2.6 ± 0.5**	0.87	144	−5.4	2.9 ± 0.9*	0.70	125	−6.2	2.8 ± 0.8*	0.78	146	−5.9
	9	2.3 ± 0.4**	0.91	155	−4.8	2.5 ± 0.8*	0.73	140	−5.4	2.5 ± 0.6*	0.82	158	−5.3
	11	1.6 ± 0.2**	0.92	176	−3.3	1.9 ± 0.5*	0.82	164	−4.2	1.9 ± 0.4**	0.88	176	−4.1
	15	1.3 ± 0.2**	0.91	187	−2.6	1.7 ± 0.4**	0.84	179	−3.6	1.6 ± 0.2**	0.92	187	−3.4
	17	0.7 ± 0.3	0.58	204	−1.4	1.1 ± 0.4	0.61	202	−2.3	1.0 ± 0.3*	0.68	207	−2.1
Pinus sylvestris	7	3.4 ± 0.6**	0.88	161	−7.0	2.0 ± 0.8	0.59	141	−4.3	2.1 ± 0.8	0.65	148	−4.5
	9	3.2 ± 0.5**	0.92	167	−6.6	1.6 ± 0.7	0.57	151	−3.5	2.1 ± 0.6*	0.76	157	−4.5
	11	3.0 ± 0.4**	0.94	179	−6.3	0.9 ± 0.5	0.46	167	−1.9	2.3 ± 0.5**	0.86	174	−4.8
	15	2.9 ± 0.4**	0.92	186	−6.1	0.4 ± 0.4	0.17	177	−0.8	2.4 ± 0.4**	0.89	183	−5.0
	17	2.8 ± 0.6**	0.85	197	−5.9	−0.2 ± 0.5	0.05	193	0.5	2.3 ± 0.5*	0.83	199	−4.9

(continued)

Table 2. Continued.

species	BBCH	2010 per ± SE	2010 R^2	2010 onset 1000 m	2010 prr	2011 per ± SE	2011 R^2	2011 onset 1000 m	2011 prr	2010/2011 per ± SE	2010/2011 R^2	2010/2011 onset 1000 m	2010/2011 prr
Acer pseudoplatanus	93	−0.2 ± 0.1	0.14	258	0.6	−0.1 ± 0.3	0.02	264	0.5	−0.2 ± 0.2	0.14	258	0.7
	95	−0.9 ± 0.1***	0.88	272	3.0	−0.5 ± 0.2	0.31	282	2.2	−0.7 ± 0.1***	0.75	276	2.7
	96	−1.2 ± 0.2***	0.84	282	3.9	−0.5 ± 0.3	0.18	291	2.2	−0.9 ± 0.2**	0.65	286	3.6
	97	−2.8 ± 0.7**	0.66	294	9.3	−0.6 ± 0.6	0.09	305	2.6	−2.0 ± 0.6**	0.58	301	7.7
Fagus sylvatica	93	−0.5 ± 0.2*	0.50	258	1.8	−1.1 ± 0.6	0.30	254	4.8	−1.0 ± 0.4*	0.49	255	3.7
	95	−2.0 ± 0.4***	0.81	274	6.7	−1.8 ± 0.4**	0.71	277	8.0	−1.9 ± 0.4**	0.79	275	7.4
	96	−2.0 ± 0.2***	0.91	284	6.7	−1.8 ± 0.3***	0.82	292	8.0	−1.9 ± 0.2***	0.90	288	7.4
	97	−2.3 ± 0.3***	0.90	303	7.7	−1.9 ± 0.4**	0.74	320	8.6	−2.1 ± 0.3***	0.90	313	8.0
mean tlr used to calculate prr	Spring	−0.48				−0.46				−0.47			
	Autumn	−0.30				−0.22				−0.26			

Phenological elevational rate (per; days 100 m⁻¹) with SE and significance level (*P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001); R^2, onset day at 1000 m elevation (day of year); phenological response rate (prr = per × (1/tlr), days °C⁻¹); mean temperature lapse rate (tlr).
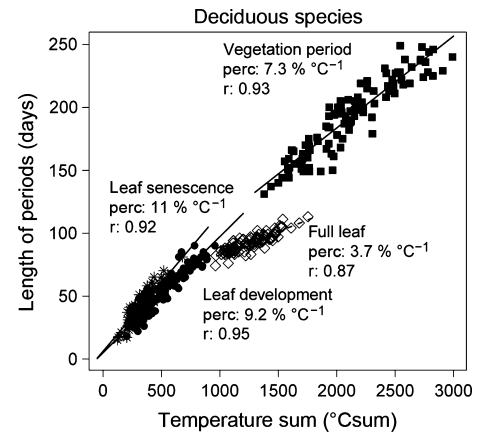

Fig. 4. Correlation between the length of phenological periods and the corresponding temperature sums. Percentaage increase (perc) of the period length per degree and Pearson's correlation coefficients r are given.

temperature (Vitasse *et al.* 2009a; Čufar *et al.* 2012). We were also able to quantify (ii) responses from a set of phenological phases. As expected, they were different, but we found a homogenous pattern: spring response rates decrease and autumn response rates increase again with later phases. Between species groups (iii), bud burst and end of leaf development onset dates were similar between ME and HE, and about 4 weeks earlier for MD. However, sensitivity of bud burst to elevation and temperature was high for MD and HE, but smaller for ME. Moreover, elevational and temperature response rates strongly decreased with later phases (end of leaf development) in MD and HE, but less so in ME. Regarding the role of spring and autumn phases in lengthening the vegetation period (iv), we found the same or even a stronger influence of delayed autumn phases. This result is probably highly influenced by the warm autumn 2011. But this circumstance shows clearly that the contribution of phenological periods to the lengthening of the vegetation period strongly depends on the time of the year experiencing the highest warming. Last but not least, we showed that (v) the two deciduous species (*A. pseudoplatanus* and *F. sylvatica*) seem to reveal approximately the same correlation between reduced chilling days and increased forcing temperature, in contrast to the other species.

Meteorological data

For calculations of the phenological response rates, of course, there is a high influence of the lapse rates used. Lapse rates smooth temperature variations to a linear reduction with elevation and neglect, for example, special microclimates due to topography or thermal inversions. However, our dense measurement network directly at the phenological observation sites allows us to calculate lapse rates, and especially temperature sums, individually for all transects, sites and seasons. Compared to other published lapse rates in the alpine region (*e.g.* −0.54 to −0.58 °C 100 m⁻¹; Rolland 2003) and the commonly used mean lapse rate of −0.65 °C 100 m⁻¹ (Minder *et al.* 2010), our measured lapse rates were less expressed due to the temperature buffer effect of the forest (loggers are installed within the forest). Other studies reported annual mean lapse rates around −0.47 to −0.48 °C 100 m⁻¹ for the Bavarian Alps (Ewald 1997) and −0.32 (December) to −0.62 °C 100 m⁻¹

Table 3. Extension of the length of phenological periods with increasing temperature for 2010, 2011 and 2010/2011 data.

species	period BBCH	2010			2011			2010/2011		
		perc ± SE	R^2	mL	perc ± SE	R^2	mL	perc ± SE	R^2	mL
Abies alba	1–17	9.6 ± 0.9***	0.91	72	9.1 ± 1.1***	0.86	72	8.7 ± 0.8***	0.83	72
Acer pseudoplatanus	1–97	6.3 ± 0.6***	0.83	160	4.9 ± 0.4***	0.86	204	7.0 ± 0.4***	0.86	183
	1–17	9.1 ± 0.8***	0.85	36	7.9 ± 0.7***	0.85	67	9.8 ± 0.4***	0.93	52
	17–93	3.5 ± 0.4***	0.81	90	3.7 ± 0.3***	0.82	97	3.9 ± 0.3***	0.81	93
	93–97	14.2 ± 1.2***	0.83	32	11.4 ± 1.0***	0.82	40	12.0 ± 0.7***	0.84	36
Fagus sylvatica	1–97	7.2 ± 0.6***	0.83	184	5.2 ± 0.6***	0.79	224	7.1 ± 0.4***	0.89	204
	1–17	10.1 ± 1.2***	0.74	48	6.5 ± 0.7***	0.77	73	8.4 ± 0.4***	0.88	60
	17–93	2.7 ± 0.5***	0.60	93	4.2 ± 0.5***	0.77	93	3.5 ± 0.3***	0.68	93
	93–97	11.4 ± 1.4***	0.70	43	8.1 ± 0.9***	0.76	58	9.0 ± 0.5***	0.84	50
Larix decidua	1–17	9.1 ± 1.1**	0.96	36	8.0 ± 1.2***	0.91	72	10.0 ± 1.0***	0.91	57
Picea abies	1–17	7.5 ± 0.4***	0.91	60	6.2 ± 0.2***	0.96	68	6.9 ± 0.4***	0.83	64
Pinus mugo	1–17	4.7 ± 0.6***	0.87	56	4.8 ± 0.8***	0.78	74	5.8 ± 1.1***	0.56	65
Pinus sylvestris	1–17	6.5 ± 1.4**	0.84	51	5.3 ± 0.8**	0.92	70	7.4 ± 1.1***	0.82	61

Percentage increase (perc, % °C^{-1}) with SE and significance level (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$); R^2; mean length of the periods (mL, days).
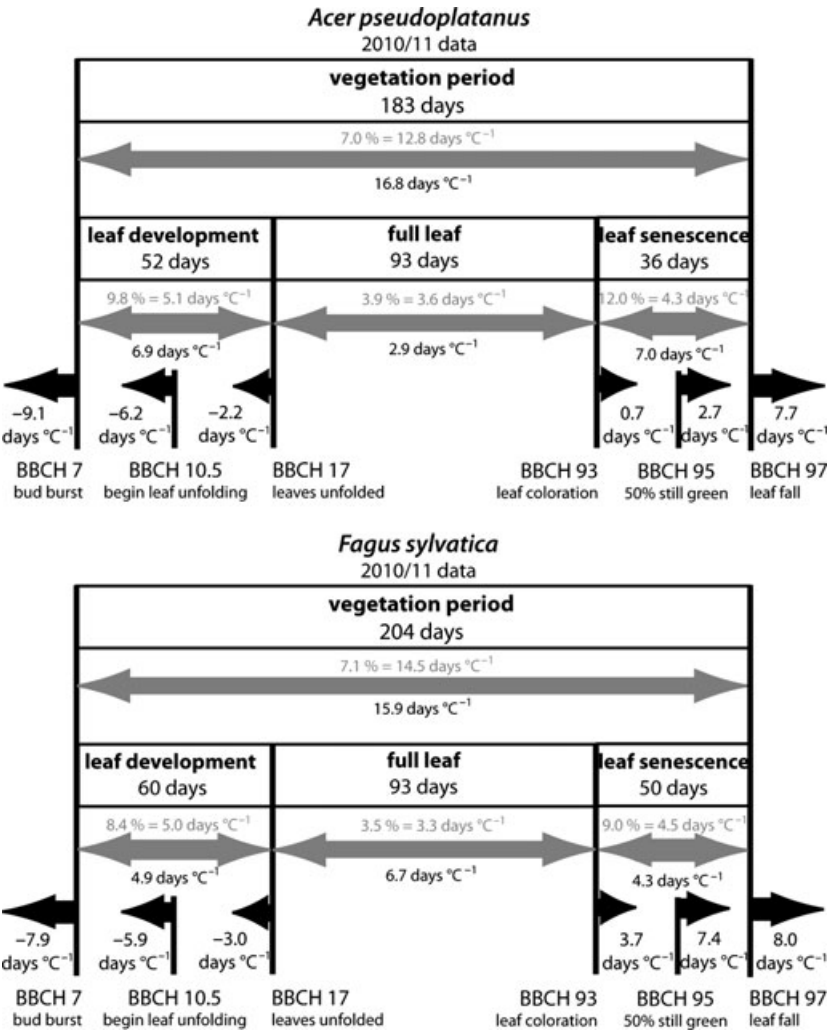

Fig. 5. Advance of spring and delay of autumn onset dates based on the lapse rate calculation (black arrows) and extension of phenological periods based on two methods [lapse rates (black values at two-sided arrows) and percentage increase determined on site-specific temperature sums (grey values at two-sided arrows)] for *Acer pseudoplatanus* and *Fagus sylvatica* 2010/2011 data obtained along the elevational transects.

(spring; Kirchner *et al.* 2012) in Garmisch-Partenkirchen. Here, our measured lapse rates (with mean lapse rate of −0.47 °C 100 m^{-1}) yield similar values due to the regional proximity of the study areas. The regional and annual differences in lapse rates underline the importance of site-specific temperature measurements at the sites and transects, instead of
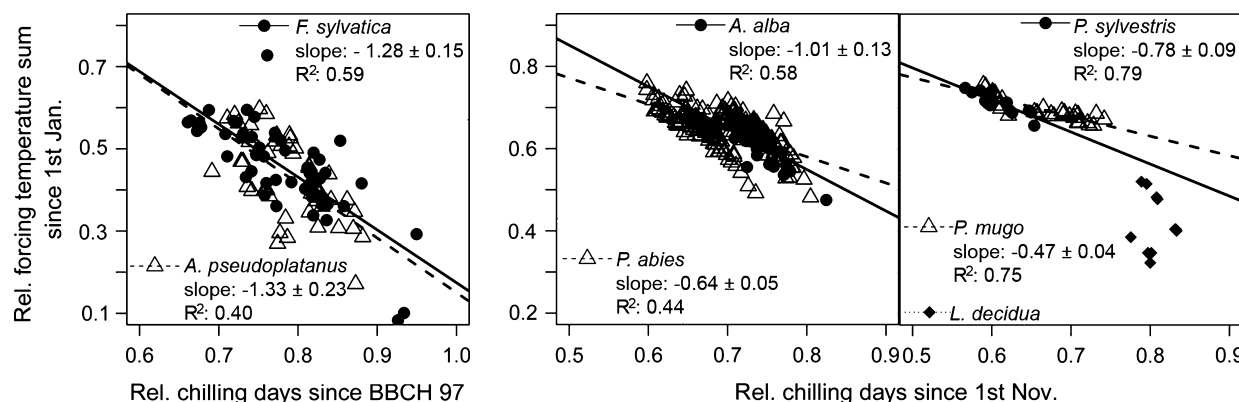
Fig. 6. Linear correlation between relative number of chilling days (≤5 °C, BBCH 97 − BBCH 7 for deciduous and 1 November − BBCH 7 for evergreen species) and relative number of forcing temperature sum before bud burst (>5 °C, 1 January − BBCH 7) in 2011.

commonly used values. Since temperature loggers became affordable, in most studies, site-specific measurements in phenological studies have become more and more common. With these data, it is also possible to focus on phenological differences due to small-scale meteorological conditions found in complex terrain of mountainous regions. Any variations in seasonal weather conditions from year-to-year (e.g. 2010 versus 2011) would definitely result in different phenological elevational rates. However, taking into account results in temperature lapse rates including thermal inversion situations will result in more precise temperature response rates.

Phenological elevational and response rates

In this study, differences between N- and S-facing aspects have not been included, since our first analyses of the 2-year data set did not lead to consistent results. Since we expect phenological differences related to aspect, a long-term study would be necessary. Moreover, comparing the 2 years, 2010 and 2011, phenological elevational rates were within their standard errors, except for L. decidua and P. sylvestris. Due to the specialised occurrence of these species in the mountainous forest, we had a small number of individuals for L. decidua and P. sylvestris in our study, which obviously was not sufficient to achieve consistent results. More observation years and more individuals included in the study would likely consolidate the results. Since the elevational transects range over 1000 m, and not all species have the same elevational distribution (e.g. L. decidua and P. mugo in high elevations), there is also some uncertainty through mixing responses from different ecotypes. Our response rates for these species therefore have to be handled with care and could be revised from continuing studies.

Phenological elevational rates and phenological response rates in Table 2 confirm an advance of spring and a delay of autumn phases with increasing temperature. Our phenological elevational rates for F. sylvatica and A. pseudoplatanus bud burst and leaf unfolding (BBCH 7 and BBCH 10.5) in southern Germany fit perfectly to rates reported in the literature: vertical changes in F. sylvatica flushing are reported as 1–4 days 100 m^{-1} (Schnelle 1955; König & Mayer 1988; Menzel 1997; Pellerin et al. 2012). Vitasse et al. (2009b) found advanced flushing of 1.9–6.6 days °C^{-1} and delayed senescence

of 0.0–5.6 days °C^{-1} for deciduous trees in the Pyrenean mountains. For leaf unfolding of Pinus species and A. alba, Davi et al. (2011) determined phenological elevational rates of 4.4 and 2.8 days 100 m^{-1}. Our rates are somehow lower, but in the same range. Comparing the species, A. pseudoplatanus, L. decidua and P. abies, phenology turned out to be highly sensitive to elevation and temperature (response of >4 days 100 m^{-1}). Surprisingly, F. sylvatica, which is known to be less sensitive to temperature (Vitasse et al. 2009a; Čufar et al. 2012), followed closely (3.7 days 100 m^{-1}). A. alba and the two Pinus species had smaller response rates <3 days 100 m^{-1}.

Phenological elevational rates determined by linear trends are quite reliable. However, the determination of temperature response rates through combining phenological elevational rates with temperature lapse rates is an approximation. Lapse rates are smoothing real site conditions and give the linear temperature response with elevation. But to interpret them for temperature responses in the future under global warming conditions, it must be remembered that temperature sensitivity becomes non-linear with increased warming (Pope et al. 2013). Then, other factors (reduced chilling, photoperiod) could gain relevance, especially in autumn, where photoperiod plays an important role as well as temperature (Migliavacca et al. 2008). However, the advantage of our method is that it can determine responses to temperature in a relatively short time of observations and is more accurate and site-specific than common elevational rates.

As shown, elevation and temperature sensitivity strongly depend on the BBCH phase. Early-spring and late-autumn phases show higher values than late-spring and early-autumn phases. Most likely this is a consequence of a more explicit vertical temperature decrease in early spring and late autumn compared to the middle of the vegetation period. But this also means that leaf development and senescence processes are faster at higher elevations. This could be due to several factors, which remain to be verified: either trees at high elevations are adapted to a shorter vegetation period and/or they produce smaller leaves than in the valley. Also, since spring phases at high elevations start later, the increase in temperature from day-to-day is much faster than in early spring, which could lead to more rapid development. Moreover, our results underline the need to clearly define observed phases in phenological

studies; otherwise, comparing values of different studies will lead to inaccurate conclusions.

Species groups

Mean values of species groups (MD, ME and HE) show obvious traits. Later spring onset dates for evergreen species compared to deciduous species can be explained by the fact that they have no need to expose themselves to the risk of late frosts since they are able to start photosynthesis at any time. Late onset dates of high-elevation species can easily be explained from the temperature conditions required only being fulfilled later in the year. ME temperature response rates also differ in another feature from MD and HE. Whereas response rates of the latter decreased from bud burst to end of leaf unfolding, the ME response is relatively unchanged during spring development. This could be interpreted as species of MD and HE groups have to be more flexible to react to temperature since they are forced to adapt their leaf development to given environmental conditions, whereas evergreen species with late leaf-out seem to be relatively fixed in their course of leaf development. However, in the method based on temperature sums, lengthening of the leaf development period per degree did not reveal any large differences between the groups. Since these groups are only represented by a few species, it might be too early to draw general conclusions.

Extension of phenological periods

Correlations of the length of phenological periods with corresponding temperature sums revealed the expected result of higher temperature leading to a longer vegetation period. In our study, not only the vegetation period, but also phenological periods and lengths between single phenological phases were extended with higher temperature sums available. With earlier onset in the year, more time might be necessary to fulfil required temperature sums. An observed lengthening of the vegetation period with warming due to earlier bud burst and later leaf fall has often been reported (Menzel & Fabian 1999; Vitasse *et al.* 2009b). For *F. sylvatica*, Vitasse *et al.* (2009b) found an extended vegetation period of 6.7–13 days °C^{-1}, Dittmar & Elling (2006) reported changes of 2.7–3.4 days 100 m^{-1}, which is equal to an extension of the vegetation period by 5.7–7.2 days °C^{-1} (based on our 0.47 days °C^{-1} spring lapse rate).

Changes in autumn period are reported as smaller (Menzel & Fabian 1999; Estrella & Menzel 2006; Röthlisberger 2010) or similar (Vitasse *et al.* 2009b) to the advance of phenological spring phases. However, principal climate factors inducing the start of leaf colouring have not yet been clearly identified (Estrella & Menzel 2006). Besides temperature, daylength may be an important parameter (Larcher 2003). Between individuals at the same site, start of colouring is highly variable but not the end of leaf fall (Röthlisberger 2010). Both facts may explain why leaf colouring in our study showed less dependency on elevation and temperature than leaf fall. Davi *et al.* (2006) reported a 55% contribution of early leaf unfolding to extension of the vegetation period and a 45% contribution of delayed leaf fall, which fits almost perfectly to advanced bud burst and delayed leaf fall dates using the lapse rate method for *A. pseudoplatanus*. But, in general, we found leaf senescence was as sensitive to temperature as leaf development, since it

made the same or an even higher contribution to vegetation period lengthening. On the one hand, there is a high influence of the mean spring and autumn lapse rates used, since a smaller lapse rate (*e.g.* in autumn 2011) leads to a higher calculated phenological response rate. In 2011, autumn temperatures were 3 °C higher than in 2010, but spring temperatures only increased by <1 °C; this therefore influenced extension of the leaf senescence period in this study. But, consequently, the period experiencing higher warming will mainly influence lengthening of the vegetation period. As we showed, the full-leaf period is extended with increasing temperature (even though less so than leaf development and senescence) due to an earlier end to leaf development and a later start to leaf colouration. This provides advantages, especially for deciduous trees, through a longer period of photosynthesis and secondary stem growth.

There are only slight differences in the results using the lapse rate or the temperature sum calculation (Fig. 5). However, results from both methods were influenced by the extremely warm autumn 2011. We assume the results based on site-specific temperature sums could be more accurate than the method based on lapse rates, since lapse rates neglect or soften the effect of site-specific microclimate and inversion influences.

Chilling and forcing

Chilling thresholds are reported to be between 0 and 7.2 °C (Eggert 1951); however, exact thresholds and range of temperatures for chilling are still unknown. The definition of a uniform 5 °C threshold for chilling and forcing, as well as the two starting points – 1 November for chilling for evergreen species and 1 January for forcing temperatures – in this study are arbitrary, but often and commonly used in the literature (Murray *et al.* 1989; Hunter & Lechowicz 1992). Moreover, differences between species in the required threshold are less studied and may be highly variable (Cesaraccio *et al.* 2004). This is definitively true for *L. decidua*, since it was the one of the seven species without a clear linear relationship of chilling and forcing temperatures with the 5 °C threshold.

For the other species, our results were similar to several other studies (Murray *et al.* 1989; Chuine & Cour 1999; Heide 2003), showing that with increasing chilling period, decreasing forcing temperature was required for bud burst. The slopes in the regression between chilling days and forcing days, which mainly vary slightly around −1.25, can be interpreted as: for a 4% increase in chilling days, 5% less forcing days are required. The correlation between chilling days and temperature sums, however, differs between deciduous and evergreen trees. For deciduous species, an increase in chilling highly reduces forcing temperature requirements, which is consistent with previous studies (Heide 2003). Moreover, *F. sylvatica* is known to have high chilling requirements compared to other deciduous vspecies (Caffarra & Donnelly 2011). For evergreen species in our study, the effect of longer chilling leading to lower required forcing temperature is less distinct and highly variable between species. The obvious difference between deciduous and evergreen species may also be related to the different starting dates for the calculation of chilling (end of leaf fall as a 'true' phenological phase, varying from mid-October to mid-November, for deciduous, and from 1 November for evergreen species). However, it is obvious that the two deciduous species seem to

have much the same reaction to reduced chilling, whereas a comparison of evergreen species to each other showed highly variable chilling requirements. In the literature, where only a few species are generally discussed, there are also different chilling requirements for evergreen species (Nienstaedt 1967; Hänninen & Pelkonen 1989; Hänninen *et al.* 2007). Thus, under future global warming conditions, especially bud burst of deciduous trees might be delayed due to decreasing chilling, partly counterbalancing spring warming (Heide 2003).

A natural chilling requirement of 145 days, as reported in Murray *et al.* (1989), was only achieved at high elevations, surely also influenced by the warm spring 2011. But this value should not be generalised for all species; in some studies, higher temperatures induce negative chilling when exceeding the upper threshold, whereas temperatures below a lower threshold (generally 0 °C) are not considered effective for chilling (Richardson *et al.* 1974; Cesaraccio *et al.* 2004). The idea that negative temperatures would also have a negative chilling effect would even mean that trees at high elevations experience less chilling than those at lower elevations.

CONCLUSIONS

The phenological sensitivity of species to elevation and temperature is similar, whether based on lapse rates or temperature sums. However, in the complex terrain of mountainous regions, microclimate at different locations is highly variable and does not always follow the lapse rate. Thus, results calculated with temperature sums originating from each specific site seem to be more reliable. Seasonal variation in elevational and temperature response rates of the single phenological phases observed here (decrease with later spring, increase with later autumn phases) underline the importance of clearly defined phenological phases when comparing results from different studies. Spring temperature responses of deciduous and high-elevation species seem to be more distinct and therefore more flexible than of evergreen species, because the latter are less forced to benefit from short-term favourable growing conditions. Instead, leaf development of evergreen species seems to

be more independent once the temperature threshold for bud burst is reached. However, the effect of a reduced chilling period on the required temperature sum for bud burst is more distinct for deciduous species, which could somewhat counterbalance the advance in spring with increasing temperatures.

The lengths of the vegetation period and phenological periods (leaf development, full leaf, leaf senescence) increased with increasing temperature. This could be due to earlier onset dates leading to a longer time span necessary until temperature sum requirements for the next phase are fulfilled. In our study, senescence phases were delayed to similar magnitudes as leaf development phases advanced. Thus, the period during which higher warming is experienced mainly influences length of the vegetation period. Senescence phases therefore could have been underestimated in terms of their influence on lengthening of the vegetation period. According to our results, this plays an important role as to which time of the year temperatures will change most under future climate warming, especially since phenological response varied between species, phenological periods and phenological phases.

Some questions remain unanswered and could be investigated through long-term observations along elevational transects: how does N and S aspect influence phenology; what are the differences between mature and juvenile tree phenology; how do changes in flowering and seed development phenology affect the reproduction of trees; and how much do the different tree species profit from a lengthened vegetation period for secondary stem growth and carbon allocation? Answers to all these parts of the mosaic of interactions between climate and biosphere will finally lead to a more complete picture.

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